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Microbial activity in peatlands

Patterns of fungal and bacterial carbon mineralization across northern European peatlands

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Abstract

The fungal and bacterial activity was determined in 20 northern European peatlands ranging from *ombrotrophic* bogs to *eutrophic* fens with key differences in degree of humification, pH, dry bulk density, carbon (C) content and vegetation communities using the selective inhibition (SI) technique. These peatlands were partly disturbed and the respective water tables lowered below the surface layer. Basal respiration ranged from 24 to 128 µg CO_2-C g^{-1} dry peat d^{-1}. Bacterial contributions to CO_2 production were high in most peatlands and showed the following pattern: eutrophic>>transitional≥mesotrophic>> ombrotrophic peatland types. The fungal-to-bacterial (F:B) ratios varied substantially within peatland type, and this was mainly attributed to differences in peat botanical compositions and chemistry. The computed mean Inhibitor Additivity Ratio (IAR) was quite close to 1 to suggest that the SI techniques can be used to partition eukaryotic and prokaryotic activity in wide range of peatlands. Overall, basal respiration, microbial biomass-C, fungal and bacterial activities varied across the studied

peatland types, and such differences could have consequences for C- and nutrient-cycling as well as how bogs and fens will respond to environmental changes.

Keywords

antibiotics, basal respiration, carbon dioxide, microbial activity, microbial biomass, peat

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Introduction

Northern peatlands contain 30% of the global soil C that corresponds to 455 Pg C (Gorham 1991). Carbon mineralization in these peatlands is principally controlled by geochemical, environmental and microbiological factors. According to Updegraff et al. (1996), the C mineralization rates in most peatlands correlated well with the chemical compositions of peats such as water and acid soluble carbohydrates, the C/N and lignin/N ratios, or lignin contents and the peat-forming vegetation (e.g., *Bryophytes*, *Carex*, *Sedge*, *Eriophorum* or shrub/tree plants). The hydrological conditions including the position of redox boundaries associated with the water table and peat moisture content are also known to influence the amount and rate of C mineralization in peatlands where short periods of flooding may stimulate decomposition, while prolonged flooding slow rates (Baker et al. 2001). Severe drought, and subsequent re-wetting, could also destabilize peatland carbon stocks (Fenner and Freeman 2011). Similarly, the decomposition of complex organic matter of peats to carbon dioxide (CO_2), methane and dissolved organic carbon is controlled by climatic factors. CO_2 emission, for instance, tends to increase by a factor of 2 to 3 for every 10 ^{0}C temperature increase (Yavitt et al. 1997).
The importance of microorganisms as a factor of controlling the rate and amount of C mineralization is also widely recognized across a range of peatlands (Andersen et al. 2006; Jaatinen et al. 2007; Martani 2005; Thormann 2006) although there are still gaps in our understanding of the types of and controls on microbes responsible for C mineralization. Broadly, fungi are believed to play fundamental roles in the decomposition processes of organic matter in many acidic terrestrial ecosystems (Andersen et al. 2006; Martani 2005; Thormann et al. 2002; Williams and Crawford 1983), as they have extensive hyphal growth habit and ability

to translocate nutrients through their hyphal networks. They are also tolerant to nutrient limited environments because of their lower biomass N and other nutrient requirements. Fungi principally occupy oxic layers with the exception of certain yeasts and moulds that can carry out fermentation. In contrast, bacteria might have a competitive advantage over fungi in deeper and/or more anoxic soil layers as they can also utilize alternative electron acceptors (Killham and Prosser 2007). However, bacterial diversity has been shown decrease with increasing acidity across a large range of soil types (Fierer and Jackson 2006).

In peatland ecosystems, a range of diversity of fungi, bacteria, archaea, protists, animals and plants have been described (Nuyim 2000). In some studies, fungi have been described as being an important group of decomposers (Andersen et al. 2006; Martani 2005; Jaatinen et al. 2007). In a microscopy-based study, Golovchenko et al. (2007) have reported fungal biomass dominance in ombrotrophic sites while bacterial biomass dominates the minerotrophic sites. However, recent studies by Myers et al. (2012) and Winsborough and Basiliko (2010) have indicated that metabolic activity in peatlands is dominated by bacteria. These authors observed bacterial dominance over fungi in acidic *Sphagnum* derived Canadian bogs and poor fens as well as in a near neutral wetter rich fen with sedge peat. Lin et al. (2012) also reported strong bacterial dominance over fungi with *Acidobacteria* and *Firmicutes* as the dominant microbial groups in bogs and fens of northwestern Minnesota peatlands, respectively. The above findings warrant research to more fully understand the contribution of fungi and bacteria in peatland C cycling; as these microorganisms differ significantly in their physiology and metabolic activity (Poll et al. 2006), and perhaps thus in their responses to environmental changes .

The fungal and bacterial activities in soils can be measured using various techniques; and the selective inhibition (SI) techniques have been used to describe important characteristics of soil functioning by partitioning glucose-induced bacterial and fungal respiration in a range of agricultural and forest soils (Alphei et al. 1995; Ananyeva et al. 2006, Anderson and Domsch 1975; Bailey et al. 2003). Recent studies by Myers et al. (2012) and Winsborough and Basiliko (2010) used SI techniques to effectively inhibit and therefore quantify fungal and bacterial activity in Canadian peatlands, but only after optimizing the antibiotic and glucose additions. Here, we measured bacterial and fungal activity in northern European *eutrophic, ombrotrophic, mesotrophic* and *transitional* peatlands using the SI approach. We hypothesized that ombrotrophic (bog) sites would be more dominated by fungi, while the mesotrophic and eutrophic sites would favor bacteria. We also characterized bulk microbial C mineralization and performed correlation analyses between physical, chemical, and microbiological parameters to evaluate potential controls on C loss from our large range of peats.

Materials and Methods

Characteristics of sampled peatlands

Samples from 20 peatlands of 7 European countries were included in this study (Table 1). These peatlands were partly disturbed (i.e., particularly through the construction of drainage ditches) and their respective water tables have been lowered below the surface layer. The living vegetation has also been scraped to facilitate peat mining for horticultural and other uses. In this study, surface peats (up to 20 cm) were considered as the drainage structures expected to affect the moisture content of the upper peat layers. From each peatland, peats were taken in 3 plastic bags (each has a volume of ≈30L). Each bag contained peats taken from six random places. They

were sampled in the month of September, packed in coolers, and transported to the Leibniz University of Hannover for analysis. All wood, bark and roots were removed and sieved to pass 5 mm sieve. Each bag was then considered as a replicate. Based on the source of water and nutrients in sites (Stewart and Kantrud 1971), the studied peatlands were classified into ombrotrophic (*n = 9*), transitional (*n = 6*), mesotrophic (*n = 3*) and eutrophic (*n = 2*). The ombrotrophic peatlands, or bogs, are entirely dependent on precipitation for hydrologic inputs and are generally nutrient poor environments (Shotyk 1988; Steinmann and Shotyk 1997). The mesotrophic and eutrophic sites, or fens, received more mineral rich ground and/or surface waters. Transitional sites receive some ground/surface water, but are still influenced substantially by mineral-poor precipitation inputs.

The botanical compositions in the sampled peats were identified following Heikurainen and Huikari (1952). Briefly, air dried peat was crushed carefully with a mortar and a representative subsample (100-200 ml) soaked in deionized water for a minimum of 2 h. Botanical identification was then made from the peat remains using a high resolution microscope (Meiji Company, Japan). Critical identification markers such as smallest pore holes, cell structure, and mid and/or tip parts of the leaf were used to ascertain different plant remains. The original plant remains within a given peat sample grouped into *Sphagnum*, *Carex*, *Bryales*, *Eriophorum*, ericoid shrubs and soft/hard wood, where *Sphagnum* and *Carex* were found to be the two major peat-forming groups (Amha et al. 2010; Amha 2011). The degree of humification was determined according to the von Post humification scale (von Post 1924). In this qualitative method, a small amount of moist peat was squeezed by hand and the value determined from the

color of the running water as well as from the nature of the residue. The physical and chemical properties of these peatlands were analyzed and previously reported by Amha et al. (2010).

Sample preparation for incubation

The water content in each bag was adjusted to 40% of the corresponding water filled pore space (WFPS; *eq.* 1) with distilled and deionized water (if necessary), and stored in 4 °C room. The WFPS, as oppose to moisture content, measures the influence of moisture on microbial activity and gives direct information on the availability of water in the samples (Robertson and Groffman 2007). Subsamples were then taken and conditioned for a week at 20°C (Rumed®, Rubarth Apparate GmbH, Germany). These homogenized subsamples were used in the basal respiration and microbial biomass measurements, in glucose and antibiotics optimization experiments as well as in a SI experiment.

$$WFPS = \frac{W_m * D_{BD}}{\rho H_2O * P_S} * 100 \quad (1)$$

Where, *WFPS*, W_m, D_{BD}, ρH_2O and P_S represent water filled pore space (%), gravimetric water content (Mg/Mg), peat dry bulk density (Mg m^{-3}), density of water (Mg m^{-3}) and total pore space (%), respectively.

Basal respiration measurement

Basal respiration in the conditioned peat samples was measured without any amendment. Briefly, triplicate conditioned subsamples (each corresponding to 10 g oven dry weight, odw) were incubated in 1.5 l glass jars for 10 d at 25 °C. The final water content was adjusted to 60% of the corresponding WFPS. Microbial respiration in these peatlands was found to increase considerably with the additions of water up to 60% of their respective WFPS (Amha and Bohne

2011). Incubating KNO_3 treated peat samples at 60% WFPS also did not induce a sizable amount of anaerobic respiration, as evidenced by small emission of (N_2O+N_2)–N over 24 hrs. Headspace gas was taken at the beginning and end of incubation period and analysed for CO_2 on a Perkin Elmer Autosystem XL gas chromatograph equipped with a thermal conductivity detector. CO_2 production (μg CO_2–C g^{-1} dry peat d^{-1}) was calculated from a calibration with four commercial standards.

Microbial biomass

Microbial biomass was estimated by a Substrate Induced Respiration (SIR) method (Anderson and Domsch 1975) as modified by West (1986). Briefly, glucose solution was added to 10 g moist sample (*n = 3*) to achieve the peat-to-solution ratio of 1:2 (w/v). The final glucose concentration in the sample solution was adjusted to 30 mg glucose ml^{-1}. Jars containing samples (each 250 ml capacity) were closed ≈15 min after glucose addition and incubated at 22 °C. Headspace gas was sampled at 0, 1, 2, 3, 4, 5, and 6 h after the jars were sealed. Following each headspace sampling, an equivalent volume of ambient air was injected back into the closed glass jar to avoid a drop in pressure. Microbial biomass-C (MB-C_{SIR}) was calculated according to the revised equation of Sparling et al. (1990) where MB-C_{SIR} (μg g^{-1} dry peat) = 50 x (μl CO_2 g^{-1} dry peat h^{-1}).

Glucose and antibiotics optimization experiments

One peat sample from each peat-forming environment (#9, #12, #17 and #19; Table 1) was used to determine the amount of glucose and antibiotics to be added in a SI experiment. The selected peat samples had similar humification degree (H4-H5). Moreover, the dominant peat-forming plant species in three of the four peat samples was *S. fuscum* (i.e., it accounted for >60% of the

identified *Sphagnum* residues). Optimum concentration of glucose was achieved by incubating 50 ml of conditioned sample with eight glucose concentrations (0, 0.05, 0.1, 0.2, 0.4, 0.6, 0.8 and 1.2 g C l^{-1} dry peat). Peat subsamples, equivalent to 50 ml each, were determined according to VDLUFA (2002) and their respective water content adjusted to 60% WFPS. Jars containing peats were closed ~15 min after amendments and incubated at 25 °C. The CO_2 concentrations in the headspace were measured at the beginning and after 24 h (Winsborough and Basiliko 2010). To determine optimum concentration of antibiotics, triplicate conditioned subsamples (10 g each) were weighed into 100 ml beakers and subsequently treated with six concentrations of streptomycin or cycloheximide (0, 1.5, 3.0, 4.5, 6.0 and 10 mg g^{-1} moist weight). All beakers were then sealed with parafilm (Parafilm®, Menasha, WI, USA) and incubated at room temperature for about 24 h. Each treatment had then received glucose solution at rates of 0.8 g C l^{-1} dry peat. Each beaker was kept inside a-1.5 l glass jar and its respective moisture content adjusted to 60% WFPS. All treatments were incubated at 25 °C. The headspace gases were taken with syringes (0 and 24 h) and analyzed for CO_2.

Selective inhibition experiment

We use the selective inhibition on each sample, after optimizing for glucose (0.8 g C l^{-1} dry peat), streptomycin (3.0 mg g^{-1} moist peat) and cycloheximide (4.5 mg g^{-1} moist peat). Selective inhibition of microbial activity was performed according to Anderson and Domsch (1975) with some modifications. From each peatland, 10 g moist peat subsample (n = 3) was amended with (A) glucose, (B) glucose + streptomycin, (C) glucose + cycloheximide, and (D) glucose + both antibiotics. The final moisture content in each treatment was adjusted to 60% WFPS and incubated at 25 °C. Headspace gases were taken at initial and after 24 h, and analyzed for CO_2.

Calculations and statistical analyses

The relative inhibitions of streptomycin, cycloheximide and their mixture to substrate-induced respiration were calculated according to Bailey et al. (2002) and Beare et al. (1990). The fungal-to-bacterial (F:B) ratio was computed as a ratio of fungal respiration to bacterial respiration. Since the dry bulk density of the studied peatlands differed considerably (Amha et al. 2010), comparisons of fungal and bacterial activity were made on a unit volume basis. Inhibitor Additivity Ratios (IARs) were also calculated as measures of the inhibition of non-target organisms by one or both antibiotics (Beare et al. 1990). An IAR of 1 would thus indicate there is no overlapping or antagonistic effect while IAR >1 illustrates the presence of overlapping antibiotic effect (i.e., substantial non-target inhibition by one or both antibiotics). IAR becomes <1 when there is an antagonistic effect (i.e., the combined addition of antibiotics being more efficient than the separate addition). The relative proportions of fungal and bacterial activity were also compressed to fit an IAR of 1.0 after checking the data for normality and homogeneity of variance. Broad categorical comparisons with ANOVA were made for the selected microbiological data on the basis of peatland types. The coefficient of variations (CV, %) were calculated according to s/x, where s represents the deviation between the peat samples means and x is overall mean value. The Pearson correlation coefficients with Bonferroni probabilities were also computed between the microbiological data and a wide range of physicochemical parameters to evaluate their relations and potential controls on one another using R statistical software, version 3.1.0, 2014.

Results

Peats were quite variable in their degree of humification, pH, dry bulk density and total C content (Table 2). The humification degree ranged from H3 to H7; where H1 represents peat with fully intact plant material and H10 represents completely humified peat. The pH of all peats (in water; 1:5 w/v) was acidic and varied between 3.91 and 5.19 units. However, there was no clear relationship between humification and the peatland types. Dry bulk density was determined according to VDLUFA (2002) and ranged from 44 to 170 g l^{-1}, with an overall mean value of 82.6 g l^{-1}. Total C varied between 46.9 and 52.2% and tended to increase with degree of humification within each peatland type (Table 2).

Basal respiration ranged from 24 to 128 µg CO_2-C g^{-1} dry peat d^{-1} (Table 2). The highest CO_2 (mean ± standard error) was measured from eutrophic sites (121±7 µg g^{-1} dry peat d^{-1}), which is followed by transitional (60±9 µg g^{-1} dry peat d^{-1}), mesotrophic (60±24 µg g^{-1} dry peat d^{-1}) and ombrotrophic (95±8 µg g^{-1} dry peat d^{-1}) sites. Peat from both eutrophic sites had similarly the high rates of respiration irrespective of their degree of humification (H5 vs. H7, respectively) and the peat-forming plant species (*Sphagnum* vs. *Carex* species). CO_2 production from peats containing *S. imbricatum* (#8, #9, #14, #16 and #18) was considerably lower (36–62 µg CO_2-C g^{-1} dry peat d^{-1}) than the overall mean value (77 µg CO_2-C g^{-1} dry peat d^{-1}; *n = 20*) indicating C mineralization in the studied peatlands is affected not only by peatland type but also by the specific plant species composition. CO_2 production was highest in peat from Finish sites than those in any other countries, regardless of peats humification degree, peat botanical compositions, or peatland type (Table 2).

In the SIR method, the response of microorganisms to added glucose seem to vary considerably between peatlands but it did not show any pattern on the basis of geographic locations,

humification degree and peat-forming vegetation. While the rates of CO_2 production in the Lithuanian (*n = 3*) and Latvian (*n = 2*) peats decreased over 3 and 5 h, respectively, they increased after 1 h in the Estonian (*n = 2*), Finish (*n = 5*), German (*n = 2*) and Swedish (*n = 1*) peat samples (data not shown). However, the concentration of CO_2 was nearly stable over the incubation period in the Irish (*n = 2*), Estonian (#15) and the remaining two German peats (#12 and #17). In this study, the maximum initial respiratory response to the added glucose ranged from 5.52 to 36.04 µl CO_2 g^{-1} dry peat h^{-1}, which corresponded to 276 to 1802 µg MB-C g^{-1} dry peat (Table 2).

The glucose optimization experiment indicated that substrate-induced microbial respiration in four moderately decomposed peat samples increased with increasing glucose-C although the rates varied considerably between peatland types (Fig. 1). The substrate-induced CO_2-C in the transitional, mesotrophic and eutrophic peats showed steep increases with increasing glucose concentrations up to 0.8 g C l^{-1}. However, this was happened only up to 0.2 g C l^{-1} in ombrotrophic peat (#9) whereby further glucose additions did not result in a significant CO_2 evolution. We, therefore, decided to add 0.8 g C l^{-1} (i.e., 2000 µg glucose ml^{-1} peat) in the SI experiment. Substrate-induced respiration after streptomycin addition increased slightly in ombrotrophic peat sample but decreased considerably in other peat samples (Fig 2a). The maximal bacterial inhibition in eutrophic peat was attained at higher streptomycin concentration (6.0 mg g^{-1} moist peat) compared to transitional peat (4.5 mg g^{-1} moist peat) and mesotrophic peat (3.0 mg g^{-1} moist peat). In contrast, the pattern of respiratory responses to increasing concentrations of cycloheximide was similar for all peatlands (Fig. 2b). Addition of

cycloheximide up to 4.5 mg g^{-1} moist peat suppressed fungal activity considerably although the inhibition in eutrophic peat was maximal at rate of 1.5 mg g^{-1} moist peat.

In the SI experiment, production of CO_2 from the control treatment (0.8 g glucose-C l^{-1} received peat sample) ranged from 103 to 673 mg l^{-1} dry peat d^{-1} (Table 3). The rates of substrate-induced microbial respiration in most ombrotrophic peatland samples were lower than the overall mean value of 227 mg CO_2 l^{-1} dry peat d^{-1}. In contrast, the highest CO_2 evolution (>300 mg l^{-1}) was measured from the eutrophic peats. Bacterial respiration in 3 ombrotrophic peats (#1, #2 and #9) was slightly increased (2.9, 4.4 and 3.8% of control, respectively) after the addition of 3.0 mg streptomycin g^{-1} moist peat. Bacterial inhibition in the remaining peats ranged from 5.3 to 78.0%, with an overall mean value of 34.5%. In similar comparison, 35.7% of substrate-induced respiration was reduced by the addition of 4.5 mg cycloheximide g^{-1} moist peat. Combined introduction of antibiotics across all peats suppressed substrate-induced respiration by 39.9 to 85.6 % (Table 3). The reductions of CO_2 evolution after combined additions were comparatively low in mesotrophic, transitional and eutrophic peats compared to reductions by the sum of separate additions of streptomycin and cycloheximide. However, there was no clear trend for samples from ombrotrophic peatlands.

The F:B ratio in mesotrophic, eutrophic and transitional peats (but not peat #12) were between 0.10 and 0.91. In contrast, ombrotrophic peats (after excluding the above 3 peats from the calculation) had an F:B ratio of >1 indicating proportionally lower bacterial contributions to total C mineralization. The presence of overlapping or antagonistic effect was also compared on the basis of IAR (Table 3); and additions of 3.0 mg streptomycin and 4.5 mg cycloheximide g^{-1} moist peat resulted in IAR of 0.97 to 1.48. The relative proportions of fungal and bacterial

activity compressed to fit an IAR of 1.0 (Fig. 3), where most transitional and mesotrophic peats showed an overlapping effect and ombrotrophic peat samples an antagonistic effect. Based on the computed relative proportions, bacterial and fungal inhibitions ranged from 11.2 to 91.1% and from 7.3 to 87.7%, respectively. Overall, in terms of most measured microbiological variables (Table 2 & 3), there were no differences between transitional and mesotrophic peat samples to suggest that these two peatland types shall be treated as one group.

Basal respiration and MB-C_{SIR} showed significant ($P < 0.01$) correlations with total C, N/P and C/P ratio but correlated poorly ($P > 0.05$) with total N, pH, dry bulk density, C/N ratio and the von Post decomposition degree (Table 4). In similar comparison, other microbiological data (i.e., fungal respiration, bacterial respiration, F:B ratio and IAR) had poor correlations with many of the above physicochemical variables.

Discussion

Peat mineralization patterns and controls

The rate of basal respiration is often used as a measure of microbial activity across soil types and varied considerably between the studied peatlands (Table 2). Rates in eutrophic peatlands were considerably higher than ombrotrophic, transitional, or mesotrophic sites; and indicating that the rates of C-cycling in eutrophic peatlands were not constrained by the availability of easily degradable C- and/or nutrient-sources. According to Shotyk (1988) and Steinmann and Shotyk (1997), eutrophic peat is generally richer in nutrients and has more bioavailable C, and thus is more decomposable. The botanical composition in our peatlands also affected the rates of basal respiration as this attribute also determines the chemical nature of organic matter inputs in peatlands. In this study, CO_2 production in peats containing *S. imbricatum* was low compared to

peats containing other bryophytes residues suggesting that organic compounds in the *S. imbricatum* residues could be either relatively resistant to microbial degradation or have antagonistic effects on microorganisms. Moreover, the rates of C mineralization in a wide range of north European peatlands might be explained by total C, N:P and C:P ratios as these variables showed strong correlations with basal respiration (Table 4).

The role of fungi and bacteria in peat decomposition

The contribution of fungi to substrate-induced respiration was high in ombrotrophic peats (Table 3), which is in line with Golovchenko et al. (2007) findings who reported fungi dominance in such sites. Our results also seem to support another cultivation-dependent study by Thormann (2006) who observed fast growth of fungi in ombrotrphic peatlands. He pointed out that fungal growth in these peatlands is primarily favored by inherent acidic pH, low nutrient availability, recalcitrant organic matter, and high C/N ratio. Since the pH in our peatlands was acidic (Table 1) and pH did not correlate with measured microbiological data (Table 4), the high F:B ratios might be explained by low nutrients and oxygenated surface horizons in the ombrotrophic bogs. The presence of mycorrhizal fungi could be another explanation for the higher F:B ratios in ombrotrophic peats. Analyses on the botanical compositions of peat residues confirmed that most peats contained remnant of ericoid shrubs (e.g., *Empetrum nigrum*) and other woody plant species. The ericoid mycorrhizal fungal strains, which are found in bogs and fens, have the ability to decompose lignin, cellulose, chitin, starch, pectin, and gelatin (Rice and Currah 2001), and these non-obligate plant symbionts might contribute to the higher fungal respiration in the ombrotrophic peatlands.

Bacterial contributions to CO_2 production were high in most peatlands and showed the following pattern: eutrophic>>transitional≥mesotrophic>>ombrotrophic peatlands (Table 3). Winsborough and Basiliko (2010) have also demonstrated bacterial dominance over fungi on three Canadian peatlands using the same technique. However, the range of F:B ratios in the current study is wider than Winsborough and Basiliko (2010) findings (F:B of 0.31-0.68). Similarly, Lin et al. (2012) and Myers et al. (2012) observed prokaryotic dominance in peatland microbial communities although they used different methodologies (i.e., pyrosequencing and clone library construction of phylogenetic marker genes vs. the SI method).

Combined additions of streptomycin and cycloheximide did not result in a complete inhibition of microbial activity (Table 3). According to Heilmann et al. (1995), the sources of CO_2 from both streptomycin and cycloheximide treated sample is attributed to surviving fungal and bacterial populations or active constitutive enzymes in the peat samples. With regard to the later reason, β-glucosidase (Fenner et al. 2005) and phosphatase (Bonnett et al. 2006) are known to be present in wide range of peatlands. CO_2 production, following the additions of both antibiotics, might also come from non-target organisms as peat microbiota also can comprise protozoa (e.g. testate amoeba), archaea, microalgae and micromotazoa (Payne et al. 2010). Our range (39.9–85.6%) is, however, higher than the mean values observed for most soils (40–70%; Beare et al. 1990; West 1986). Slightly increased bacterial respiration in 3 of the 9 ombrotrophic peatland samples after bactericide additions (Table 3) elucidated that streptomycin may have been used as a substrate source by non-target or resistant microorganisms in these peatlands. In literature, antibiotic utilization by non-target/resistant microorganisms (Badalucco et al. 1994) and adsorption/modification of antibiotic(s) by the soil components (Alphei et al. 1995; Lin and

Brookes 1999) are mentioned as plausible reasons for increased microbial activity after streptomycin addition.

Our samples were obtained from partly disturbed peatlands where the respective water tables lowered below the surface layer to facilitate peat mining for horticultural and other uses. These human interventions and changes in land-use are expected to affect the functioning and structure of fungal and bacterial communities. However, recent study by Preston et al. (2012) demonstrated that bacterial community structure in North American and European bogs and fens tends to be less affected by land-use change (i.e., natural, mined and resorted) although these peatlands differed considerably in peat physicochemical characteristics, geographic locations and vegetation types. Basiliko et al. (2013) also supported the above findings and concluded that bacterial communities appeared to be more resistant or resilient to substrate change brought about by land-use change and other interventions. In contrast, fungal community and structure are strongly related to vegetation and litter chemistry in the peatlands (Trinder et al. 2008) where these two parameters have larger roles in structuring fungal communities than water table position. Trinder et al. (2008) findings suggest that lowering the water table below the surface layer might have had little impact on the fungal communities in our peatlands given that the time interval between drainage ditches construction and peat sampling period was relatively short (June/July vs. September).

Although we did not identify the type and number of bacterial species found in the studied peatlands, the bacterial community in an acidic *Sphagnum* dominated peat bog includes *Acidobacteria, Alphaproteobacteria, Actinobacteria, Deltaproteobacteria, Chloroflexi, Verrucomicrobia,* and *Planctomycetes* (Dedysh et al. 2006). Lin et al. (2012) also reported

Acidobacteria and *Firmicutes* are the dominant microbial groups in bog and fen of northwestern Minnesota peatlands, respectively. Most of these bacterial groups, particularly *Acidobacteria*, have the ability to degrade aromatic and other organic compounds in peatland ecosystems (Ausec et al. 2009). Likewise, the largest fungal group in peatlands is known to be *ascomycetes* followed by *basidiomycetes*, *zygomycetes* and *chytridiomycetes* (Thormann and Rice 2007). The first two fungal groups are also known to predominate surface peatlands (Thormann et al., 2002; Thormann 2006) and could degrade dissolved organic matter (e.g., cellulose and polyphenolic compounds) and variety of C substrates of bryophilous residues under oxic condition. The dominant fungi group in the studied peats is speculated to be filamentous fungi compared to yeast as these peats contained lower amount of readily soluble carbohydrates (Amha 2011). According to Thormann et al. (2007), yeasts are involved in the degradation of mostly simple polymers, including sugars, alcohols, and amino acids, and they appear to play minor or no roles in the degradation of complex polymers, such as cellulose, pectin, and lignin and its derivatives. Yeasts are also accounted for about 10% of fungi known from peatlands.

With regard to the SI method, the concentrations of antibiotics that effectively partitioned eukaryotic and prokaryotic activity tended to vary between peatland types (Fig 2a & b); and additions of 3 mg streptomycin and 4.5 mg cycloheximide g^{-1} moist peat were considered to be the lowest concentrations producing maximum bacterial and fungal inhibition, respectively. These concentrations were considerably higher than what are commonly added into mineral soils (Alphei et al. 1995; Ananyeva et al. 2006; Bailey et al. 2003) as soils with higher organic matter contents and lower pH (both are the cases for our sampled peatlands; Table 2) require higher concentration of antibiotics to achieve maximum inhibition. The amount of cycloheximide added

in this experiment was considerably higher than Winsborough and Basiliko (2010) who achieved maximum fungal inhibition with an addition of 1.3 µg cycloheximide ml^{-1} of bog peat, rich fen peat or poor fen peat. In contrast, they had added higher streptomycin concentrations (13–26 mg ml^{-1} peat) as the activity of microorganisms in their sampled peats were dominated by bacteria. The IARs range in this study (Table 3) was generally higher than Winsborough and Basiliko (2010) but lower than Imberger and Chiu (2001) who worked in different ecosystem and soil types. Overall, the computed mean IAR was quite close to 1 suggesting that SI techniques can be used to partition fungal and bacterial activities in wide range of peatlands. This approach could, therefore, be used to examine microbial and carbon cycling feedbacks to environmental and global change across a large range of peatlands.

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Table 1 Details on the peat-forming environment and botanical composition of peat samples obtained from seven European countries.

Peat No.	Country	Area of extraction	[a]Relevant *Sphagnum* species	Peat-forming environment
#1	Latvia	Turkums	2, 5, 8	ombrotrophic bog
#2	Lithuania	Gabolinus	4, 8, 11, 15	ombrotrophic bog
#3	Estonia	West Estonia	2, 6, 8, 10	ombrotrophic bog
#4	Finland	Lapua	5, 8, 10, 15	ombrotrophic bog
#5	Finland	Seinajoki	1, 10	ombrotrophic bog
#6	Finland	Närpio	1, 8, 10	ombrotrophic bog
#7	Latvia	LaFlora	1, 6, 8, 10	ombrotrophic bog
#8	Ireland	Brehony	1, 8, 9	ombrotrophic bog
#9	Estonia	P-27	4, 8, 9	ombrotrophic bog
#10	Lithuania	-	1, 6, 8, 10	fen-bog transition
#11	Lithuania	15b Laukas	1, 3, 10, 14	fen-bog transition
#12	Germany	Osnabrück	8, 10, 13	fen-bog transition
#13	Sweden	Drakamyr	8	fen-bog transition
#14	Germany	P-2	9	fen-bog transition
#15	Estonia	West Estonia	[b]Absent	fen-bog transition
#16	Ireland	Sharagh	9, 13	mesotrophic fen
#17	Germany	Vechta	7, 8, 12, 13	mesotrophic fen
#18	Germany	Vehmemoor	9, 12, 13	mesotrophic fen
#19	Finland	Kikilla	16	eutrophic fen
#20	Finland	Kikilla	Absent	eutrophic fen

[a]according to Heikurainen and Huikari (1952): 1) *S. angustifolium;* 2) *S. balticum;* 3) *S. capillifolium;* 4) *S. centrale;* 5) *S. compactum;* 6) *S. cuspidatum;* 7) *S. fallax;* 8) *S. fuscum;* 9) *S. imbricatum;* 10) *S. magellanicum;* 11) *S. molle;* 12) *S. palustria;* 13) *S. papillosum;* 14) *S. riparium;* 15) *S. russowii;* 16) *S. subsecunda*

[b]dominated by *Carex* species

Table 2 Selected physicochemical and microbiological characteristics of the peats

[x]Peat	Country	Humification degree (H)	pH in water (1:5 w/v)	Dry bulk density (g L^{-1})	Total Carbon (%)	Basal respiration (µg CO_2-C g^{-1} peat d^{-1})	Microbial biomass (µg C g^{-1} peat)
#1	Latvia	3	4.62	45	48.5	70	739
#2	Lithuania	3	4.42	44	49.0	73	983
#3	Estonia	3	4.71	79	49.1	102	1464
#4	Finland	3	4.28	58	47.8	111	1091
#5	Finland	3	4.46	87	49.3	102	1798
#6	Finland	3	4.60	54	47.2	103	1802
#7	Latvia	4	4.75	49	49.3	91	990
#8	Estonia	5	4.62	90	51.2	62	1058
#9	Ireland	5	4.62	54	50.9	38	586
#10	Lithuania	3	4.60	46	49.0	63	669
#11	Lithuania	4	4.77	74	50.0	76	1236
#12	Germany	4	4.46	80	50.5	73	1069
#13	Sweden	5	4.58	90	48.9	82	1279
#14	Germany	7	4.74	107	52.2	41	515
#15	Estonia	7	5.19	155	50.2	24	276
#16	Ireland	4	4.91	61	50.7	36	517
#17	Germany	5	4.80	109	48.8	107	1368
#18	Germany	6	3.91	123	51.5	37	393
#19	Finland	5	4.29	76	46.9	128	1653
#20	Finland	7	4.97	170	51.2	113	1384
Mean			**4.60**	**82.6**	**49.6**	**77**	**1044**
CV			**5.88**	**43.2**	**3**	**40**	**44**

[x]see Table 1 for the descriptions of the peat samples

Table 3 Percent of bacterial, fungal and combined inhibitions with respect to control, fungal-to-bacterial ratio (F:B), and inhibition additivity ratio (IAR) in a wide range of peat samples subjected to antibiotics. All peat samples received 0.8 g glucose-C and 0.4 g NO_3^-–N. The moisture content was adjusted to 60% water filled pore space and incubated at 25 °C.

[v]Peat	Control (mg CO_2 L^{-1} d^{-1})	% inhibition			F:B	IAR
		Streptomyci	Cycloheximid	[w]Combine		
#1[x]	[y]139 ± 8	-2.4 ± 0.9	54.2 ± 1.9	67.6 ± 0.7	nc	nc
#2[x]	136 ± 9	-3.8 ± 0.4	46.6 ± 7.6	49.3 ± 7.0	nc	nc
#3	318 ± 39	9.4 ± 1.0	73.3 ± 2.8	83.6 ± 2.8	7.88 ± 1.11	0.99 ±
#4	242 ± 16	12.3 ± 4.1	67.2 ± 10.2	82.0 ±	5.63 ± 1.07	0.97 ±
#5	264 ± 22	5.3 ± 0.1	38.3 ± 0.8	43.1 ± 0.3	7.21 ± 0.34	1.01 ±
#6	153 ± 10	8.1 ± 1.8	58.0 ± 5.0	67.3 ±	7.22 ± 0.94	0.99 ±
#7	180 ± 1	8.3 ± 2.6	36.2 ± 4.8	43.7 ± 4.0	4.48 ± 0.80	1.01 ±
#8	103 ± 3	19.9 ± 2.0	30.7 ± 5.2	39.9 ± 6.8	1.54 ± 0.10	1.27 ±
#9[x]	106 ± 38	-4.1 ± 3.2	44.0 ± 1.6	52.9 ± 5.7	nc	nc
#10	124 ± 16	40.4 ± 3.0	30.5 ± 2.0	53.6 ± 2.6	0.76 ± 0.01	1.32 ±
#11	372 ± 2	40.9 ± 3.0	18.9 ± 4.3	49.9 ± 5.4	0.46 ± 0.07	1.20 ±
#12	156 ± 5	31.3 ± 4.2	37.5 ± 4.5	68.7 ± 8.5	1.20 ± 0.02	1.00 ±
#13	212 ± 10	30.0 ± 0.2	27.0 ± 0.4	43.5 ± 3.8	0.90 ± 0.01	1.32 ±
#14	242 ± 10	53.5 ± 2.1	38.0 ± 0.2	86.7 ± 3.9	0.71 ± 0.03	1.06 ±
#15	196 ± 18	45.8 ± 2.0	28.2 ± 0.9	58.1 ± 3.1	0.62 ± 0.01	1.28 ±
#16	108 ± 5	49.1 ± 2.2	38.7 ± 3.2	59.5 ± 0.4	0.79 ± 0.10	1.48 ±
#17	143 ± 17	44.1 ± 1.8	35.5 ± 4.1	61.2 ± 7.0	0.80 ± 0.06	1.30 ±
#18	332 ± 15	37.5 ± 0.8	33.9 ± 3.2	55.5 ± 2.0	0.91 ± 0.11	1.31 ±
#19	340 ± 16	78.0 ±0.8	8.0 ± 0.3	85.6 ± 3.3	0.11 ± 0.02	1.01 ±
#20	673 ± 58	72.5 ± 1.8	7.3 ± 0.2	78.2 ± 0.1	0.10 ± 0.01	1.02 ±
Ombrotrophi	**210**	**10.6**	**50.6**	**59.9**	**5.66**	**1.04**
Transitional	**217**	**40.3**	**30.0**	**60.1**	**0.78**	**1.20**
Mesotrophic	**194**	**43.6**	**36.0**	**58.7**	**0.83**	**1.36**
Eutrophic	**507**	**75.3**	**7.7**	**81.9**	**0.11**	**1.02**

***P*-level**		***	***	*	**	**ns**

[v]see Table 1 for the descriptions of the peat samples

[w]combined addition of 3.0 mg streptomycin and 4.5 mg cycloheximide g^{-1} moist peat

[x]peats with negative inhibition after addition of streptomycin not included in categorical analysis

[y]mean ± standard deviation;

ns, *, **or *** denotes significant level at $P>0.05$, $P \leq 0.05$, $P \leq 0.01$ or $P \leq 0.001$, respectively.

Table 4 Pearson correlation coefficient (*r*) computed between microbiological data and some of the selected physicochemical properties

Variables	Microbial Biomass-C	Basal Respiration	Fungal Respiration	Bacterial Respiration	Fungal-to-Bacterial Ratio	IAR
Humification degree	–0.34	–0.39	–0.26	0.51*	–0.66**	0.21
Dry Bulk Density	–0.27	-0.21	0.06	0.60*	–0.41	0.11
pH	–0.09	–0.19	–0.23	0.10	–0.16	0.19
Total Carbon (C)	–0.56**	–0.57*	–0.12	0.30	–0.46	0.17
Total Nitrogen (N)	–0.10	–0.19	0.05	0.51*	–0.27	–0.01
Inorganic N	0.49	0.47	0.07	0.04	0.29	–0.50*
C/N	–0.15	–0.02	–0.19	–0.59*	0.18	0.17
N/Phosphorous (P)	–0.66**	–0.68**	–0.13	0.18	–0.36	0.25
C/P	–0.66**	–0.67**	–0.27	–0.25	–0.23	0.39
N/Potassium (K)	–0.41	–0.43	0.11	0.35	–0.22	0.12

* or ** donates significant level at $P \leq 0.05$ or $P \leq 0.01$respectively.

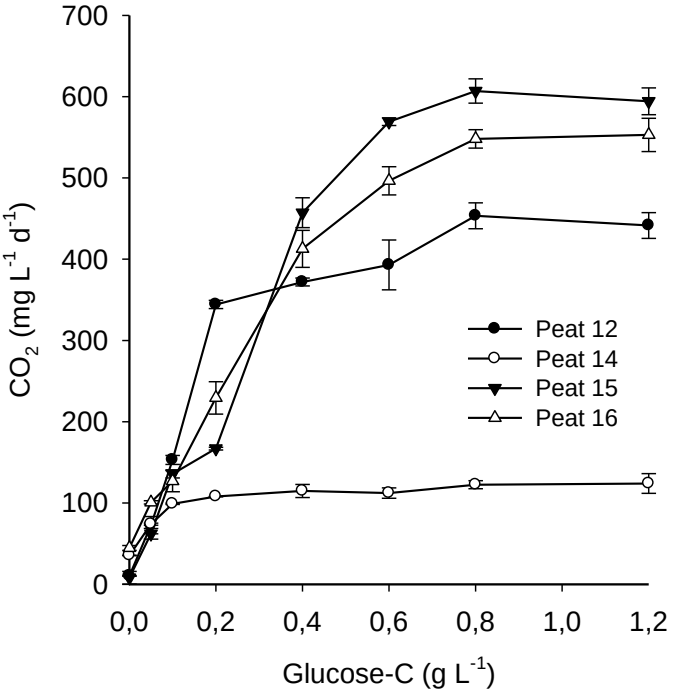

Figure 1 CO_2 evolution from four moderately decomposed peat samples as influenced by the added glucose concentrations. The moisture content in each treatment was adjusted to 60% water filled pore space and incubated at 25 °C for 24 h. Each point was the mean of 3 measurements and the vertical bars indicate standard deviations. See Table 1 for the descriptions of the peatlands.

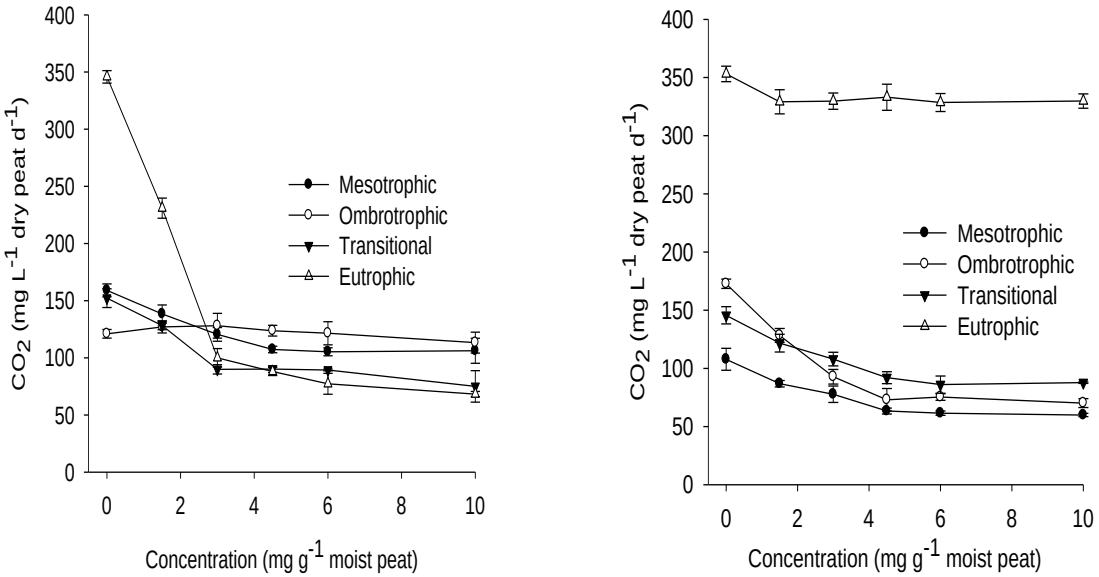

Figure 2 Evolved CO_2 from four moderately decomposed peat samples after additions of streptomycin (a) and cycloheximide (b). Glucose and NO_3^-–N were added to each treatment at rates of 0.8 g C and 0.4 g N L^{-1} dry peat, respectively. The moisture content in all treatments was 60% water filled pore space and samples were incubated at 25 °C for 24 h. Each point was the mean of 3 measurements and the vertical bars indicate standard deviations.

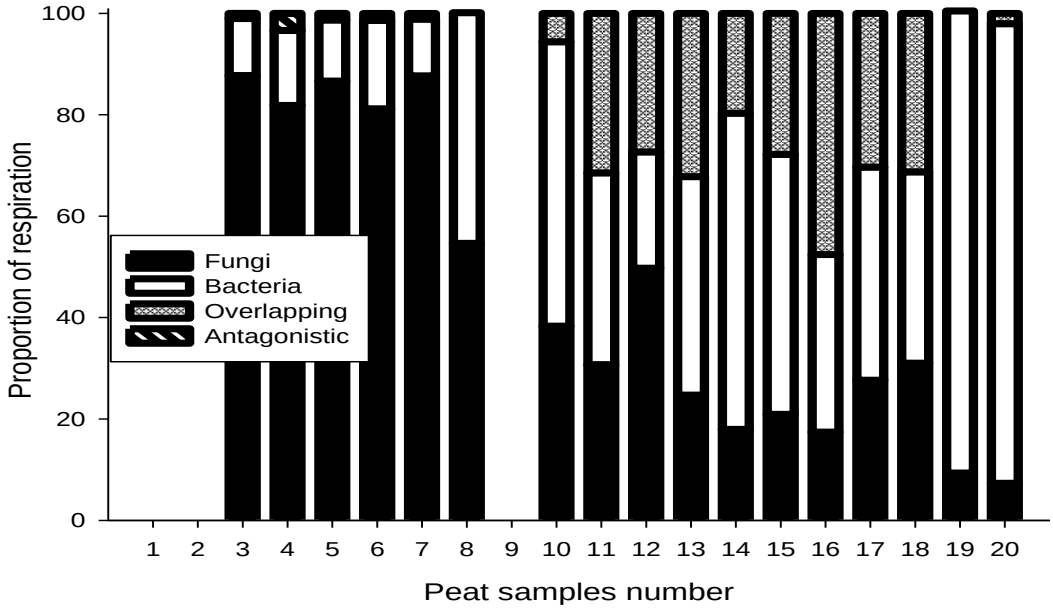

Figure 3 The proportion of overlapping or antagonistic effect by the added antibiotics when the inhibition additivity ratio compressed to 1. Peatland #1, #2 and #9 are not included in the calculation as an addition of streptomycin in these samples resulted in a slight increased C evolution compared to the control. See Table 1 for the descriptions of the peatlands.