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Aerobic carbon-cycle related microbial communities in boreal peatlands: responses to water-level drawdown

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Academic dissertation

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Title: Aerobic carbon-cycle related microbial communities in boreal peatlands: responses to water-level drawdown

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ABSTRACT

Boreal peatlands represent a considerable portion of the global carbon (C) pool. These environments are vulnerable to changes in water level (WL), which can vary dramatically in response to climate or land-use change. Water-level drawdown (WLD) causes peatland drying and induces a vegetation change, which in turn affects the decomposition of soil organic matter and the release of greenhouse gases (CO_2 and CH_4) into the atmosphere. The objective of this thesis was to study the microbial communities related to the C cycle and their response to WLD in two boreal peatlands.

The first study site (Lakkasuo) is a boreal peatland complex that was partly drained in 1961 to investigate the long-term effects of WLD, and includes three site types with different nutrient levels. At the same location, an experiment simulating the predicted effect of climate change was carried out in 2001 to study the short-term effects of WLD. The second study site (Suonukkasuo) is a boreal fen with a WL gradient caused by a groundwater extraction plant; the undisturbed fen grades into a pine-dominated peatland forest. Microbial communities were studied with phospholipid fatty acid (PLFA) analysis, PCR-DGGE and multivariate analysis.

Both sampling depth and site type had a strong impact on all microbial communities. In general, bacteria dominated the deeper layers of the nutrient-rich fen and the wettest surfaces of the nutrient-poor bog sites, whereas fungi seemed more abundant in the drier surfaces of the nutrient-poor bog. WLD clearly affected the microbial communities but the effect was dependent on site type. Fungi and Gram-negative bacteria seemed to benefit and actinobacteria to suffer from the WLD in the fens. The fungal and methane-oxidizing bacteria (MOB) community composition changed at all sites but the actinobacterial community response was apparent only in the nutrient-rich fen after WLD.

The actinobacterial response to WLD was minor compared to that of the fungal community. The response was greatest in the nutrient-rich fen and least in the nutrient-poor bog. Microbial communities became more similar among sites after long-term WLD. Litter quality had a large impact on community composition, whereas the effects of site type and WLD were relatively minor. The decomposition rate of fresh organic matter was influenced slightly by actinobacteria, but not at all by fungi. Overall, the results were in line with patterns of vegetation change in the study sites.

Field respiration measurements in the northern fen indicated that short term WLD accelerates the decomposition of soil organic matter. In addition, a correlation between activity and certain fungal sequences indicated that community composition affects the decomposition of old organic matter in deeper layers of the peat profile. Fungal sequences were matched to taxa capable of utilizing a broad range of substrates. Most of the actinobacterial sequences could not be matched to characterized taxa in reference databases. WLD had a negative impact on CH_4 oxidation, especially in the oligotrophic fen.

This thesis represents the first investigation of microbial communities and their response to WLD among a variety of boreal peatland habitats. The results indicate that microbial community responses to WLD are complex but dependent on peatland type, litter quality, depth, and variable among microbes.

Keywords: boreal peatlands, carbon cycling, water level drawdown, drainage, climate change, litter quality, decomposer communities, fungi, actinobacteria, MOB

To the memory of Nuutti

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Kerava, Spring 2010, Krista Peltoniemi

LIST OF ORIGINAL ARTICLES

This thesis in based on the following papers, referred to in the text by their Roman numerals:

I Jaatinen, K., Fritze, H., Laine, J. and Laiho, R. 2007. Effects of short- and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. Global Change Biology, 13: 491–510. doi:10.1111/j.1365-2486.2006.01312.x

II Peltoniemi, K., Fritze, H. and Laiho, R. 2009. Response of fungal and actinobacterial communities to water-level drawdown in boreal peatland sites. Soil Biology and Biochemistry, 41: 1902–1914. doi:10.1016/j.soilbio.2009.06.018

III Jaatinen, K., Tuittila, E-S., Laine, J., Yrjälä, K. and Fritze, H. 2005. Methane-oxidizing bacteria (MOB) in a Finnish raised mire complex: effects of site fertility and drainage. Microbial Ecology, 50: 429–439. doi:10.1007/s00248-004-0219-z

IV Jaatinen, K., Laiho, R., Vuorenmaa, A., del Castillo, U., Minkkinen, K., Pennanen, P., Penttilä, T. and Fritze, H. 2008. Responses of aerobic microbial communities and soil respiration to water-level drawdown in a northern boreal fen. Environmental Microbiology, 10: 339–353. doi:10.1111/j.1462-2920.2007.01455.x

V Peltoniemi, K., Fritze, H., Alvira Iraizoz, P., Pennanen, T., Straková, P. and Laiho, R. The influence of litter quality, site nutrient level, water-level drawdown and the state of litter decomposition on fungal and actinobacterial decomposer communities in boreal peatlands. Manuscript.

AUTHOR'S CONTRIBUTIONS

Krista Peltoniemi (nee Jaatinen) had the main responsibility for the microbial analyses based on molecular methods and the writing process in all papers. She participated in sampling (**I-III**) and conducted the multivariate data analyses together with Raija Laiho (**I, II, IV, V**). Raija Laiho was responsible for the CO_2 respiration (**I, IV**) and CH_4 oxidation (**III**) models. Hannu Fritze was responsible for the guidance in practical microbiological laboratory work in all papers. Jukka Laine was in charge of the field experimental layout at Lakkasuo (**I, II, III**). Taina Pennanen was responsible for the fungal in-growth (mesh bag) experiment, and Kari Minkkinen and Timo Penttilä conducted the CO_2 field measurements (**IV**). Raija Laiho and Petra Straková were responsible for the layout of the litter experiment, and Petra for the preparation of the litter material and their chemical analyses (**V**). The other coauthors participated in the data analyses, writing process and discussion of the results.

CONTENTS

ABBREVIATIONS

a.s.l.	above sea level
bp	base pair
CA	correspondence analysis
CCA	canonical correspondence analysis
cDNA	complementary deoxyribonucleic acid
d.d.	unit degree days
DGGE	denaturing gradient gel electrophoresis
DCA	detrended correspondence analysis
DNA	deoxyribonucleic acid
ECM	ectomycorrhiza
ERM	ericoid mycorrhiza
GC	gas chromatography
Ho	hollow
Hu	hummock
ICP-A	ESinductively coupled plasma atomic emission spectrometer
IRGA	infra-red gas analyser
ITS	internal transcribed spacer
La	lawn
LTD	long-term water-level drawdown
ME	mesotrophic
mmoX	alpha-subunit of the hydroxylase component of the sMMO
MOB	methane-oxidizing bacteria
mRNA	messenger ribosomal ribonucleic acid
NMDS	non-metric multidimensional scaling
NPP	net primary production
P	pristine
PCA	principal component analysis
PCR	polymerase chain reaction
PLFA	phospholipid fatty acid
pMMO	particulate methane-monooxygenase
pmoA	A-subunit of the pMMO
OL	oligotrophic
OM	ombrotrophic
o.m.	organic matter
Pg	petagram (1 x 1015 g)
ppb(v)	parts per billion (per volume)
ppm(v)	parts per million (per volume)
RDA	redundancy analysis
RDP	ribosomal database project
RIGLS	restricted iterative generalized least square
rRNA	ribosomal ribonucleic acid
RT-PCR	reverse transcriptase polymerase chain reaction
sMMO	soluble methane-monooxygenase
STD	short-term water-level drawdown
Tg	teragram (10^{12} grams = megatonne)
WL	water level
WLD	water-level drawdown

1 INTRODUCTION

1.1 Peatland ecosystems

Peatlands are defined by the presence of peat, a substance composed mainly of partially decomposed plants and being over 65% organic matter and less than 20-35% inorganic content (Clymo 1983). The International Mire Conservation Group (Joosten and Clarke 2002) requires a 30 cm minimum depth of peat for a site to be classified as peatland. A 'mire' is a water-saturated and peat-forming peatland. The main physical factor in peatland functional ecology is the high water level (WL), which reduces the decomposition rate of organic matter and enables peat to form (Päivänen and Vasander 1994). The height of the WL varies in time and space within and among peatlands. Environmental factors, such as a cool climate and low evaporation maintain conditions that promote peat formation.

Based on ecohydrology and the consequent nutrient status, boreal peatlands are classified into two main trophic classes: minerotrophic and ombrotrophic (Rydin and Jeglum 2006). Minerotrophic peatlands, i.e., fens, receive nutrients from input water that drains nearby mineral soils (Ingram 1992) and they are richer in cations such as Mg^{2+}, K^{+}, and Ca^{2+} (Malmer et al. 1992). Minerotrophic fens can be further divided into three classes according to their nutrient availability: oligotrophic (poor), mesotrophic (intermediate) and eutrophic (rich) (Rydin and Jeglum 2006). Fens are typically characterized by herbaceous species and sedges (e.g., Cyperaceae) that have aerenchymatic tissues enabling them to live in waterlogged conditions. The surface of ombrotrophic peatlands, i.e., bogs, is isolated from the throughflow and groundwater of the surrounding catchment area; therefore, they receive water and chemical elements from atmospheric deposition only. Bogs are typically dominated by dwarf shrubs and *Sphagnum* mosses. While differences in ecohydrology, moisture-aeration and pH-base richness largely determine peatland vegetation, variation in the nutrient level and wetness of a site produces heterogenic peatland habitats that provide different suites of environmental resources to microbial communities. In general, fungal biomass tends to dominate (55–99%) in ombrotrophic peatland, while bacterial biomass is the most abundant (55–86%) in minerotrophic peatlands (Golovchenko et al. 2007).

Subarctic and boreal peatlands store about 460 Pg of C, which is ca. 30% of the global soil C pool (Gorham 1991). The accumulation of C in peatlands is a balance between the C input of the litter-forming vegetation and C output of decomposer organisms. Carbon dioxide ($CO_{2)}$ is bound to vegetation via photosynthesis and is released by microbial decomposition of the produced organic matter. Decomposition is largely dependent on litter quality, e.g., *Sphagnum* litter types decompose significantly slower than *Carex* litter (Scheffer et al. 2001) and that of deciduous shrubs, trees and graminoids (Aerts et al. 1999). Decomposition efficiency may be related to the chemical composition of litters, since *Sphagnum* litters have low P and N concentration (Aerts et al. 1999) and high concentrations of decay-resistant phenolic compounds (Johnson and Damman 1991). Indeed, it has been shown that polyphenol/element (N/P/K) and C/element ratios mainly affect the decomposition of *Sphagnum* litter, and the C/P ratio controlled the decomposition of graminoids along a minerotrophic-ombrotrophic gradient in a bog (Bragazza et al. 2007).

Peatlands and other wetlands are also the main natural source of the second most important greenhouse gas, methane (CH_4) (Moore and Knowles 1989). CH_4 is produced in the anoxic peat horizon and is partially oxidized by microbes before it escapes into the atmosphere. Both methane production and oxidation are processes mediated by microbes. Thus, peatlands sequester CO_2 (the main green house gas) from the atmosphere as peat while they emit large

quantities of both CO_2 and CH_4. So, the C cycle of peatland is dependent on (i) CO_2 fixation and release, (ii) CH_4 production and consumption, and (iii) the in- and outflow of dissolved organic carbon (DOC) (Urban et al. 1989, Sallantaus 1992). The release of DOC can be associated with desorption of organic C from the soil, from the decomposition of peat and plant tissues by soil organisms, or through the exudation of organic C from plant roots (Fenner et al. 2005, Trinder et al. 2008). DOC output is usually higher than input, which results in a net loss from the peatland by the throughflow of water; net losses of 5–9 g C m^{-2} a^{-1} have been measured at a peatland in central Finland (Sallantaus 1992, Sallantaus and Kaipainen 1996). Globally, peatlands contribute 30–40 Tg of the total 500–550 Tg annual emission of CH_4 (Cicerone and Ormland 1988, Khalil and Rasmussen 1983, Lassey et al. 2000), and the ca. 9 million hectares of Finnish peatlands emit ca. 0.5 Tg CH_4 annually (Minkkinen et al. 2002). Temperature, soil structure and plant cover are suggested to associate with depth profiles of O_2, CO_2 and CH_4, and therefore also with gas emission rates (Shephard et al. 2007).

1.2 Peatland aerobic microbial communities involved in CO_2 release

1.2.1 Bacteria

Fragmentation of plant material is initiated by the soil macrofauna (e.g., spiders and millipedes). These are followed by the meso- (e.g., mites, collembolans and enchytraied potworms) and microfauna (e.g., nematodes, tardigrades, rotifers and amoebae) that mainly feed on bacteria and fungi. In an anoxic environment, where oxygen availability is limiting decomposition, the fermenting or strictly anaerobic bacteria and archaea are responsible for most microbial activity. Yet, aerobic bacteria (probably also archaea) and fungi are the most important and effective decomposers of organic matter in the upper, oxic layers of peat, since they are responsible for the final mineral release even from the most recalcitrant chemical components. During the decomposition of organic matter, microbes release CO_2 as a product of heterotrophic respiration.

Knowledge of bacterial communities in peatlands has been largely based on cultivation studies in the 1970's. These early peatland studies reported on the isolation of aerobic bacterial genera such as *Achromobacter* (Betaproteobacteria), *Arthrobacter* (Actinobacteria), *Bacillus* (Firmicutes), *Cytophaga* (Sphingobacteria), *Chromobacterium* (Betaproteobacteria), *Micrococcus* (Actinobacteria), *Pseudomonas* (Gammaproteobacteria), *Actinomyces* (Actinobacteria), and *Streptomyces* (Actinobacteria) (Given and Dickinson 1975). Later, Williams and Crawford (1983) complemented the list of peatland genera with *Clostridium* (Firmicutes), *Mycobacterium* (Actinobacteria), *Micromonospora* (Actinobacteria) and *Nocardia* (Actinobacteria). In a Scottish raised bog, aerobic bacteria (*Bacillus*) dominated (50–60%), whereas the other main groups were Gram-negative non-sporing rods (30%) and *Arthrobacter* (5%) (Wheatley et al. 1996). A study based on microbial biomass (excluding fungi) and plate counting from a drained *Sphagnum fallax-Carex rostrata* fen in France revealed that testate amoebae (48% of the microbial biomass), heterotrophic bacteria (15%), cyanobacteria (14%) and diatoms (Bacillariophyceae; 13%) were the dominant groups (Gilbert et al. 1998). Another biomass study of five different *Sphagnum*-dominated peatlands in Switzerland, Finland, Netherlands, Sweden, and England showed that heterotrophic bacteria dominated in all sites, whereas fungi, microalgae or testate amoebae were the second dominant groups, depending on site (Mitchell et al. 2003).

During the past decade, a few attempts have been made to broaden the view of bacterial diversity and distribution in peatlands with the use of molecular identification methods. The

main groups of clones found from a *Sphagnum*-dominated peatland in Siberia were affiliated with the phyla Acidobacteria, Alphaproteobacteria, Verrucomicrobia, Actinobacteria, Deltaproteobacteria, Chloroflexi and Planctomycetes (Dedysh et al. 2006). The majority of bacterial clones from two drained fen sites in Slovenia consisted of Acidobacteria (23%), Alpha- (16%), Beta- (12%), Gamma- (8%) and Deltaproteobacteria (17%), Planctomycetes (7%) and Actinobacteria (6%) (Kraigher et al. 2006). In addition, bacterial clones from *Sphagnum*-dominated peatlands in NE USA (New England) were dominated by Proteobacteria (54%), Firmicutes and Acidobacteria (11%), and the rest of the clones were similar to Verrucomicrobia, Actinobacteria and Planctomycetes (Morales et al. 2006). According to a decomposition study of *Sphagnum*, Alphaproteobacteria play the dominant role in the early stages of decomposition, whereas Actinobacteria or Planctomycetes become more important as the material degrades (Kulichevskaya et al. 2007).

Over thirty years ago, Khan and Williams (1975) suggested that acidophilic actinobacteria are important decomposers in acidic environments. Over half of the cultivated bacterial genera from peatlands were identified as actinobacteria (Given and Dickinson 1975, Williams and Crawford 1983). Furthermore, actinobacteria are believed to contribute significantly to the decomposition of organic matter since they are mainly strict aerobes (Goodfellow and Williams 1983) and contain members that can degrade a variety of polymers (e.g., lignin, celluloses, pectin, chitin and humic materials) released during the process (Berg and McClaugherty 2003, Schrempf 2001, McCarthy 1987). Furthermore, Pankratov et al. (2006) suggested that actinobacteria play the leading role in cellulose processing of *Sphagnum* bogs. Many of the clones obtained from peat samples are similar to known actinobacteria (Rheims et al. 1996, Dedysh et al. 2006) and enrichment cultures have verified three groups similar to either *Acidimicrobium ferrooxidans* or *Rubrobacter radiotolerans* (Rheims et al. 1999). Although actinobacteria represent a considerable portion of the soil microbial community, conclusions regarding their abundance and importance in peatlands vary (see the references above). Most studies concerning microbial (including actinobacteria) communities have been conducted in *Sphagnum*-dominated peatlands, and the generality of their findings or the influence of habitat are uncertain.

1.2.1.1 Methane-oxidizing bacteria (MOB)

Since MOB are the only organisms capable of biological oxidation of CH_4, they are important organisms in C cycle regulation. When CH_4 produced by methanogenic archaea in underlying peat layers reaches the upper aerobic part, MOB oxidize a portion of it to CO_2. Efficiency estimates of the oxidation of autogenic CH_4 in different peatlands vary considerably from 20% in *Carex* dominated fens (Popp et al. 2000) to 78% in *Sphagnum* dominated bogs (Yavit and Lang 1987). Ombrotrophic peatlands consume the majority of upward-diffusing CH_4, whereas flux rates to the atmosphere from minerotrophic peatlands remain high because of the gas transport through the aerenchyma of vascular plants (Hornibrook et al. 2009).

MOB are traditionally divided into two taxonomic groups within the Proteobacteria. Type I MOB include the Gammaproteobacteria *Methylobacter*, *Methylomicrobium*, *Methylomonas*, *Methylocaldum*, *Methylosphaera*, *Methylothermus*, *Methylosarcina* and *Methylococcus* (Hanson and Hanson 1996). Type II MOB include the Alphaproteobacteria *Methylocystis*, *Methylosinus*, *Methylocella* and *Methylocapsa* (Hanson and Hanson 1996). These types differ in their carbon assimilation pathways, phylogenetic affiliation, and intracellular membrane arrangement (Hanson and Hanson 1996). In addition, *Methylocapsa acidophila* was suggested to form a novel type III since it has a divergent intracytoplasmic membrane structure (Dedysh

et al. 2002). Newly characterized MOB have been found in extreme environments, e.g., type I-related *Methylohalobius crimeensis* from hypersaline lakes of Crimea (Heyer et al. 2005) and phylum Verrucomicrobia-related MOB from highly acidic geothermal areas (Dunfield et al. 2007, Pol et al. 2007). The first step in CH_4 oxidation is carried out by the key enzyme MMO that catalyzes the initial oxidation of CH_4 into methanol (CH_3OH). MMO exists in two forms, a particulate membrane-bound (pMMO) and a soluble cytoplasmic form (sMMO). The particulate form is present in all known aerobic methanotrophs (Hanson and Hanson 1996) except *Methylocella* spp. (Dedysh et al. 2000, 2004, Dunfield et al. 2003). *Methylocella* are also known to be facultative since they can utilize single- and multicarbon compounds, e.g., methanol, acetate, pyruvate, succinate, malate, and ethanol (Dedysh et al. 2005). The cytoplasmic soluble form of the enzyme is present only in certain MOB strains (Murrell et al. 2000).

Peatland MOB activity is highest just above the WL, where CH_4 and oxygen levels are adequate for CH_4 oxidation (Sundh et al. 1994). A maximum concentration of methanotroph-specific phospholipid fatty acids (PLFAs) were found at an intermediate depth in the more nutrient rich and drier surface of the ombrotrophic mixed peatland site compared to wetter medium-rich fen site (Sundh et al. 1997). Identification of MOB-specific PLFAs revealed the presence of both types I and II MOB in peatland soil (Krumholz et al. 1995, Sundh et al. 1994, 1995). Type I MOB dominate in nutrient-rich environments (Amaral et al. 1995, Fisk et al. 2003, Wise et al. 1999) whereas type II MOB dominate in nutrient-poor bogs (Edwards et al. 1998). Studies from Russian and German bogs showed that 60–95% of MOB belonged to type II with *Methylocystis* being the dominant genus (Dedysh et al. 2003). A new type II strain (*Methylocystis heyeri*) was isolated from an acidic *Sphagnum* peat bog lake in Germany and an acidic tropical forest soil in Thailand. This strain contained PLFA 16:1ω8c, which was previously considered as a signature PLFA of type I MOB (Dedysh et al. 2007). Representatives from two novel acidophilic genera, *Methylocella palustris* and *Methylocapsa acidiphila*, were also discovered from acidic peat bogs (Dedysh et al. 2000, 2002). Subsequently, two other *Methylocella* strains were identified; *M. silvestris* from acidic forest (Dunfield et al. 2003) and *M. tundrae* from acidic tundra peatlands (Dedysh et al. 2004). It has been suggested that *Methylocella* could be key players in CH_4 oxidation in natural peatlands (Dedysh et al. 2001).

A study conducted from blanket peat samples in England combined PLFA analysis with stable isotope probing (SIP), mRNA and microarray techniques (Chen et al. 2008). They found that only pMMO was active and that *Methylocystis* and *Methylosinus* were the dominant MOB and largely responsible for CH_4 oxidation. They also detected an unique group of peat-associated type I MOB and a novel group of uncultivated type II MOB related to *Methylocapsa*. Another study based on fluorescence *in situ* hybridization (FISH) with the 16S rRNA gene suggested that partly endophytic methanotrophs in the hyaline cells of submerged *Sphagnum* mosses consume CH_4 and are a significant (10–15%) C source for *Sphagnum* in peat bogs by coupling the CO_2 needed for photosynthesis with the CO_2 released from CH_4 oxidation (Raghoebarsing et al. 2005). In a boreal peatland survey, 23 different *Sphagnum* species oxidized CH_4 and those analyzed possessed a *Methylocystis* signature (Larmola et al. 2010). As for other bacterial groups, studies of MOB diversity and activity have been largely conducted in *Sphagnum*-dominated peatlands and knowledge of other habitats remains incomplete.

1.2.2. Fungi

Several studies have shown that fungal biomass and production dominates that of bacteria in peatlands, and which is likely due to their higher tolerance of acidity (Latter et al. 1967, Williams and Crawford 1983). Cellulose-degrading fungi are more abundant in peatlands than their bacterial counterparts (Hiroki and Watanabe 1996) and nowadays fungi are considered to be the main aerobic decomposers in these habitats (e.g., Thormann 2006a, 2006b). In pristine wet peatlands, fungal decomposers are mostly limited to the uppermost surface layers (Latter et al. 1967, Nilsson and Rülcker 1992). Many microfungal species have been isolated from living and decomposing *Sphagnum fuscum*, and their ability to decompose various organic compounds, e.g., tannic acids, cellulose and pectine, is well described (Thormann et al. 2001, 2002). From a taxonomic point of view, anamorphic ascomycetes were the largest group (62%) of microfungi and genera *Penicillium* and *Acremonium* were the dominant groups in peatland isolation studies (Thormann 2006a). Zygomycetes (*Mortierella*) were also frequently isolated (10% of all species). Both chytridiomycetes and basidiomycetes comprised 4% of isolated species. From chytridiomycetes, *Rhizopydium*, *Phlyctochytrium* and *Septosperma* were the dominant genera. Teleomorphic ascomycetes represented 3% of isolated species, and *Chaetomium*, *Gelanisospora*, *Sordaria* and *Thielevia* predominated. 106 of 868 individual records of microfungi could not be assigned to any known taxon. In addition, many yeasts have been isolated from peatlands that are believed to play an important role in the initial stages of organic matter decomposition (Thormann et al. 2007). *Cryptococcus*, *Candida*, *Pichia* and *Rhodotorula* were the most abundant genera, accounting for 58% of known peatland yeasts.

The most effective decomposers belong to macrofungi that produce a variety of enzymes, e.g., laccases, phenol oxidases, peroxidases, to decompose the most recalcitrant and complex organic compounds derived from plant detritus. Typical macrofungal genera identified from boreal peatlands are *Cortinarius*, *Galerina*, *Hypholoma*, *Mycena*, *Collybia* and *Omphalina* (Salonen and Saari 1990). These genera include litter or wood saprotrophs and mycorrhizal fungi, which are also an important component of groundwater-driven ecosystems such as fens and wet meadows (Turner et al. 2000). A great diversity of ECM fungi was found in peatlands (Salo 1993). These include species of *Lactarius*, *Hebeloma*, *Laccaria*, *Russula*, *Tomentella*, and *Cortinarius*, which are most often collected and associated with the tree roots (e.g., *Picea, Larix, Salix* and *Betula*). Ericoid mycorrhizal (ERM) (e.g., *Rhizoscyphus ericae*, *Oidiodendron* spp.) fungi are specific to ericaceous plants (shrubs and dwarf-shrubs; *Andromeda polifolia*, *Calluna vulgaris*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium* spp.) typical of peatland. Mycorrhizal fungi have evolved repeatedly from saprotrophic precursors (Hibbett et al. 2000), and some of them seem to have retained the decomposition enzymes (Bending and Read 1997, Read et al. 2004). Indeed, some species of ECM genera such as *Lactarius* and *Tomentella* have catabolic activities in certain ecological niches (Buée et al. 2007). Thus, some mycorrhizal fungi can potentially switch between symbiont and free-living saprotroph, and may enjoy a competitive advantage (Hibbett et al. 2000). This physiological flexibility might be especially useful in the organic-rich and generally nutrient-poor soils of peatlands (Read and Perez-Moreno 2003, Read et al. 2004).

Fungi can be separated into five behavioral groups according to their substrate utilization patterns during the decomposition of organic matter (Deacon 1997). Group 1 consists of many common anamorphic molds (e.g., *Cladosporium*, *Alternaria*) that use simple sugars and other storage compounds of plants. Group 2 contains pioneer saprobes, mostly zygomycetes (e.g., *Mucor*, *Mortierella*). Group 3 are simple-polymer degrading fungi (e.g., *Fusarium*, *Trichoderma*, *Chaetomium*), group 4 includes many basidiomycetes that degrade recalcitrant

polymers and group 5 is formed of opportunistic saprobes (e.g., *Mortierella*, *Pythium*) that are common throughout the decomposition process. The latter stages of decomposition favour basidiomycetes, because they are the major decomposers of complex polymers and become dominant in the litter as the process continues (Deacon 1997). Saprotrophic fungi differ in their ability to utilize compounds as C sources (Thormann et al. 2001, 2002), and thus associate with different litter types according to their chemical composition (Thormann et al. 2004a). Indeed, differences in microfungal species distributions and succession patterns among peatland litter types have been detected; species of *Aspergillus*, *Mortierella* and *Oidiodendron* were common in *Sphagnum* litter in the bog and species of *Phialophora*, *Phialocephala*, *Fusarium*, *Dimorphospora foliicola*, *Monocillium constrictum* and several basidiomycetes were typical of *Carex* and *Salix* litters in the fen (Thormann et al. 2003, 2004b).

Although Thormann and colleagues have carried out several important studies of peatland fungal ecology, their reliance on traditional laboratory cultivation and microscopic applications risks overemphasizing the importance of more easily cultured organisms, e.g., yeasts and molds. Notably, many fungi spend most of their life cycle without forming large or hardly visible sporocarps and thus may escape detection methods based on microscopic examination of fruiting bodies. Artz et al. (2007) found that different fungal groups dominated when species lists obtained from isolate cultures and sequenced clones from the same cutover peatlands were compared. Furthermore, the hyphae-forming mantles of several species are difficult to differentiate, which complicates their identification. These technical obstacles promote the use of less equivocal and more direct molecular methods in understanding microbial diversity and functional ecology in different peatland types.

1.3 Effects of climate warming and land-use change on peatlands

1.3.1 Impact on the C cycle

The reservoir of C in peatlands is labile, since it is prone to climate variation. Two important green house gases, CO_2 and CH_4, are responsible for most of the C loss from peatlands. It has been estimated that CH_4 absorbs infrared radiation about 30 times more effectively than CO_2 and contributes up to 20% of global warming (Bouwman 1990). Global green house gas emissions due to human activities have increased since pre-industrial times, with an increase of 70% between 1970 and 2004 (IPCC 2007). The annual CO_2 concentration growth-rate was larger during the last 10 years (1995–2005 average: 1.9 ppm per year) than it has been since the beginning of continuous direct atmospheric measurements (1960–2005 average: 1.4 ppm per year) (IPCC 2007). The global atmospheric concentration of CH_4 has increased from a pre-industrial value of about 715 ppb to 1732 ppb in the early 1990s, and was 1774 ppb in 2005. It has been estimated that climatic warming together with decreased annual rainfall, as predicted by scenarios of future climate change, will lower the WLs in boreal peatlands (Gorham 1991) and if the annual mean temperature increases by 3 °C, the WL of boreal fens will drop by 14–22 cm (Roulet et al. 1992). Another estimate suggests that a temperature increase of 2 °C would increase CO_2 emission by 30% and a drop in the WL of 15–20 cm would increase it by 50–100% (Silvola et al. 1996). Because WL determines the borderline between aerobic and anaerobic conditions, lowering the WL increases aerobic decomposition and CO_2 flux from peat to atmosphere (Blodau et al. 2004). Furthermore, fluctuation of the WL influences CH_4 emission from peatlands (Kettunen et al. 1999) so greater variation in climate extremes will affect the peatland C cycle. It has also been suggested that a higher temperature will increase the release of DOC from peatlands (Freeman et al. 2001a) and an

experimentally lowered WL caused an immediate export of DOC followed by higher DOC concentrations in the pore-water of the drained peatland (Strack et al. 2008).

Direct human activity in peatlands, e.g., drainage for forestry, affects the natural C store. In Finland, about 4.5 million hectares of peatland area has already been drained and 54% of that area has been converted to forests (Hökkä et al. 2002). CO_2 emissions usually increase in drained or hydrologically-altered peatlands (Silvola 1986, Moore and Dalva 1993, Silvola et al. 1996) and Nykänen et al. (1998) found that drainage converted an oligotrophic fen site from a CH_4 source into a small CH_4 sink. In addition, as the thickness of the aerobic surface layer increases, anaerobic generation of CH_4 decreases, which diminishes the total CH_4 emission by 30–100% depending on the WL and peatland type (Nykänen et al. 1998). Decomposition studies have produced partly contradictory results; in field experiments, drainage either did not affect (Domisch et al. 2000) or induced both increased (Lieffers 1988, Minkkinen et al. 1999) and decreased decomposition rates (Laiho et al. 2004). Hydrology undisputedly affects C balance in peatlands, but its impacts can be direct or indirect and influenced by the current climate, vegetation, litter quality, soil temperature, pH, and microbial activity. As such, it remains unclear whether peatlands inevitably transfrom from C sink to C source following WLD.

1.3.3 Impacts on aerobic microbial communities

There is some evidence that the composition and functioning of peatland microbial communities vary with environmental conditions. For example, active fungal mycelium was affected by seasonal variations in temperature and distance to WL in an oligotrophic *Sphagnum*-dominated mire (Nilsson and Rülcker 1992), and both depth-related factors (e.g., oxygen content) and land-use induced changes (e.g., plant cover and moisture) affected microbial activity and biomass in raised bogs (Brake et al. 1999). As WL changes influence plant community structure (Weltzin et al. 2000, 2003, Laiho et al. 2003), the succession may also induce changes in the microbial community. Indeed, microbial responses to the prevailing peatland flora have been observed with substrate-induced respiration (SIR), substrate utilization patterns (BIOLOG) and with PLFA analysis (Borgå et al. 1994, Fisk et al. 2003). Interestingly, a significant response of the fungal community was linked to a vegetation succession induced by regeneration of cutover peatlands (Artz et al. 2007). Peatland vegetation, possibly via the quality of litter produced, is believed to be the key determinant of changes in the microbial community structure following WLD. However, a comprehensive investigation of litter types in peatland habitats with different vegetation (nutrient level) and hydrology (WL) has yet to be completed and many peatland ecologists are forced to speculate.

Although microbial responses to nutrient levels and litter types are poorly studied, the effects of WL or hydrology have been investigated. In the early studies based on counts and biomass estimates, a lowered WL resulted in lower abundances of bacteria and yeasts (Huikari 1953) and increased abundances of aerobic moulds (Huikari 1953), cellulose-decomposing microbes (Paarlahti and Vartiovaara 1958), and aerobic bacteria (Karsisto 1979) in surface peat. A significant decline in the abundance of genes of eubacteria (16S rRNA), denitrifiers (*nirS*) and methanogens (*mcrA*) was detected in a short-term drought experiment in a British fen and bog (Kim et al. 2008). When phenol oxidase activity was used as a measure of microbial activity, it was found to increase and caused a greater diversity and abundance of phenolic-catabolizing bacteria after simulated drought in a Welsh peatland (Fenner et al. 2005). Polyphenolics inhibit decomposition by binding to the reactive site of extracellular enzymes and through the formation of phenolic complexes (Horner et al. 1988) in low temperatures

(Freeman et al. 2001b), oxygen (Pind et al. 1994, Freeman et al. 2001a) and pH (Ruggiero and Radogna 1984, Pind et al. 1994). Thus, activity of phenol oxidases is believed to be a key regulator of peatland C cycling and storage (Freeman et al. 2001b, 2004) and known microbial producers include fungi (Bending and Read 1997) and bacteria (Hullo et al. 2001, Endo et al. 2003, Fenner et al. 2005). However, litter and organic soil phenol oxidase activity was found to be positively correlated with moisture content, which suggests that enzyme activity may require an optimal moisture level and be limited by drought in shallow organic soils (Toberman et al. 2008).

Microfungal communities in a Swedish mire decreased strongly as site wetness increased (Nilsson et al. 1992). Also, Mitchell et al. (2003) found out that fungal biomass correlated positively with the increasing WL, pH and total phosphorus. Yet, it has also been shown that abundance and growth of some mycorrhizae might be limited in dry or flooded soil (Lodge 1989). Mycorrhizal fungi are able to colonize woody plants in peatland habitats even when fully submerged (Glenn et al. 1991, Baar et al. 2002). In a study of the fungal communities from a Scottish heath-moorland gradient, moisture was suspected to be the strongest determinant behind the detected community change (Anderson et al. 2003b).

Unfortunately, relatively little is known about the effects of WL lowering or drainage on the activity and community structure of MOB in peatlands. WL has been cited as the key environmental factor regulating methanotrophy in *Sphagnum* (Larmola et al. 2010). Hypothetically, if lower WL increases aeration of the peatland and decreases the amount of CH_4 released, this could induce a change from a MOB community characteristic of peatlands toward a community typical of upland soils capable of oxidizing atmospheric CH_4 (Knief et al. 2003). In the bog, a more moderate response of the MOB community to WLD would be expected; WL causes more dramatic changes to vegetation and soil pH in nutrient-rich fens compared to nutrient-poor bogs (Minkkinen et al. 1999, Laiho et al. 2003). Yet, contradictory findings about the correlation of MOB activity and pH exist; both higher (Dunfield et al. 1993) and non-significant (Moore and Dalva 1997) changes in CH_4 oxidation rate at a higher soil pH have been reported. In summary, even though there is evidence that hydrology clearly affects microbial communities and their activity rates in peatlands, specific environmental factors linked to changes in WL and their relative impact on the microbial community are poorly understood.

2 AIMS OF THE STUDY

Traditional isolation-culture methods risk over-emphasizing more easily cultured taxa and may fail to detect potentially important organisms altogether. Limitations of the traditional approach can be navigated with chemical markers (e.g., PLFAs), which can be identified to group-level and taxon-specific genetic markers (e.g., rRNA gene), which can be subjected to selective amplification (e.g., PCR), community fingerprinting (e.g., DGGE) and finally sequenced and compared to reference databases for identification. The aims of this thesis were to use such methods to survey the activity, diversity and structure of aerobic microbial communities in a diverse set of boreal peatland sites with different hydrology and nutrient levels. The following questions were examined in the articles comprising this thesis:

I How does the total microbial community of different boreal peatland sites, as represented by the PLFA composition, respond to site nutrient level and short- and long-term WLD?

II How does the fungal and actinobacterial community of different boreal peatland sites respond to site nutrient level and a short- and long-term WLD?

III How does methane-oxidizing bacteria (MOB) diversity and activity of different boreal peatland sites respond to site nutrient level and a long-term WLD?

IV How do fungal and actinobacterial communities specifically, and microbial activity generally respond to gradual WLD in a northern boreal fen?

V How does the active community of litter-decomposing fungi and actinobacteria respond to litter quality, site type, WLD and decompostion stage in boreal peatlands?

3 MATERIALS AND METHODS

3.1 Study sites and sampling

3.1.1 Lakkasuo

Lakkasuo (61°47'N, 24°18'E, ca. 150 m a.s.l.) is a boreal raised bog complex in Central Finland containing a variety of site types (Laine et al. 2004, Figure 1). Annual rainfall in this area is 710 mm, of which about a third falls as snow. Average temperatures for January and July are -8.9 and 15.3 °C, respectively. Approximately half of the peatland was ditch-drained to encourage tree growth in 1961. This drained portion was used to estimate the long-term effects of WLD. An experimental WLD treatment simulating the predicted effect of climate change was carried out in 2001 in the undrained part of the peatland (Laine et al. 2004). This design was used to estimate the short-term effects of a persistent WLD. Three sites differing in their nutrient levels were included in the studies: two in the minerotrophic, mesotrophic and oligotrophic fens and one in the ombrotrophic bog. Study sites included a pristine control plot, a plot with short-term WLD, and a plot with long-term WLD, all of which had uniform vegetation and soil properties before disturbance (Laine et al. 2004). Together, these plots formed a gradient towards a peatland forest ecosystem (Laiho et al. 2003) in which WL-induced changes to the microbial community could be extensively studied in each plot. The pristine and short-term WLD plots at the ombrotrophic site included microtopographic variation typical of the site type: hummock, lawn-level and hollow microforms. The detailed information on vegetation patterns, site nutrient levels (fertility) and WL between peatland sites are found in papers I and III. Average WL, pH and element concentrations of each sampling plot and layers are presented in Table 1.

Samples were taken with a box corer in triplicate per plot during May 2004 (I, II) and August 2003 (III). The litter-bag experiment was started in the summer of 2006 (V). The first and the second set of litter-bags were collected during October of 2006 and 2007 (V). Sample sites and plots are shown in Figure 1.

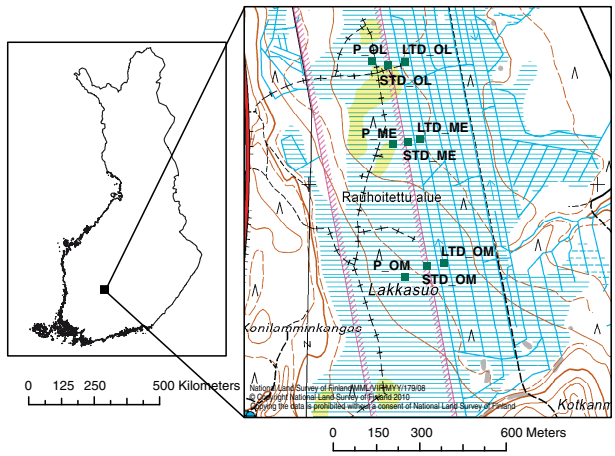

Figure 1. Map of Finland showing the location of Lakkasuo study site and sampling plots. Following abbreviations for sampling plots are used in figure: ME, mesotrophic, OL, oligotrophic; OM, ombrotrophic; P, pristine; STD, short-term water-level drawdown; LTD, long-term water-level drawdown.

Table 1. Average WL, pH and element concentrations (mg kg^{-1}) for study plots at Lakkasuo (I–III, V).

Plot	Layer[a]	WL[b]	pH	N (%)	P	K	Ca	Cu	Fe	Mg	Mn	Zn	C (%)
P ME	L1	0	5.9 (0.2)	2.11 (0.21)	851 (74)	1021 (190)	5910 (804)	5.93 (0.61)	13273 (4520)	774 (54)	45.7 (4.8)	37.60 (2.17)	44.70 (0.95)
P ME	L2		5.7 (0.2)	2.38 (0.02)	814 (17)	786 (64)	6410 (703)	6.08 (0.57)	4900 (1383)	739 (44)	20.4 (3.0)	29.43 (0.45)	46.77 (0.37)
P ME	L4		5.3 (0.0)	2.61 (0.15)	558 (43)	96 (2)	6277 (433)	2.27 (0.35)	3223 (581)	614 (45)	13.1 (0.4)	4.86 (0.75)	51.30 (0.96)
STD ME	L1	-15	5.4 (0.2)	2.08 (0.15)	933 (39)	1015 (90)	8317 (1230)	6.53 (0.09)	12167 (433)	1163 (156)	74.2 (19.5)	49.67 (6.41)	44.80 (0.10)
STD ME	L2		5.5 (0.1)	2.93 (0.10)	1110 (68)	620 (71)	5797 (282)	6.75 (0.85)	7713 (2650)	793 (50)	20.2 (5.1)	26.03 (1.15)	46.23 (0.92)
STD ME	L4		5.0 (0.1)	2.40 (0.03)	553 (23)	89 (14)	6370 (297)	2.19 (0.06)	5150 (535)	617 (14)	20.0 (2.1)	5.10 (0.81)	52.80 (0.29)
LTD ME	L1	-15	3.8 (0.1)	1.52 (0.11)	704 (68)	851 (208)	3177 (352)	5.39 (0.96)	2647 (983)	516 (26)	37.7 (12.9)	38.80 (18.70)	48.80 (0.90)
LTD ME	L2		3.8 (0.1)	2.04 (0.34)	766 (116)	322 (17)	3247 (1012)	4.45 (0.26)	6293 (133)	218 (19)	6.9 (1.1)	20.11 (11.93)	45.27 (1.78)
LTD ME	L4		4.5 (0.0)	2.52 (0.21)	540 (40)	40 (3)	5127 (767)	2.53 (0.50)	6743 (570)	181 (34)	5.2 (0.8)	3.56 (0.25)	52.10 (0.20)
P OL	L1	-11	4.6 (0.1)	1.23 (0.03)	338 (24)	958 (139)	5407 (122)	8.54 (2.03)	13743 (3276)	934 (40)	253.7 (18.9)	30.50 (1.82)	46.17 (0.13)
P OL	L2		4.6 (0.1)	1.56 (0.12)	474 (36)	314 (37)	4423 (405)	16.37 (3.30)	24167 (3762)	697 (65)	205.3 (12.9)	26.10 (1.47)	45.17 (0.62)
P OL	L4		4.8 (0.0)	2.54 (0.19)	806 (76)	57 (14)	3813 (128)	3.84 (0.13)	4157 (474)	450 (9)	91.0 (9.1)	14.30 (2.31)	53.60 (0.35)
STD OL	L1	-30	4.9 (0.3)	1.36 (0.12)	401 (32)	1156 (214)	6830 (1203)	6.23 (0.83)	12120 (1516)	1239 (273)	350.3 (116.4)	38.10 (1.49)	47.40 (0.61)
STD OL	L2		4.9 (0.3)	1.93 (0.11)	781 (46)	401 (47)	5237 (997)	10.52 (1.00)	13520 (2705)	826 (177)	178.3 (107.0)	22.10 (2.35)	43.37 (1.76)
STD OL	L4		4.9 (0.1)	2.54 (0.05)	806 (14)	50 (10)	3830 (101)	3.78 (0.31)	3593 (81)	456 (28)	93.1 (23.0)	12.22 (1.71)	55.27 (0.18)
LTD OL	L1	-30	3.9 (0.1)	2.21 (0.20)	1330 (119)	734 (196)	3720 (465)	8.04 (0.85)	7577 (1107)	279 (35)	44.5 (13.2)	22.20 (7.16)	48.80 (0.55)
LTD OL	L2		4.2 (0.1)	2.97 (0.04)	1243 (38)	189 (42)	2473 (238)	6.17 (0.80)	5803 (517)	125 (27)	8.2 (0.6)	10.67 (4.20)	51.13 (2.02)
LTD OL	L4		4.6 (0.1)	2.42 (0.05)	762 (19)	30 (0)	3183 (74)	3.82 (0.11)	4240 (17)	136 (29)	19.6 (5.9)	4.82 (0.77)	55.57 (0.19)
P OM Hu	L1	-22	4.0 (0.1)	0.92 (0.07)	236 (27)	2017 (286)	1500 (32)	3.43 (0.19)	281 (13)	458 (10)	272.0 (43.1)	33.80 (0.57)	49.33 (0.37)
P OM Hu	L2		3.8 (0.0)	0.84 (0.08)	213 (18)	830 (215)	1327 (41)	3.25 (0.32)	425 (12)	465 (17)	143.7 (20.5)	46.60 (0.71)	49.43 (0.09)
P OM Hu	L4		3.6 (0.0)	1.10 (0.05)	276 (23)	161 (11)	1263 (43)	4.81 (0.23)	585 (11)	509 (9)	46.8 (2.3)	54.23 (1.59)	49.50 (0.17)
P OM La	L1	-6	4.4 (0.1)	0.87 (0.03)	170 (27)	1917 (406)	1180 (59)	2.80 (0.34)	390 (50)	491 (14)	109.8 (19.5)	53.33 (5.47)	48.97 (0.37)
P OM La	L2		3.9 (0.1)	0.93 (0.11)	200 (19)	609 (88)	1203 (58)	1.97 (0.12)	410 (18)	456 (18)	83.2 (9.3)	56.87 (5.39)	49.10 (0.32)
P OM La	L4		3.7 (0.1)	1.08 (0.07)	223 (13)	94 (10)	981 (80)	3.37 (0.42)	490 (31)	347 (27)	24.9 (2.9)	29.17 (2.51)	49.53 (0.33)
P OM Ho	L1	-3	4.0 (0.1)	0.83 (0.03)	189 (16)	659 (318)	798 (18)	1.69 (0.35)	358 (35)	366 (28)	37.1 (4.6)	30.80 (4.28)	48.70 (0.15)
P OM Ho	L2		4.0 (0.0)	1.05 (0.06)	190 (28)	205 (68)	731 (8)	2.36 (0.22)	353 (57)	334 (13)	28.1 (1.8)	25.00 (2.03)	48.33 (0.09)
P OM Ho	L4		3.9 (0.1)	1.27 (0.04)	183 (12)	81 (14)	622 (55)	2.40 (0.31)	349 (46)	248 (9)	17.4 (0.3)	17.63 (1.62)	49.10 (0.51)
STD OM Hu	L1	-24	4.0 (0.1)	0.92 (0.01)	278 (41)	1305 (192)	1593 (149)	4.05 (0.31)	297 (18)	522 (4)	314.3 (60.3)	41.83 (2.50)	48.33 (0.23)
STD OM Hu	L2		3.6 (0.0)	0.96 (0.01)	248 (27)	795 (59)	1247 (15)	3.03 (0.44)	462 (27)	540 (29)	144.7 (20.7)	66.33 (8.10)	48.47 (0.30)
STD OM Hu	L4		3.6 (0.0)	1.18 (0.03)	280 (28)	222 (27)	1323 (98)	3.21 (0.48)	586 (31)	583 (25)	48.6 (6.8)	55.80 (7.35)	48.17 (0.32)
STD OM La	L1	-15	3.8 (0.1)	1.09 (0.13)	286 (35)	1152 (254)	1180 (49)	2.69 (0.43)	445 (77)	523 (27)	146.0 (36.1)	99.47 (54.47)	47.67 (0.30)
STD OM La	L2		3.7 (0.0)	1.11 (0.09)	278 (55)	464 (28)	1233 (110)	2.76 (0.32)	591 (87)	560 (26)	91.4 (20.5)	97.47 (39.30)	47.77 (0.09)
STD OM La	L4		3.8 (0.1)	1.18 (0.02)	240 (19)	101 (25)	998 (119)	2.84 (0.70)	488 (62)	449 (51)	26.9 (9.6)	32.30 (6.86)	47.60 (0.45)
STD OM Ho	L1	-10	4.0 (0.0)	1.09 (0.12)	297 (32)	601 (82)	1023 (9)	2.16 (0.24)	475 (36)	460 (24)	66.4 (4.1)	44.43 (1.65)	46.40 (0.40)
STD OM Ho	L2		4.1 (0.1)	1.20 (0.10)	246 (49)	216 (64)	825 (10)	3.24 (0.28)	346 (8)	382 (21)	40.7 (2.0)	31.80 (2.42)	46.20 (0.46)
STD OM Ho	L4		3.9 (0.1)	1.36 (0.12)	228 (33)	57 (3)	721 (129)	0.99 (0.14)	412 (37)	286 (63)	18.7 (6.4)	15.00 (3.43)	48.70 (0.21)
LTD OM	L1	-15	3.7 (0.2)	1.48 (0.06)	814 (58)	791 (66)	2923 (156)	7.34 (0.08)	898 (22)	470 (78)	155.0 (29.2)	72.03 (7.58)	50.40 (0.53)
LTD OM	L2		3.6 (0.0)	1.02 (0.05)	461 (38)	393 (59)	2197 (202)	3.45 (0.46)	819 (237)	466 (55)	41.8 (18.1)	61.30 (1.30)	47.43 (0.39)
LTD OM	L4		3.6 (0.0)	1.13 (0.05)	260 (12)	52 (4)	1147 (208)	1.17 (0.18)	833 (18)	349 (19)	4.6 (0.8)	20.77 (4.13)	47.60 (0.15)

[a] L1, 0–5 cm; L2, 5–10 cm; L3, 10–20 cm; L4, 20–30 cm. [b] cm from the peat surface. SE in parentheses

3.1.2 Suonukkasuo

Suonukkasuo is a mesotrophic pine fen located in Rovaniemi, northern Finland (66°28'N, 25°51'E) within the aapa mire zone (Figure 2). Mesotrophic pine fens (RhSR in the Finnish peatland site type nomenclature of Laine and Vasander 2005) are typically sites where wet lawns and drier hummocks form a mosaic-like vegetation pattern. A ground-water extraction plant on an esker bordering and downstream of the peatland has affected WL at the study site since 1959, resulting in a clear hydrological gradient where the undisturbed fen (location S4) becomes slightly disturbed (location S3), semi-disturbed (location S2), and finally a pine-dominated mesotrophic peatland forest (location S1) (Figure 2, IV). Intact triplicate soil cores were taken in September 2004 (IV). A tentative fungal in-growth mesh bag experiment was installed to sample the ECM fungal community. Mesh bags were buried at the four hydrologically-different locations (S1–S4) during June 2005 and harvested four months later. The average WL, pH and element concentrations of each sampling location and layer are presented in Table 2.

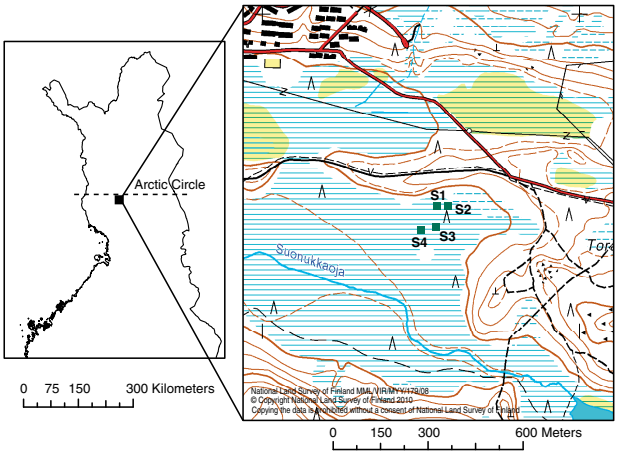

Figure 2. Map showing the location of Suonukkasuo study site and sampling plots. Sampling plots represent four locations: S1, S2, S3 and S4 described in the text.

Table 2. Average WL, pH and peat element concentrations (mg kg^{-1}) for the study locations in Suonukkasuo (IV).

Plot	Layer[a]	WL	pH (S.E.)	N (%)	P	K	Ca	Cu	Fe	Mg	Mn	Zn	C (%)
S1	L1	-24	3.8 (0.1)	2.31	1480	389	2350	15.3	21400	575	571	9.06	48.6
	L2		3.9 (0.1)	2.36	1430	241	2500	21.4	22500	531	212	4.57	51.2
	L3		4.6 (0.0)	2.19	1450	312	2640	25.2	24000	591	254	5.21	51.5
	L4		4.6 (0.1)	2.20	1370	1040	2930	38.9	24500	1620	409	13.90	45.2
S2	L1	-25	4.6 (0.0)	2.29	1380	444	2370	9.9	12900	570	174	8.52	49.9
	L2		4.5 (0.1)	2.86	1640	186	2170	11.5	12400	404	155	6.20	53.3
	L3		4.6 (0.1)	2.79	1540	111	2260	14.6	16500	334	200	5.21	54.8
	L4		4.9 (0.1)	2.66	1340	123	2700	20.1	21800	405	375	4.01	54.0
S3	L1	-19	4.6 (0.1)	2.28	1260	410	2520	5.6	16800	471	289	11.70	51.0
	L2		4.7 (0.1)	2.84	1340	101	2240	5.3	13500	277	283	5.91	54.4
	L3		4.8 (0.0)	2.77	1240	54	2550	6.4	16600	281	413	5.25	55.9
S4	L1	-12	4.1 (0.2)	2.47	1250	412	1990	4.1	13400	343	239	9.59	51.9
	L2		4.3 (0.2)	2.69	1210	99	2250	4.5	15300	204	270	6.98	54.4

a. L1, 0–10 cm; L2, 10–20 cm; L3, 20–30 cm; L4, 30–40 cm. b. unit kg m^{-3}. c. measured from a depth of 30–50 cm

3.2 Analyses

A short description of the methods and analyses is given below and summarized in Table 3. Further information can be found in the attached papers (I–V). PCR primers for each of the studied microbial groups are presented in Table 4.

3.2.1. Chemical analyses

Dry weight was determined after drying at 105 °C overnight (I–IV) and soil pH was determined in distilled water (1:3, vol/vol) using fresh peat soil (I–IV). Concentrations of carbon and nitrogen were determined from air-dried samples with a LECO CHN-1000 analyzer and the concentration of other elements with an inductively coupled plasma atomic emission spectrometer (ICP-AES, ARL 3580) (II, IV).

3.2.2 Microbiological analyses

Microbial biomass and total community structure was investigated by PLFA analysis (I, IV). Identification of microbial groups was based on differences in the relative composition of cell membrane PLFAs. Briefly, the sum of PLFAs i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7t, i17:0, a17:0, 17:0, cy17:0, 18:1ω7 and cy19:0 was considered to be predominantly of bacterial origin and chosen as an index of bacterial abundance (Frostegård and Bååth 1996). PLFAs a15:0, i16:0 and a17:0 have been found to be clearly more common in Gram-positive bacteria (Haack et al. 1994) and thus the sum of these was used as an indicator of their abundance. Correspondingly, PLFAs 16:1ω9, 16:1ω7t, 16:1ω5, cy17:0, 18:1ω7 and a19:1 are suggested to be common in Gram-negative bacteria (Wilkinson 1988) and thus the sum of these was used as an indicator of their abundance. The PLFAs 10Me16, 10Me17, 10Me18 were considered to be of actinobacterial origin (Kroppenstedt, 1985). The quantity of 18:2ω6 was used as an indicator of fungal abundance, because it is suggested to be mainly of fungal origin in soil (Federle 1986) and collerates well with the amount of ergosterol (Frostegård and Bååth 1996).

Fungal, actinobacterial and MOB communities were analyzed by molecular methods (II–V). DGGE is based on the electrophoresis of amplified PCR products in polyacrylamide gels containing a gradient of chemical DNA denaturants. Partial DNA fragments with different base pairs in their sequences have unique melting temperatures and thus migrate differentially. Some limitations of the method are known in that PCR primer bias may produce chimeric sequences when using DNA extracted directly from environmental samples (Jumpponen 2007). In addition, small amounts of microbial DNA may PCR poorly and escape detection in DGGE. Direct sequencing of DGGE bands that are incompletely resolved may also be problematic if they cannot be separated by excision. In spite of these technical obstacles, direct PCR-DGGE-sequencing offers a relatively rapid method of analyzing a large number of samples, such as in this study.

Fungal communities were studied with partial small subunit (SSU) or 18S rRNA gene (II, V) and ITS region (IV). The ITS region is located between 18S rRNA and 25S rRNA genes and consist of two non-coding spaces (ITS1 and ITS2) that are separated by the 5.8S rRNA gene. ITS is a highly variable region that can provide greater taxonomic resolution than 18S rRNA alone and enables more precise identification (Anderson et al. 2003a). Former research teams in our laboratory have found 18S rRNA to be a suitable marker for fungal community studies (Vainio and Hantula 2000, Pennanen et al. 2001), and it was therefore

Table 3. Analyses and methods used in the papers of this thesis.

Target of analyses and used methods	In paper
Chemical characterization	
Element concentrations	
C and N with LECO CHN-1000	II, IV
Dry ashing and HCl with ICP-AES ARL 3580	II, IV
Peat soil pH	
Water suspension (1:3; vol:vol)	I–IV
Dry matter (d.m.)	
+105 °C	I–IV
Microbial activity	
Basal respiration	
potential CO_2 evolution with GC	I, IV
Field respiration	
CO_2 evolution in the field with IRGA	IV
Activity of MOB	
Potential CH_4 oxidation with GC	III
Microbial community structure	
Total microbial community	
PLFA extraction and analysis with GC	I, IV
Fungal, actinobacterial and MOB community	
DNA extractions from mycelia	IV
DNA extraction from soil	II, III, IV
PCR-DGGE and sequencing	II, III, IV
Active fungal and actinobacterial community	
RNA extraction from litters	V
Reverse-transcription of RNA to cDNA	V
PCR-DGGE and sequencing	V
Diversity of fungi and actinobacteria	
Shannon-Weaver diversity index	II, V
Phylogenetic analyses (ARB)	II, III, IV, V
Testing of microbial community response	
Patterns of DGGE band composition	
Multivariate methods:	
DCA, PCA, RDA, CA, CCA (CANOCO 4.5)	I, II, IV, V
NMDS (PC-ORD 4.0)	III
Diversity indices	
Two-way ANOVA (SYSTAT 10)	II
MOB community and environmental variables	
Pearson's correlation (Statistix 8)	III
Respiration and CH_4 oxidation models	
Linear mixed models (MLwiN 2.02)	I, III, IV

Table 4. PCR-primers used in the papers II–V.

Target	Marker	Primer	Sequence 5'→ 3'	Fragment length (bp)	Reference
Fungi	18S rRNA	FF390 FR1[1]	CGA TAA CGA ACG AGA CCT GAI CCA TTC AAT CGG TAI T	390	Vainio & Hantula 2000
	ITS	ITS1F[2] ITS2	CTT GGT CAT TTA GAG GAA GTA A GCT GCG TTC TTC ATC GAT GC	290	Gardes & Bruns 1993 White et al. 1990
Actino-bacteria	16S rRNA	S-C-Act-235-a-s-20[3] S-C-Act-878-a-A-19	CGC GGC CTA TCA GCT TGT TG CCG TAC TCC CCA GGC GGG G	643	Stach et al. 2003
MOB	pmoA	A189f[4] A682r	GGS GAC TGG GAC TTC TGG GAA SGC NGA GAA GAA SGC	500	Holmes et al. 1995
	mmoX	mmoxA[4] mmoxB	ACC AAG GAR CAR TTC AAG TGG CAC TCR TAR CGC TC	1100	Auman et al. 2000

gc-clamps: [1] CCCCCGCCGCGCGCGGCGGGCGGGGCGGGGGCACGGGCC, [2] CGCCCGCCGCGCGCGGCGGGCGGGGCGGGGGCACGGGGGG,
[3] CCCCCCCCCCCCCGCCCACCGCCCCCCGCCCCCGCCGCCC, [4] CCCCCCCCCCCCCGCCCCCCGCCCCCCGCCCCCGCCGCCC

chosen for the first fungal community study in Lakkasuo (II). Preliminary fungal community analyses with both 18S rRNA and ITS markers were conducted at Suonukkasuo as part of an earlier Master's thesis (Vuorenmaa 2005) and ITS was selected for further analyses because it yielded better separation between sampling locations (IV). Reverse transcription products of 18S rRNA gene were of a higher quality than those of ITS and it was also chosen to determine fungal community in litter samples (V).

Actinobacterial communities were studied with partial 16S rRNA gene analysis (II, IV, V). Ribosomal RNA is an excellent molecule to identify microbes since it is found abundantly in all living cells and contains sufficient genetic variation to be a useful genus/species marker (Woese 1987). The sequence of nucleotides in rRNA is highly conserved, and evolutionary relationships among all life forms can be inferred by comparing rRNA sequences (Woese 1998).

For peat soil analyses, we used extracted rRNA gene that can also be obtained from dormant or dead cells (II, IV). Notably DNA-based analyses can potentially detect the entire community irrespective of organismal activity. Metabolically active species synthesize larger amounts of RNA. Thus, the direct recovery of rRNA from environmental samples enables the metabolically active microbes to be detected and measured (Aneja et al. 2004, Girvan et al. 2004, Pennanen et al. 2004). For the litter analyses, extracted RNA was immediately reverse transcribed into cDNA, which can be further PCR amplified and used in additional analyses (V). MOB were characterized with two partial functional genes, *pmoA* (Holmes et al. 1995) and *mmoX* (Auman et al. 2000), which encode the A-subunit of the pMMO and the α-subunit of the hydroxylase component of the sMMO, respectively (III). DGGE bands with separate positions in gels were excised, re-amplified, purified, sequenced and subjected to a BLAST search of databases maintained by the National Center for Biotechnology Information (NCBI) and SeqMatch search of Ribosomal Database Project (RDP) releases 9.44 or 10 (Cole et al. 2005, 2009). Alignments and phylogenetic trees were created with the ARB package (Ludvig et al. 2004) to explore the diversity and taxonomic affiliation of the sequenced microbial DGGE bands.

Basal respiration or potential microbial activity in fresh peat samples was measured under laboratory conditions as the amount of CO_2 evolved in 66 h (I, IV). Field respiration was

conducted at the study site to measure total heterotrophic microbial activity in peat soil, and fluxes were calculated as a linear change of CO_2 concentration in chamber headspace over time (IV). MOB activity was measured in the laboratory as a linear decrease of CH_4 in the bottle headspace over time (III).

3.2.3 Multivariate and statistical analyses

Communities were screened for the presence (1) or absence (0) of observed bands in DGGE. Several multivariate analyses were used to detect changes in microbial communities since they offer tools for explaining and interpreting the complex microbial ecological data, its dissimilarities, similarities, and relationships between environmental variables (Ramette 2007). Multivariate analyses were conducted using the Canoco for Windows 4.5 software (Lepš and Šmilauer 2003). First, heterogeneity in the data was examined using DCA and, depending on the gradient lengths, linear (PCA, RDA) or unimodal (CA, CCA) methods were applied to PLFA composition and DGGE binary data. Significance of the axes was evaluated with Monte Carlo permutation tests (500 or 1000 permutations with reduced model). We used the Jaccard coefficient and NMDS method (Ellison 2000) for MOB-derived DGGE binary data (III). NMDS was simply chosen to illustrate similarity among communities. Pearson's correlation analysis was performed among pH, CH_4 oxidation rate, and amount of *pmoA* DGGE bands (Analytical Software Statistix 8) (III). A mixed (multilevel) regression model (Goldstein 1995) was applied to quantify the effects of environmental variables on basal/field respiration, CH_4 oxidation, and their relationships to different microbial communities (III, IV). We applied the RIGLS method, which is recommended for small samples (Rasbash et al. 2000). Shannon-Weaver diversity indices (Shannon and Weaver 1963) were calculated for fungi and actinobacteria in each peat core (i.e., integrating layers L1–L3 per sampling location) (II) and for replicate litter samples in each plot (V). The diversity indices were subjected to two-way analysis of variance (ANOVA) with General Linear Models in the SYSTAT v. 10 package (II).

4 RESULTS AND DISCUSSION

Environmental influences will be presented first followed by changes in microbial community structure and activity.

4.1 Factors affecting microbial communities

4.1.1 Site type

Microbial communities clearly responded to the nutrient status of peat soils, since the PLFA composition differed among pristine peatland sites with different nutrient levels in Lakkasuo (I). Also fungal communities differed between the fen sites and the bog in Lakkasuo according to fungal 18S rRNA gene sequence data (II). The results are congruent with the vegetation pattern (Laine et al. 1995), which is more similar between the two fens than between either of the fens and the bog, and may reflect variation in substrate quality and heterogeneity.

Results from papers II and IV showed similar trends with the findings from earlier studies where the microfungal community composition was related to peatland type and wetness (Nilsson et al. 1992), and where a moorland-forest moisture gradient determined the fungal sequence composition (Anderson et al. 2003b). Site type also affected the active fungal and actinobacterial community composition in litter (V). Fungal communities of the surveyed sites probably follow ecohydrology and, consequently, the physical and chemical characteristics (e.g., pH, substrate quality, gas exchange) of the peatland types (Laine et al. 2004). Despite differences detected between fens and bogs, actinobacterial community found in the pristine Lakkasuo sites were not influenced by environmental variables (II). The oligotrophic fen and ombrotrophic bog sites possessed different MOB community (III).

Some sequences exhibited a random distribution pattern among sampling plots and/or layers. Thus, differences observed in the fungal response patterns among sites may not imply real differences in all cases, but may be artificial and due to the limited coverage of sample cores. Also, a high spatial variability of microbial distribution patterns must be kept in mind when sampling (Pennanen et al. 1999, Malmivaara-Lämsä et al. 2008). On the other hand, it has been suggested that an observable and predictable distribution pattern of soil organisms exists and might be linked to, e.g., vegetation, fine roots and the aggregation of organic matter or soil carbon (Ettema and Wardle 2002).

4.1.2 Depth

Sampling depth was inevitably one of the main factors shaping the total PLFA distribution both in Lakkasuo and Suonukkasuo (I, IV). This result was expected, since the importance of peat depth has been emphasized before (Artz et al. 2006). O_2 availability likely explains part of the fundamental differences in PLFA composition since an earlier study found it had a strong effect on PLFA patterns in two wetlands differing in carbon quality, storage and water-holding capacity (D'Angelo et al. 2005).

The fungal communities of the surface and deeper layers diverged both in Lakkasuo and Suonukkasuo, and correlated positively with distance from WL (II, IV). Indeed, the surface fungal community differed clearly between locations, whereas that of deeper layers had become more similar in Suonukkasuo (Fig. 3 in IV). The result may be explained by homogeneity in layers containing old peat, e.g., substrate quality and O_2 availability have become more stable than in the surface peat, where fresh litter may feed a more diverse fungal

community. Actinobacteria of all sites in Lakkasuo and different locations in Suonukkasuo separated clearly according to sampling depth (II, IV). Actinobacteria may be dependent on some other depth-related factor than moisture or aeration, e.g., substrate quality generally decreases downwards along with the state of decomposition (Hogg et al. 1992, Hogg 1993). In addition, the *pmoA*-possessing MOB were also affected, since DGGE bands increased with sample depth (III).

4.1.3 Water level drawdown (WLD)

A clear change in the PLFA composition of peat soils following WLD was detected in all three sites with different nutrient levels in Lakkasuo (I) and along the WL gradient between the sampling locations in Suonukkasuo (IV). Changes after short-term WLD were smaller in both sites compared to long-term WLD, and the change was most prominent in the nutrient-rich mesotrophic fen and least prominent in the ombrotrophic bog (I). Thus, WLD induced changes in microbial communities seem to correspond with nutrient level, as well as changes in vegetation (Laine et al. 1995) and litter quality (Laiho et al. 2003). Similarly, the WL gradient was the strongest determinant for the PLFA composition in Suonukkasuo; the greatest separation was seen between the driest and wettest locations (IV).

WLD affected fungal communities at all peatland sites (II) and locations (IV) as well as active fungal and actinobacterial community composition in litters (V). Fungal communities became somewhat similar between sites after long-term WLD (II). Fungal diversity increased after short-term WLD, but not after long-term WLD (Table 2 in II) and patterns of change for most fungal sequences that responded to WLD were often dependent on site (Table 3 in II). One explanation for this could be that short-term WLD has created transient environmental conditions that induce a colonization of common aerobes leading to higher overall diversity. Following long-term WLD, upon establishment of the drier conditions the environment dramatically differs from the pristine one (Laiho 2006) and continued gradual replacement of specialists by generalists leads to lowered diversity. Similar patterns of succession have been noted in plants (Laine et al. 1995, Vasander et al. 1997).

The greatest difference in Suonukkasuo was detected between the driest and the wettest locations, which are also the most floristically different, i.e., drier locations had more shrubs and trees compared to the wettest location (IV). In Suonukkasuo, the actinobacterial community was rather homogeneous among locations although WL was variable (IV). Results indicate that actinobacterial response to hydrological change, whether drastic or gradual, is minor (II, IV), and it seems that most actinobacteria in boreal peatlands may be rather resilient to a fluctuating environment. The MOB community also clearly changed in the oligorophic fen and the ombrotrophic bog sites following WLD (III).

4.1.4. Substrate quality (for litter decomposers)

The litters of the litterbag experiment represented rather fresh organic matter, while peat soil is an older substrate of generally increasing age and decomposition with depth. Litter type had the greatest impact on active fungal and actinobacterial communities after the first and second years of decomposition (V). The result agrees with earlier findings that litter quality is the main regulator of initial decomposition and fungal community structure (Trinder et al. 2008). Different fungal sequences were typical of certain litter types in different years, indicating that the decomposition stage affects communities as well (Table 5). Indeed, decomposition

stage is known to affect fungal colonization in needles (Osono et al. 2006). The effect of decomposition stage on actinobacterial communities was minor (Table 5).

Litter chemical composition explained most (30–40%) of the variation among microbial communities (Table 2 in V). This variation is difficult to interpret because of its multidimensional nature due to numerous chemical variables. In general, after the first year of decomposition, the concentrations of some nutrient elements, e.g., lignin, lignin-like compounds and hemicelluloses, had the greatest influence on fungal community structure (Table 3 in V). In the second year of decomposition, the influence of carbon related compounds increased while that of some initial nutrient element concentrations decreased. Manganese, which is an important component of certain ligninolytic fungal enzymes (Morgenstern et al. 2008), was influential in the first and second years of decomposition. Variables that seemed to have some relevance for the actinobacterial community composition in both years were total carbon and Klason lignin (Table 3 in V).

Fungal diversities between litter types varied considerably and were highest in graminoid leaf litters (Table 4 in V). The lowest fungal diversities were detected on branches and in foliar litter after the first and second year of decomposition, respectively. The result from the first year of decomposition likely involves the lower litter quality which fewer fungi can utilize. In the second year, foliar litters were already so well decomposed which might have affected the rRNA yield and further to fungal diversity in them.

Foliar litter and needles had the greatest actinobacterial diversity after the first and second year of decomposition, respectively (Table 4 in V). The lowest actinobacterial diversity in both sampling sets was detected on branches, which may reflect the lack of organisms capable of using wooden substrates.

4.1.5 The explanatory power of different factors

The response of microbial communities to environmental factors was explored across a variable set of boreal peatland sites from both fresh and older substrate. Firstly, litter quality had the greatest impact on the structure of active microbial decomposer communities, especially fungi (V). Secondly, the site of decomposition as well as their hydrological status influenced the active microbial community composition but to a lesser extent. Thirdly, microbial function (defined as litter-mass loss after the two-year-decomposition period) could not be explained in terms of fungal community composition and only to a minor extent by actinobacterial community composition after the second year of decomposition (V).

Sampling depth and site had the greatest, and WLD the second greatest impact on total microbial communities in Lakkasuo (I). Notably, interactive effects of sampling depth and WLD had greater explanatory power than these two variables separately. Site and WLD had the greatest, and depth the second greatest effect on the fungal community (II). The combined effects of the sampling depth and WLD explained more of the variation than these factors alone in the oligotrophic fen and in the ombrotrophic bog (II). Sampling depth had the greatest, and site the second greatest effect on the actinobacterial community, and WLD was also influential in the mesotrophic fen (II). Both WLD and sampling depth had strong effects on the total microbial and fungal community, whereas only sampling depth significantly affected the actinobacterial community in Suonukkasuo (IV). Although MOB community was also affected by site type, depth and WLD, community analyses were explored with NMDS and thus these factors cannot be ranked in a similar manner (III).

Table 5. Taxonomic affiliation of the sequences, and their putative ecological role in different litter types during the two-year decomposition period.

Fungi	Litter type	Taxonomic affiliation	Putative ecological role (e.g. reference)
1st year	pine needles	*Cortinarius*	ECM, saprotroph of well decomposed organic matter (Lindahl et al. 2007)
	E. vaginatum leaves	*Marasmius, Rhodocollybia*	saprotroph of fresh litter and lignin (Lindahl et al. 2007, Valášková et al. 2007)
	C. lasiocarpa leaves	*Mycena, Hygrocybe*	saprotroph of fresh litter (Griffith & Roderick 2008, Lynch & Thorn 2006)
	pine branches	*Arthonia dispersa, Leotia*	pathogen, wood-decayer (Wang et al. 2006)
	forest moss	*Meliniomyces, Phialocephala*	ERM, saprotrophs of many polymers (Currah & Tsuneda 1993, Piercey et al. 2002)
	S. fallax	*Boletaceae*	unknown
2nd year	pine needles	*Basidiomycete*	putative lignin-degrader (Blackwood et al. 2007)
	pine branches	*Hyphodiscus, Oidiodendron*	saprotrophs of various woody substrates (Bending & Read, 1997, Hosoya 2002)
	S.fallax	*Boletaceae*	unknown
Actinobacteria			
1st year	pine needles	*Frankia*	free-living saprotrophs, nitrogen-fixers (Arveby & Huss-Daniel 1988, Smolander et al. 1988, Nickel 2000)
	B. nana leaves	*Frankia*	free-living saprotrophs, nitrogen-fixers
	pine branches	ambiguous	unknown
	E. vaginatum leaves	ambiguous	unknown
	forest moss	ambiguous	unknown
	E. vaginatum basal sheats	*Frankia*	free-living saprotrophs, nitrogen-fixers
	C. lasiocarpa leaves	*Frankia*	free-living saprotrophs, nitrogen-fixers
	Sphagnum mosses	*Frankia*	free-living saprotrophs, nitrogen-fixers
	S.fallax	ambiguous	unknown
2nd year	pine needles	*Frankia*	free-living saprotrophs, nitrogen-fixers
	B. nana leaves	*Frankia*	free-living saprotrophs, nitrogen-fixers
	S.fallax	ambiguous	unknown

4.2 Microbial community composition

4.2.1 Total community

The relative proportion of bacterial PLFAs as well as the proportion of Gram-positive and Gram-negative PLFAs was higher in the minerotrophic fens than in the bog (I), and this result is in line with previous studies of sedge-dominated fens (Holding et al. 1965, Borgå et al. 1994). The dominance of mono-unsaturated PLFAs in surface layers of fen sites and the increasing amount of saturated PLFAs with depth probably reflects the presence of aerobic bacteria at the surface and anaerobic forms in deeper layers, as suggested by Sundh et al. (1997). The same trend was observed at Suonukkasuo, where the upper layers had a distinctive PLFA composition compared to deeper ones (IV).

Fungal PLFAs dominated in the drier hummock and lawn surfaces of the ombrotrophic bog, which may indicate an abundance of mycorrhizal fungi on these surfaces (I). The proportion of actinobacterial PLFAs was highest in the nutrient-rich mesotrophic fen at Lakkasuo (I) and, correspondingly, actinobacteria dominated in the surface layers of the wettest locations at Suonukkasuo (IV). The result indicates that actinobacteria play a more important role in nutrient-rich peatlands. As certain actinobacteria are suggested to decompose acidic litter above and organic matter below ground (Khan and Williams, 1975), and to act as antagonists of fungi (Dinishi Jayasinghe and Parkinson 2008), it is likely that fungi are their major competitors in acidic environments. Thus, actinobacteria might have a competitive advantage over fungi in nutrient-rich fens of a higher pH.

A lower WL increased fungal PLFAs over bacterial PLFAs only at the wettest sites, the mesotrophic fen and hollow surfaces of the bog in Lakkasuo (I). The increasing abundance of fungi after WLD may partly reflect the increase of mycorrhizal vegetation (e.g., shrubs and trees). A similar trend was detected at Suonukkasuo, where an increase of the fungal and bacterial biomass ratio in the drier locations was positively correlated with a lower WL (IV). Fungi may enjoy a competitive advantage over bacteria in drier conditions where the substrate is more recalcitrant. The typical pattern for the wetter conditions seemed to mirror a decrease of actinobacterial PLFAs after WLD at both Lakkasuo and Suonukkasuo (I, IV). On the other hand, sample depth or some other depth-related factor was more important than WLD for actinobacteria at the drier peatland sites.

Some reservations must be made when PLFAs are handled as group-specific indicators for bacteria (I and IV). Signature fatty acids are based on cultivated species, although the majority of bacteria remain to be cultivated. As new bacteria are isolated and characterized, the knowledge of different PLFAs in groups may change. For example, although iso- (i) and anteiso (a) branched fatty acids are generally considered as indicators for Gram-positive bacteria, several Gram-negative bacteria also contain significant amounts of them (e.g., Männistö and Häggblom 2006, Männistö et al. 2007).

4.2.2 Fungal community

Fungal 18S rRNA gene and ITS sequences from peat soil and cDNA-derived 18S rRNA gene sequences from litters clustered with fungi capable of utilizing a broad range of substrates (II, IV, V). Unfortunately, the fungal 18S rRNA gene marker is not sufficiently variable to provide universally decisive identification at the generic level. Furthermore, the 18S rRNA primers also amplified non-target organisms (e.g., algae and protozoa) and a sequence of common mire plant, *Menyanthes trifoliata* L., with one base pair mismatch. However, the sequence

data provided many useful insights and the majority of fungal sequences from Lakkasuo were split equally between Ascomycota and Basidiomycota (II, V). Most of the fungal ITS sequences from peat soil of Suonukkasuo were similar to Basidiomycota (IV). Interestingly, most of the sequences from Lakkasuo and Suonukkasuo were identified as different fungal taxa. This might be explained by the use of different genetic markers in these studies that, through their comparison with available databases of incomplete coverage, produced different views of fungal diversity in peatlands. ITS databases appear to be dominated by basidiomycete sequences, since this group is more commonly used for ectomycorrhizal studies (Dahlberg 2001, Horton and Bruns 2001).

A few sequences that were found in both peat and litter samples were similar to a common set of taxonomic groups (Fig. 1 in II, Fig. 4 in IV, Figs. 1 and 2 in V). These included the common soil zygomycete *Mortierella* (Deacon 1997, Thormann 2006b) and ECM genus *Russula*. These taxa may represent ubiquitous members of peatland fungal communities. In addition, identical sequences were obtained from peat and litter samples at Lakkasuo that were similar to *Podochytrium* (Chytridiomycota), *Babjevia* (Lipomycetaceae) and several genera of aero-aquatic cellulose degraders (Dothideomycetes) (Fisher et al. 1977, Abdullah and Taj-Aldeen 1989) (II, V).

Quite unexpectedly, sequences similar to the common and fast growing genera *Mucor* and *Penicillium* were not detected at any of our sites (II, IV, V) even though their presence in peatlands has been confirmed elsewhere (e.g., Given and Dickinson 1975, Thormann 2006a, 2006b). It is unlikely that these genera would be entirely absent from Lakkasuo and Suonukkasuo, but they are certainly not abundant (II). These fungi may constitute only a small part of the fungal biomass although they are easily detected by traditional cultivation methods (e.g., Fritze and Bååth 1993, Artz et al. 2007, Lindahl and Boberg 2008). Similarly, no arbuscular-mycorrhizal (AM) fungi (Glomeromycota) were detected among the sites although they are common in nutrient-rich fens (Wolfe et al. 2007) where they form mutualistic associations with plants such as sedges (Turner et al. 2000).

Different fungal sequences characterized the two fens and the bog site at Lakkasuo (II). For instance, sequences that were similar to, e.g., uncultured Boleaceaceae clone from aspen rhizosphere (Lesaulnier et al. 2008) and a clone clustering in the same clade with *Mortierella* were typical of the fen. Another sequence that was most similar to Dothideomycetes (e.g, *Helicoon* and *Tyrannosorus)* was typical of the bog. The latter includes cellulose degraders (Fisher et al. 1977) and major decomposers of wood and plant litter as well as plant parasites and biotrophs (Goos 1987). In addition, a sequence similar to ECM-forming *Russula* was found in almost all of the pristine sites. This result agrees that ECM fungi are common in peatlands (Thormann et al. 1999), but does not confirm that they have a rather narrow tolerance of site wetness (Lodge 1989).

Collectively, the results suggest that WLD may have a greater effect on basidiomycetes than ascomycetes (Table 3 in II). Only one ascomycete sequence showed a response (positive) to long-term WLD. This sequence was similar to Sordariales, which is a diverse group containing lignicolous, herbicolous, coprophilous and soil-dwelling taxa (Huhndorf et al. 2004). In addition, the response to WLD was variable and taxon specific. For instance, a sequence similar to the wood-decomposing genera *Cymatoderma* and *Panus* appeared in the oligotrophic fen and in the hummock-surfaces of the ombrotrophic bog after short-term WLD, and another sequence similar to *Clavulina* disappeared in the mesotrophic fen and the bog after long-term WLD. The response of chytrids to WLD was also variable but appeared to be site dependent.

Most of the fungal ITS sequences from Suonukkasuo were typical of drier locations (IV). Typical sequences of wetter sites clustered with both Ascomycota (*Cercophora*) and Basidiomycota (e.g., *Russula*, *Tylospora*, Theleporaceae, *Hypholoma*). Sequences of the ECM fungi *Russula nitida* and *Tylospora fibrillosa* were more typical of surface layers, whereas those similar to *Cercophora* were commonly found in deeper layers. Most of the ITS sequences derived from in-growth mesh bags represented mycorrhizal fungi (IV). The results support the view that some ECM fungi are able to switch from symbiotic mycorrhizal to a saprotrophic lifestyle (Hibbett et al. 2000), and their limited ability to use certain complex compounds, e.g., tannic aid, lignin, cellulose and pectin (Hutchison 1990, Bending and Read 1997) may confer a competitive advantage in organic-rich soils Read and Perez-Moreno 2003, Read et al. 2004).

Fungal sequences that were typical of site, WLD or both were observed (Table 6). Since the litters analysed were not sterilized, microbes that were present prior to field establishment might have affected the initial community composition and subsequent succession. For example, it has been reported that phyllosphere fungi change the litter quality and in turn affect its subsequent decomposition and fungal succession (Osono 2003). Phyllosphere fungi might contain primary saprotrophs (Hudson 1968) that readily utilize carbohydrates and generate a more favourable environment for the colonization of fungi capable of decomposing more recalcitrant substances. Müller et al. (2001) found that endophytic fungi act as pioneer decomposers in surface-sterilized spruce needles when incubated for 5 months on sterile and non-sterile soils. Furthermore, endophytic fungi were an active part of the needle-decay community during the entire two-year decomposition study (Korkama-Rajala et al. 2007).

Table 6. Taxonomic affiliation of the sequences, and their putative ecological role in different sites or plots during the two-year decomposition period.

Fungi	Site or plot	Taxonomic affiliation	Putative ecological role (e.g. reference)
1st year	LTD ME	*Russula*	ECM
	LTD OM	*Meliniomyces, Phialocephala, Cladophialophora*	ERM, saprotrophs of many polymers (Currah & Tsuneda 1993, Piercey et al. 2002, Davey & Currah 2007)
2nd year	OM	*mitosporic Herpotrichiellaceae*	saprotrophs of litters, wood and soil (Domsch et al. 1980)
	LTD ME	*zygomycete, Phlebia*	soil saprotrops, white-rot fungi capable of lignin decaying (Hatakka 1994)
Actinobacteria			
1st year	ME	*Frankia*	free-living saprotrophs, nitrogen-fixers (Arveby & Huss-Daniel 1988, Smolander et al. 1988, Nickel 2000)
	OM	*Rhodococcus*	saprotrophs of many compounds (Bell et al. 1998, Häggblom et al. 1988, van der Geize and Dijkhuizen 2004, Larkin et al. 2005)
	LTD ME	*Mycobacterium*	saprotroph, pathogen (Kazda et al. 1990, Torkko et al. 2000, Tortoli 2003)
2nd year	ME	ambiguous	unknown
	OM	ambiguous	unknown

4.2.3. Actinobacterial community

Collectively, results (II, IV, V) suggest that public databases currently offer a limited reference set of sequences for actinobacteria, and agrees with the earlier suggestion that relatively few of the soil bacteria have been described (Joseph et al. 2003). A BLAST search for the most actinobacterial 16S rRNA sequences derived from either DNA or rRNA from Lakkasuo and Suonukkasuo matched to a set of "unknown actinobacterial clones" or "isolates from a variety of environments" (II, IV and V).

Ribosomal Database Project (RDP) classifier software (Wang et al. 2007) was tested to search for the closest similarity to the quality checked full-length 16S rRNA gene sequences of the known actinobacterial taxa in the RDP database (Appendix A. in the thesis). Lakkasuo litter-derived sequences (V) were classified with the most diverse set of known actinobacterial taxa compared to peat-derived sequences (II) and sequences from Suonukkasuo (IV) (Appendix A.). The RDP classifier revealed that the confidence values for sequences are rather low with most of the known taxa and most sequences remain unclassified within the taxa. This further proves that the obtained sequences are only distantly related to any known taxa.

Since sequences similar to *Mycobacterium* were found in peat and litter samples of both Lakkasuo (II, V) and Suonukkasuo (IV), this reflects their common occurrence and abundance. Sequences similar to *Rhodococcus* seem to be important at Lakkasuo since they were found in both from peat and litter samples (II, V). Although 16S rRNA is a relatively conserved marker in *Mycobacterium* (Turenne et al. 2001), Lakkasuo sequences (II) clustered with pathogenic species as well as groups that are considered purely saprotrophic, e.g., *M. cookii* from *Sphagnum* in New Zealand (Kazda et al. 1990) and slow-growing strains of *M. xenopi* and *M. botniense* (Torkko et al. 2000) and sequences from Suonukkasuo (IV) were similar to *M. chlorophenolicum*, known to mineralize pentachlorophenol (Briglia et al. 1994, Häggblom et al. 1994, Apajalahti et al. 1986). Some members of *Rhodococcus* are well known for their metabolic versatility and capacity to degrade environmentally hazardous chemicals (Bell et al. 1998, Häggblom et al. 1988, van der Geize and Dijkhuizen 2004, Larkin et al. 2005). Presumably, some of these taxa can also degrade the complex hydrocarbons accumulating in peat soils. In summary, the broader range of soil pH and vegetation patterns at Lakkasuo may partly explain the more diverse actinobacterial community compared to that in the Suonukkasuo fen.

The peat soil actinobacterial community at Lakkasuo was not affected by site type (II). However, the occurrence of a few actinobacterial sequences after short-term or long-term WLD was codependent on nutrient level (II). Various sequences were more typical of drier locations and a few of them characterized wetter locations (IV). Because precise identifications could not be made, the ecological significance of these actinobacteria remains unclear. Some specific sequence patterns were found among litters that were typical of site, WLD or both (Table 6). Distantly *Frankia*-related actinobacteria might play a general role in fens and species similar to *Mycobacterium* might become increasingly important after WLD. In contrast, *Rhodococcus*-related actinobacteria appear to thrive in the bog. *Frankia* are atmospheric nitrogen fixing bacteria that live as symbionts in root nodules of, e.g., *Alnus* and *Myrica*. *Frankia* are also known to produce carbohydrases (Safo-Sampah and Torrey 1988, Igual et al. 2001) and to live as free soil bacteria in acid forests devoid of actinorhizal plants (e.g., Smolander and Sundman 1987, Arveby and Huss-Daniel 1988, Smolander et al. 1988). Whether members of *Frankia* are saprotrophic in these litters and derive from soils as earlier reported (Nickel, 2000) or play some other role cannot be assessed on the basis of these results.

4.2.4 MOB community

Only type I MOB were detected in the oligotrophic fen, whereas the ombrotrophic bog had both types I and II MOB, thereby supporting the findings of earlier studies (Amaral et al. 1995, Graham et al. 1993, Wise et al. 1999) (III). Notably, the *pmoA*-specific primer pair that was used in paper III failed to amplify *pmoA* in peat samples from two other boreal fen sites (personal observations; Tuomivirta et al. 2009). Type II MOB-related *pmoA* sequences were successfully amplified from these fen sites using A189f and a new reverse primer (A621r: Tuomivirta et al. 2009). This new reverse primer was designed to substitute A682r, which together with A189f are known to cause PCR bias and nonspecific products (Bourne et al. 2001). Thus, it is possible that type II MOB were not detected in the fen site because of mispriming. However, type I MOB-related *pmoA* sequences were most similar to sequences found in other Finnish organic soils (accession numbers AJ317928 and AJ317926) and type II MOB-related *pmoA* sequences were most similar to *Methylocystis*.

The number of *pmoA*-derived DGGE bands increased with depth and was positively correlated with soil pH. It is unlikely that pH is directly responsible for MOB diversity, but indirect influences are possible via the vegetation it supports. Deep-rooting sedges, which push photosynthetic C and O_2 into deep peat layers, are typical of fens, whereas the *Sphagnum* mosses that characterize bogs cannot do so. Thus, overall differences in MOB communities among peatland sites and sampling depths are most likely related to vegetation that in turn creates the vertical peat profile. Sequences of sMMO-possessing MOB were found only in the bog and were distantly related to any known MOB. These sequences may represent a novel lineage since they were grouped with a large set of *mmoX* sequences that represented a novel group of acidophilic or acid-tolerant methanotrophs and accounted for more than two-thirds of the *mmoX* clone library from a *Calluna*-covered soil sample (Chen et al. 2008). Earlier studies have clearly detected sMMO in bogs (McDonald et al. 1996, 1999, Morris et al. 2002) and emphasized the distinction of MOB communities inhabiting fens and bogs. Yet, a limited diversity of sMMO-possessing MOB was observed, suggesting constraints on genetic diversity of this enzyme due to the essential conservation of function (McDonald et al. 2006).

The MOB community in the oligotrophic fen became more similar to that of the ombrotrophic bog after WLD. We did not detect a change towards a "high-affinity" MOB community that is characteristic of upland soils after WLD. Yet, the MOB community did change following WLD and appeared to be adapted to a lower substrate (CH_4) concentration. Several *pmoA* sequences that were characteristic of the fen and bog were not detected after WLD. Furthermore, WLD caused a more dramatic decrease in the number of DGGE-derived *pmoA*-bands in the fen than the bog. WL was found to be the key environmental factor regulating methanotrophy in *Sphagnum* where a loose symbiosis between *Sphagnum* spp. and *Methylocystis* (type II MOB) was suggested to account for 10–30% of *Sphagnum* C biomass (Larmola et al. 2010). Only minor differences in the sMMO-possessing MOB community were observed with respect to WLD and depth. Recently, more specific detection methods such as mRNA-based microarrays (Bodrossy et al. 2006) and SIP-PLFA (Chen et al. 2008) have been applied to study MOB communities in environmental samples. These advanced techniques detect active MOB populations and offer precise and comprehensive tools to future investigations of peatland MOB.

4.3 Microbial activity

4.3.1 Respiration

The basal respiration values were negatively correlated with depth (I) and bulk density (IV), and positively correlated with pH (I) and water content (IV). Soil pH is one of the most important factors affecting the vegetation composition of pristine peatlands, and thus separates the types on the basis of their flora (Wheeler and Proctor 2000, Økland et al. 2001). Furthermore, WLD lowers pH especially in fens (Minkkinen et al. 1999, Table 2). Fungal and eukaryotic-specific PLFAs were positively correlated with basal respiration, indicating that fungi are responsible for a major part of microbial respiration at Lakkasuo (I). The decreasing respiration with depth in the peat profile may be a result of low substrate quality (Hogg et al. 1992). In the pristine fen sites in particular, aerobic decomposers may be absent from the deeper anoxic layers. In these sites, there is an input of fresh root litter to the deeper layers (Saarinen 1996), so substrate quality does not decrease with depth as predictably as in *Sphagnum* sites.

In contrast to basal respiration rates, field respiration rates between the driest and wettest locations in Suonukkasuo were threefold different (IV). These results indicate that basal respiration measures the aerobic decomposition potential of the substrate. In the dry locations, the decomposition potential of the surface peat may have already been completed to a great extent. Yet, field respiration measurements incorporate the entire CO_2 flow of the peat profile as a result of aerobic and CH_4 oxidation when an oxic surface layer is present. On the other hand, a high WL limits decomposition in the wet locations, which is reflected in the field respiration results. A similar trend was observed in six Finnish drained peatland sites, where average WL was shown to regulate field respiration via microbial community structure (Mäkiranta et al. 2009). Many PLFAs and fungal ITS sequences correlated with basal respiration, whereas sequences representing the fungal saprotrophs *Lasiosphaeria* (Miller and Huhndorf 2004), *Cercophora* (Fallah and Shearer 2001) and *Hypholoma* correlated positively with field respiration rates (IV).

4.3.2 Mass loss

When the effects of site, WLD and litter type were eliminated, microbial function (litter-mass loss) after the two-year decomposition period only explained a small amount of variation in actinobacterial community composition after the second year of decomposition (Table 2 in V) and none of the variation for fungi. These results echo those of a similar study that found no relationship between the active endophytic fungal community and the mass loss of needle litter after two years of decomposition (Korkama-Rajala et al. 2007). Recently, Salminen et al. (2009) showed that removal of the soil fauna changed the composition of the bacterial community in a coniferous forest but these structural changes did not influence the decomposition rate of cellulose or wooden discs. Thus, these results support the idea of functional redundancy, which suggests that at a fundamental level the actual microbial species composition may irrelevant since most organic decomposition processes eventually lead to intermediates or end products (e.g., pyryvate, acetyl CoA, and various compounds in tricarboxylic acid cycle) of respiration (Fierer et al. 2009).

4.3.3 Potential CH_4 oxidation

The highest CH_4 oxidation activity was found 20–40 cm above the WL at the pristine oligotrophic fen and the activity decreased to almost zero in the vicinity of the WL (III). In the pristine ombrotrophic bog, the highest activity was detected at a deeper layer than in the fen, but in contrast oxidation rates were still observed at the WL and 10 cm below it. The differential distribution of CH_4 oxidation between pristine fen and bog cannot be explained with the variables measured here. The number of *pmoA*-derived DGGE bands did not correlate with maximum CH_4 oxidation rate in any of the sites. The amount of *pmoA* amplicons obtained with A189f and the newly designed A621r primers were positively correlated with potential CH_4 oxidation rates in two other fen sites (Tuomivirta et al. 2009). However, these results are strictly not comparable since the latter study was based on quantitative real-time PCR.

WLD reduced the potential CH_4 oxidation at the fen and bog sites. The results agree with previous studies that showed how WL significantly influences CH_4 oxidation (Moore and Knowles 1989, Nykänen et al. 1998, Kettunen et al. 1999). Even though WLD generally lowered peat soil pH (Table 1), a correlation between soil pH and potential CH_4 oxidation was not detected (III), echoing the results of Moore and Dalva (1997). However, contradictary results exist in that higher *in vitro* CH_4 oxidation rates were measured at an elevated pH (Dunfield et al. 1993), and indications about relationship between CH_4 oxidation rates and soil pH have been detected (Amaral et al. 1995, Hütch et al. 1994). In other words, even if CH_4 flux has been noticed to correlate with WL, it does not necessarily correlate with water chemistry (pH, Ca, Mg and K_{corr}) (Bubier 1995).

A potential mechanism for WL control could be that surface subsidence and an increase in peat bulk density caused by a lowered WL reduces the diffusion of CH_4 and O_2 (Nykänen et al. 1998), which in turn limits CH_4 oxidation. Peatland type may be a critical factor affecting CH_4 flux; in a mesocosm study from a northern peatland, pore water chemistry and plant productivity controlled CH_4 flux in the bog, whereas WL controlled CH_4 flux in the fen through its effects on CH_4 oxidation rates (White et al. 2008). Thus, the indirect effects of climate change, e.g., vegetation and peat chemistry, may be as important as the direct effects of WL in controlling CH_4 production and oxidation in peatlands.

5 CONCLUSIONS AND FUTURE PROSPECTS

This thesis represents the first investigation of microbial communities among an extensive set of samples that circumscribe many types of boreal peatlands. In general, microbial community responses to environmental change were variable and detected at multiple taxonomic levels. The results also describe the difficulty faced when making generalisations about the direction of change, which may depend on many factors including peatland site, microform, sampling depth, litter quality and microbial group and the interactions among them.

However, sampling depth was found to be one of the main factors affecting the structure of aerobic microbial communities. Site type and microtopographic variation within the site affected the microbial community overall and the fungal community in particular. Several bacterial groups, including actinobacteria, were abundant in the nutrient-rich fen whereas fungi dominated the drier surfaces of the nutrient-poor bog. The actinobacterial community appeared to be more dependent on an undefined depth-related factor. Site also had an impact on the MOB community; a higher number of DGGE bands were detected from the oligotrophic fen compared to the ombrotrophic bog. Litter quality had the greatest impact on the structure of active decomposer communities in litters representing a 'fresh' substrate. Decomposition stage of litters affected fungi, although only to a minor extent.

Short-term and gradual WLD induced changes in the resident microbial community, and the change became more evident following long-term WLD. The results generally showed that WLD homogenizes microbial communities in sites with different nutrient levels in the long-run and that the change is greatest in the nutrient-rich mesotrophic fen and least in the nutrient-poor ombrotrophic bog, which follows the vegetation pattern. Both fungi and Gram-negative bacteria appear to benefit while actinobacteria appear to suffer from a lowered WL in the fen. Fungi either suffered or benefited depending on the microform of the bog, thus their response is at least to some extent dependent on peatland type. WLD increased fungal diversity especially in the fen, whereas actinobacterial diversity did not change. To conclude, patterns of change were different in peatland types. Basidiomycetes might be more responsive to WLD than ascomycetes.

Basal respiration was negatively correlated with depth and bulk density, and positively correlated with pH, water content and fungal PLFAs. WL at the time of measurement explained most of the variation in field respiration data. The field respiration rates indicated that climate-warming induced WLD would accelerate decomposition of soil organic matter at least in the nutrient-rich northern fen. In addition, a correlation between field respiration and saprotrophic fungal sequences indicated that species composition may play a role in the decomposition process *in situ*. Furthermore, some fungi might have a competitive advantage when peat is exposed to air and some mycorrhizal fungi might have a dual role as saprotrophs in peatlands. WLD had an impact on MOB community and activity, especially in the oligotrophic fen. Litter-mass loss showed only a minor effect on the active actinobacterial community structure, which reflects the functional redundancy of the communities.

Fungal sequences pertained to various taxa capable of utilizing a broad range of substrates. Most of the actinobacterial sequences could not be matched with any characterized taxon, although some were similar to taxa that can degrade complex hydrocarbons. The lack of precise identifications reflects the need for more reference data in public databases, and encourages the construction of a comprehensive clone library with longer genetic markers from peat and litter samples. To investigate microbial communities in peatlands further, novel applications that would utilize, e.g., high-throughput sequencing techniques and the incorporation of ^{13}C

into litter or peat soil under controlled conditions might detail the pathways and mechanisms of microbial C assimilation and the peatland C cycle.

REFERENCES

Abdullah, S.K. & Taj-Aldeen, S.J. 1989. Extracellular enzymatic activity of aquatic and aero-aquatic conidial fungi. Hydrobiologia 174: 217-223.

Aerts, R., Verhoeven, J.T.A. & Whigham, D.F. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80: 2170-2181.

Amaral, J.A., Archambault, C., Richards, S.R. & Knowles, R. 1995. Denitrification associated with groups I and II methanotrophs in a gradient enrichment system. FEMS Microbiology Ecology 18: 289-298.

—, Ren, T. & Knowles, R. 1998. Atmospheric CH_4 consumption by forest soils and extracted bacteria at different pH values. Applied & Environmental Microbiology 64: 2397-2402.

Anderson, I.C., Campbell, C.D. & Prosser, J.I. 2003a. Potential bias of fungal 18S rDNA and internal transcribed spacer polymerase chain reaction primers for estimating fungal biodiversity in soil. Environmental Microbiology 5: 36-47.

—, Campbell, C.D. & Prosser, J.I. 2003b. Diversity of fungi in organic soils under a moorland – Scots pine (Pinus sylvestris L.) gradient. Environmental Microbiology 5: 1121-1132.

Aneja, M., Sharma, S., Munch, J.C. & Schloter, M. 2004. RNA fingerprinting – a new method to screen for differences in plant litter degrading microbial communities. Journal of Microbiological Methods 59: 223-231.

Apajalahti, J.H.A., Karpanoja, P. & Salkinoja-Salonen, M.S. 1986. *Rhodococcus chlorophenolicus* sp. nov., a chlorophenol-mineralizing actinomycete. International Journal of Systematic Bacteriology 36: 246-251.

Artz, R.R.E., Chapman, S.J. & Campbell, C.D. 2006. Substrate utilisation profiles of microbial communities in peat are depth dependent and correlate with whole soil FTIR profiles. Soil Biology & Biochemistry 38: 2958-2962.

—, Anderson, I.C., Chapman, S.J., Hagn, A., Schloter, M., Potts, J.M. & Campbell, C.D. 2007. Changes in fungal community composition in response to vegetational succession during the natural regeneration of cutover peatlands. Microbial Ecology 54: 508-522.

Arveby, A.S. & Huss-Danell, K. 1988. Presence and dispersal of infective *Frankia* in peat and meadow soils in Sweden. Biology & Fertility of Soils 6: 39-44.

Auman, A.J., Stolyar, S., Costello, A.M. & Lidstrom, M. 2000. Molecular characterization of methanotrophic isolates form freshwater lake sediment. Applied & Environmental Microbiology 66: 5259-5266.

Baar, J., Bastiaans, T., van de Coevering, M.A. & Roelofs, J.G.M. 2002. Ectomycorrhizal root development in wet Alder carr forests in response to desiccation and eutrophication. Mycorrhiza 12: 147-151.

Bell, K.S. 1998. The genus *Rhodococcus*. Journal of Applied Microbiology 85: 195-210.

Bending, G.D. & Read, D.J. 1997. Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. Mycological Research 101: 1348-1354.

Berg, B. & McClaugherty, C. 2003. Plant litter – decomposition, humus formation, carbon sequestration. Springer-Verlag. Berlin. 338 p.

Blackwood, C.B., Waldrop, M.P., Zak, D.R. & Sinsabaugh, R.L. 2007. Molecular analysis of fungal communities and laccase genes in decomposing litter reveals differences among forest types but no impact of nitrogen deposition. Environmental Microbiology 9: 1306-1316.

Blodau, C., Basiliko, N. & Moore, T. 2004. Carbon turnover in peatland mesocosm exposed to different water table levels. Biogeochemistry 67: 331-351.

Bodrossy, L., Stralis-Pavese, N., Konrad-Köszler, M., Weilharter, A., Reichenauer, T., Schöfer, D. & Sessitsch, A. 2006. mRNA-based parallel detection of active methanotroph populations using a diagnostic microarray. Applied & Environmental Microbiology 72: 1672-1676.

Borgå, P., Nilsson, M. & Tunlid, A. 1994. Bacterial communities in peat in relation to botanical composition as revealed by phospholipid fatty acid analysis. Soil Biology & Biochemistry 26: 841-848.

Bourne, D.G., McDonald, I.R. & Murrell, J.C. 2001. Comparison of pmoA PCR primer sets as tools for investigating methanotroph diversity in three Danish soils. Applied & Environmental Microbiology 67: 3802-3809.

Bouwman, A.F. 1990. Introduction In: Bouwman, A.F. (ed.). Soils and the greenhouse effect, Wiley and Sons, Chichester, UK. p. 25-32.

Bubier, J.L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. Journal of Ecology 83: 403-420.

Buée, M., Courty, P.E., Mignot, D. & Garbaye, J. 2007. Soil niche effect on species diversity and catabolic activities in an ectomycorrhizal fungal community. Soil Biology & Biochemistry 39: 1947-1955.

Bragazza, L., Siffi, C., Iacumi, P. & Gerdol, R. 2007. Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. Soil Biology & Biochemistry 39: 257-267.

Brake, M., Höper, H. & Joergensen, R.G. 1999. Land use-induced changes in activity and biomass of microorganisms in raised bog peats at different depths. Soil Biology & Biochemistry 31: 1489-1497.

Briglia, M., Eggen, R.I., Van Elsas, D.J. & De Vos, W.M. 1994. Phylogenetic evidence for transfer of pentachlorophenol-mineralizing Rhodococcus chlorophenolicus PCP-I (T) to the genus Mycobacterium. International Journal of Systematic Bacteriology 44: 494-498.

Chen, Y., Dumont, M.G., McNamara, N.P., Chamberlain, P.M., Bodrossy, L., Stralis-Pavese, N. & Murrell, J.C. 2008. Diversity of the active methanotrophic community in acidic peatlands as assessed by mRNA and SIP-PLFA analyses. Environmental Microbiology 10: 446-459.

Cicerone, R.J. & Ormland, R.S. 1988. Biogeochemical aspects of atmospheric methane. Global Biogeochemical Cycles 2: 299-327.

Clymo, R.S. 1983. Peat. In: Gore, A.J.P. (ed.). Mires: Swamp, Bog, Fen, and Moor (Ecosystems of the world 4A). Elsevier, Amsterdam. p.159-224.

Cole, J.R., Wang, Q., Cardenas, E., Fish, J., Chai, B., Farris, R.J., Kulam-Syed-Mohideen, A.S., McGarrell, D.M., Marsh, T., Garrity, G.M. & Tiedje, J.M. 2009. The Ribosomal Database Project: improved alignments and new tools for rRNA analysis. Nucleic Acids Research 37 (Database issue): D141-D145; doi: 10.1093/nar/gkn879.

—, Chai, B., Farris, R.J., Wang, Q., Kulam, S.A., McGarrell, D.M., Garrity, G.M. & Tiedje, J.M. 2005. The Ribosomal Database Project (RDP-II): sequences and tools for high-throughput rRNA analysis. Nucleic Acids Research 33 (Database Issue): D294-D296. doi: 10.1093/nar/gki038.

Currah, R.S. & Tsuneda, A. 1993. Vegetative and reproductive morphology of Phialocephala fortinii (Hyphomycetes; Mycelium radicis atrovirens) in culture. Transactions of the Mycological Society of Japan 34: 345-356.

Dahlberg, A. 2001. Community ecology of ectomycorrhizal fungi: an advancing interdisciplinary field. New Phytologist 150: 150: 555-562.

D'Angelo, E.M., Karathanasis, A.D., Sparks, E.J., Ritchey, S.A. & Wehr-McChesney, S.A. 2005. Soil carbon and microbial communities at mitigated and late successional bottomland forest wetlands. Wetlands 25: 162-175.

Davey, M.L. & Currah, R.S. 2007. A new species of *Cladophialophora* (hyphomycetes) from boreal and montane bryophytes. Mycological Research 111: 106-116.

Deacon, J.W. 1997. Modern Mycology, Third Edition, Blackwell Science, Oxford, UK. 303 p.

Dedysh, S.N., Belova, S.E., Bodelier, P.L.E., Smirnova, K.V., Khmelenina, V.N. & Chidthaisong, A. 2007. *Methylocystis heyeri* sp. nov., a novel type II methanotrophic bacterium possessing 'signature' fatty acids of type I methanotrophs. International Journal of Systematics & Evolution of Microbiology 57: 472-479.

—, Berestovskaya, Y.Y., Vasylieva, L.V., Belova, S.E., Khmelenina, V.N., Suzina, N.E., Tritsenko, Y.A., Liesack, W. & Zavarzin, G.A. 2004. *Methylocella tundrae* sp. nov., a novel methanotrophic bacterium from acidic tundra peatlands. International Journal of Systematics & Evolution of Microbiology 54: 151-156.

—, Derakshani, M. & Liesack, W. 2001. Detection and enumeration of methanotrophs in acidic *Sphagnum* peat by 16S rRNA fluorescence in situ hybridization, including the use of newly developed oligonucleotide probes for *Methylocella palustris*. Applied & Environmental Microbiology 67: 4850-4857.

—, Dunfield, P.F., Derakshani, M., Stubner, S., Heyer, J. & Liesack, W. 2003. Differential detection of type II methanotrophic bacteria in acidic peatlands using newly developed 16S rRNA-targeted fluorescent oligonucleotide probes. FEMS Microbiology Ecology 43: 299-308.

—, Khmelenina, V.N., Suzina, N.E., Trotsenko, Y.A., Semrau, J.D., Liesack, W. & Tiedje, J.M. 2002. *Methylocapsa acidiphila* gen. nov., sp. nov., a novel methane-oxidizing and dinitrogen-fixing acidophilic bacterium from Sphagnum bog. International Journal of Systematics & Evolution of Microbiology 52: 251-261.

—, Knief, C. & Dunfield, P.F. 2005. *Methylocella* species are facultatively methanotrophic. Journal of Bacteriology 187: 4665-4670.

—, Liesack, W. Khmelenina, V.N., Suzina, N.E., Trotsenko, Y.A., Semrau, J.D., Bares, A.M., Panikov, N.S. & Tiedje, J.M. 2000. *Methylocella palustris* gen. nov., sp. nov., a new methane-oxidizing acidophilic bacterium from peat bogs, representing a novel subtype of serine-pathway methanotrophs. International Journal of Systematics & Evolution of Microbiology 50: 955-969.

—, Pankratov, T.A., Belova, S.E., Kulichevskaya, I.S. & Liesack, W. 2006. Phylogenetic analysis and In Situ identification of *Bacteria* community composition in an acidic *Sphagnum* peat bog. Applied & Environmental Microbiology 72: 2110-2117.

Dinishe Jayasinghe, B.A.T. & Parkinson, D. 2008. Actinomycetes as antagonists of litter decomposer fungi. Applied Soil Ecology 38: 109-118.

Domisch, T., Finér, L., Laiho, R., Karsisto, M. & Laine, J. 2000. Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. Soil Biology & Biochemistry 32: 1571-1580.

Domsch, K.H., Gams, W. & Anderson, T.H. 1980. Compendium of soil fungi. Vol 1. Academic Press, London. 859 p.

Dunfield, P.F., Khmelenina, V.N., Suzina, N.E., Trotsenko, Y.A. & Dedysh, S.N. 2003. *Methylocella silvestris* sp. nov., a novel methanotroph isolated from an acidic forest cambisol. International Journal of Systematics & Evolution of Microbiology 53: 1231-1239.

—, Knowles, R., Dumont, R. & Moore, T. 1993. Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biology & Biochemistry 25: 321-326.

—, Yuryev, A., Senin, P., Smirnova, A.V., Stott, M.B., Hou, S., Saw, J.H., Zhou, Z., Ren, Y., Wang, J., Mountain, B.W., Crowe, M.A., Weatherby, T.M., Bodelier, P.L.E., Liesack, W., Feng, L., Wang, L. & Alam, M. 2007. Methane oxidation by an extremely acidophilic bacterium of the phylum *Verrucomicrobia*. Nature 450: 879-882.

Edwards, C., Hales, B.A., Hall, G.H., McDonald, I.R., Murrell, J.C., Pickup, R., Ritchie, D.A., Saunders, J.R., Simon, B.M. & Upton, M. 1998. Microbiological processes in the terrestrial carbon cycle: methane cycling in peat. Atmospheric Environment 32: 3247-3255.

Ellison, A.M. 2000. PC-ORD version 4 review. Bulletin of Ecological Society of America 81: 127-128.

Endo, E., Hayashi, T., Hibi, T., Honsono, K., Beppu, T. & Ueda, K. 2003. Enzymological characterisation of EpoA, a laccase-like phenol oxidase produced by *Streptomyces griseus*. Journal of Biochemistry 133: 671-677.

Ettema, C.H. & Wardle, D.A. 2002. Spatial soil ecology. Trends in Ecology and Evolution 17: 177-183.

Fallah, P.M. & Shearer, C.A. 2001. Freshwater ascomycetes: new or noteworthy species from north temperate lakes in Wisconsin. Mycologia 93: 566-602.

Federle, T.W. 1986. Microbial distribution in soil - new techniques. In Megušar F. & Gantar M. (eds.). Perspectives in microbial ecology. Slovene Society of Microbiology, Ljubljana. p .493-498.

Fenner, N., Freeman, C. & Reynolds, B. 2005. Hydrological effects on the diversity of phenolic degrading bacteria in a peatlands: implications for carbon cycling. Soil Biology & Biochemistry 37: 1277-1287.

Fierer, N., Stuart Grandy, A. Six, J. & Paul, E.A. 2009. Searching for unifying principles in soil ecology. Soil Biology & Biochemistry 41: 2249-2256.

Fisher, J.P., Sharma, P.D. & Webster, J. 1977. Cellulolytic ability of aero-aquatic hyphomycetes. Transactions of the British Mycological Society 69: 495-496.

Fisk, M.C., Ruether, K.F. & Yavitt, J.B. 2003. Microbial activity and functional composition among northern peatland ecosystems. Soil Biology & Biochemistry 35: 591-602.

Freeman, C. Evans, C.D. & Monteith, D.T. 2001a. Export of organic carbon from peat soils. Nature 412: 785-786.

—, Ostle, N.J., Fenner, N. & Kang, H. 2004. A regulatory role for phenol oxidase during decomposition in peatlands. Soil Biology & Biochemistry 36: 1663-1667.

—, Ostle, N. & Kang, H. 2001b. An enzymatic 'latch' on a global carbon store. Nature 409: 149.

Fritze, H. & Bååth. E. 1993. Microfungal species composition and fungal biomass in a coniferous forest soil polluted by alkaline deposition. Microbial Ecology 25: 83-92.

Frostegård, Å. & Bååth, E. 1996. The use of phospholipid fatty acids to estimate bacterial and fungal biomass in soil. Biology & Fertility of Soils 22: 59-65.

Gardes, M. & Bruns, T.D. 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. Molecular Ecology 2: 113-118.

Gilbert, D., Amblard, C., Bourdier, G. & Francez, A.-J. 1998. The microbial loop at the surface of a peatland: structure, function, and impact of nutrient input. Microbial Ecology 35: 83-93.

Girvan, M.S., Bullimore, J., Ball, A.S., Pretty, J.N. & Osborn, A.M. 2004. Responses of active bacterial and fungal communities in soils under winter wheat to different fertilizer and pesticide regimens. Applied & Environmental Microbiology 70: 2692-2701.

Given, P.H., Dickinson, C.-H., 1975. Biochemistry, microbiology of peats. In: Paul, E.A., McLaren, A.D. (eds.). Soil Biochemisry, Vol 3. Marcel Dekker, New York. p.123-211.

Glenn, M.G., Warner, W.S. & Webb, S.L. 1991. Mycorrhizal status of mature red spruce (*Picea rubens* Sarg.) in mesic and wetland sites of northwestern New jersey. Canadian Journal of Forest Research 21: 741-749.

Goldstein, H. 1995. Multilevel Statistical Models. Kendall's Library of Statistics 3, 2nd edition. Hodder Arnold, London. 178 p.

Golovchenko, A.V., Tikhonova, E.Y. & Zvyagintsev, D.G. 2007. Abundance, biomass, structure, and activity of the microbial complexes of minerotrophic and ombrotrophic peatlands. Microbiology 76: 630-637.

Goodfellow, M. & Williams, S.T. 1983. Ecology of actinomycetes. Annual Review of Microbiology, 37: 189-216.

Goos, R.D. 1987. Fungi with a twist: the helicosporous hyphomycetes. Mycologia 79: 1-22.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1: 182-195.

Graham, D.W., Chaudhary, J.A., Hanson, R.S. & Arnold, R.G. 1993. Factors affecting competition between type I and type II methanotrophs in two-organism, continuous-flow reactors. Microbial Ecology 25: 1-17

Griffith, G.W. & Roderick, K. 2008. Saprotrophic basidiomycetes in grasslands: distribution and function. In: Boddy, L., Frankland, J.C. & van West, P. (eds.). Ecology of Saprotrophic Basidiomycetes. British Mycological Society Symposia Series. Academic press/Elsevier, Amsterdam/Boston. p 277-299.

Haack, S.K., Garchow, H., Odelson, D.A., Forney, L.J. & Klug, M.J. 1994. Accuracy, reproducibilitym and interpretation of fatty acid methyl ester profiles of model bacterial communities. Applied & Environmental Microbiology 60: 2483-2493.

Häggblom, M.M. 1988. Degradation and Omethylation of chlorinated phenolic compounds by *Rhodococcus* and *Mycobacterium* strains. Applied & Environmental Microbiology 54: 3043-3052.

—, Nohynek, L.J., Palleroni, N.J., Kronqvist, K., Nurmiaho-Lassila, E.-L., Salkinoja-Salonen, M.S., Klatte, S., Kroppenstedt, R.M. 1994. Transfer of polychlorophenol-degrading *Rhodococcus chlorophenolicus* (Apajalahti et al. 1986) to the genus *Mycobacterium* as *Mycobacterium chlorophenolicum* comb. nov. International Journal of Systematic Bacteriology 44: 485-493

Hanson, R.S. & Hanson, T.E. 1996. Methanotrophic bacteria. Microbiological Reviews 60: 439-471.

Hatakka, A. 1994. Lignin-modifying enzymes from selected white-rot fungi: production and role from in lignin degradation. FEMS Microbiology Reviews 13: 125-135.

Heyer, J., Berger, U., Hardt, M. & Dunfield, P.F. 2005. *Methylohalobius crimeensis* gen. nov. sp. nov., a moderately halophilic methanotrophic bacterium isolated from hypersaline lakes of Crimea. International Journal of Systematic & Evolutionary Microbiology 55: 1817-1826.

Hibbett, D.S., Gilbert, L.-B. & Donoghue, M.J. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. Nature (London) 407: 506-508.

Hiroki, M. & Watanabe, M.M. 1996. Microbial community and rate of cellulose decomposition in peat soils in a mire. Soil Science & Plant Nutrition 42: 893-903.

Hofrichter, M. 2002. Review: lignin conversion by manganese peroxidase (MnP). Enzyme & Microbial Technology 30: 454-466.

Hogg, E.H. 1993. Decay potential of hummock and hollow *Sphagnum* peats at different depths in a Swedish raised bog. Oikos 66: 269-278.

—, Lieffers, V.J.,Wein, R.W., 1992. Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire. Ecological Applications 2: 298-306.

Hökkä, H., Kaunisto, S., Korhonen, K.T., Päivänen, J., Reinikainen, A. & Tomppo, E. 2002. Suomen suometsät 1951–1994. Metsätieteen aikakauskirja 2B. Metsäntutkimuslaitos. Helsinki. p. 201-357.

Holding, A.J., Franklin, D.A. & Watling, R. 1965. The microflora of peat-podzol transitions. Journal of Soil Science 16: 44-59.

Holmes, A.J., Costello, A., Lidstrom, M.E. & Murrell, J.C. 1995. Evidence that particulate methane monooxygenase and ammonia monooxygenase may be evolutionarily related. FEMS Microbiological Letters 132: 203-208.

Horner, J.D., Gosz, J. & Cates, R.G. 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. The American Naturalist 132: 869-882.

Hornibrook, E.R.C, Bowes, H.L., Culbert, A. & Gallego-Sala, A.V. 2009. Methanotrophy potential versus methane supply by pore water diffusion in peatlands. Biogeosciences 6: 1491-1504.

Horton, T.R. & Bruns, T.D. 2001. The molecular revolution in ectomycorrhizal ecology: peeking into the black box. Molecular ecology 10: 1855-1871.

Hosoya, T. 2002. Hyaloscyphaceae in Japan (6)**: the genus *Hyphodiscus* in Japan and its anamorph *Catenulifera* gen. nov. Mycoscience 43: 47-57.

Hudson, H. J. 1968. The ecology of fungi on plant remains above the soil. New Phytologist 67: 837-874.

Huhndorf, S.M., Miller, A.N. & Fernández, F.A. 2004. Molecular systematics of the Sordariales: the order and the family Lasiosphaeriaceae redefined. Mycologia 96: 368-387.

Huikari, O. 1953. Tutkimuksia ojituksen ja tuhkalannoituksen vaikutuksesta eräiden soiden pieneliöstöön. Summary in English: Studies upon the effect of drainage and ash fertilization upon the microbes of some swamps. Communicationes Instituti Forestalis Fenniae 42. 18 p.

Hullo, M.F., Moszer, I., Danchin, A. & Martin-Verstraete, I., 2001. CotA of *Bacillus subtilis* is a copper-dependent laccase. Journal of Bacteriology 183: 5426-5430.

Hütch, B.W., Webster, C.P. & Powlson, D.S. 1994. Methane oxidation in soil as affected by land use, soil pH and fertilization. Soil Biology & Biochemistry 26: 1613-1622.

Hutchison, L.J. 1990. Studies on the systematic of ectomycorrhizal fungi in axenic culture. II. The enzymatic degradation on selected carbon and nitrogen compounds. Canadian Journal of Botany 68: 1522-1530.

Igual, J.M., Velazquez, E., Mateos, P.F., Rodriguez-Barrueco, C., Cervantes, E. & Martinez-Molina, E. 2001. Cellulose isoenzyme profiles in *Frankia* strains belonging to different cross-inoculation groups. Plant & Soil 229: 35-39.

Ingram, H.A.P. 1992. Introduction to the ecohydrology of mires in the context of cultural perturbation. In: Bragg, O.M., Hulme, P.D., Ingram, H.A.P. & Robertson, R.A. (eds.). Peatland Ecosystems and Man: An Impact Assessment. British Ecological Society/ International Peat Society. Dundee. p. 67-93.

IPCC 2007: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate

Change. Cambridge University Press, Cambridge, United Kingdom and New York, USA. 996 p.

Johnson, L.C. & Damman, A.W.H. 1991. Species-controlled *Sphagnum* decay on a South Swedish raised bog. Oikos. 61: 234-242.

Joosten, H. & Clarke, D. 2002. Wise use of mires and peatlands. International Mire Conservation Group and International Peat Society. 300 p.

Joseph, S.J., Hugenholtz, P., Sangwan, P., Osborne, C.A. & Janssen, P.H. 2003. Laboratory cultivation of widespread and previously uncultured soil bacteria. Applied & Environmental Microbiology. 69: 7210-7215.

Jumpponen, A. 2007. Soil fungal communities underneath willow canopies on a primary successional glacier forefront: rDNA sequence results can be affected by primer selection and chimeric data. Microbial Ecology 53: 233-246.

Karsisto, M. 1979. Effect of forest improvement measures on activity of organic matter decomposing micro-organisms in forested peatlands. Part I. Effect of drainage and NPK fertilization in the spruce and pine swamps at Kivalo and Vilppula. Suo 30: 49-58.

Kazda, J.J., Stackebrandt, E., Smida, J., Minnikin, D.E., Daffe, M., Parlett, J.H & Pitulle, C. 1990. *Mycobacterium cookii* sp. nov. International Journal of Systematic & Evolutionary Bacteriology 40: 217-223.

Kettunen, A., Kaitala, V., Lehtinen, A., Lohila, A., Alm, J., Silvola, J. & Martikainen, P.J. 1999. Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires. Soil Biology & Biochemistry 31: 1741-1749.

Khalil, M.A.K. & Rasmussen, R.A. 1983. Sources, sinks and seasonal cycles of atmospheric methane. Journal of Geophysical Research 88: 5131-5151.

Khan, M.R. & Williams, S.T. 1975. Studies on the ecology of actinomycetes in soil – VIII. Distribution and characteristics of acidophilic actinomycetes. Soil Biology & Biochemistry 7: 345-348.

Kim, S.Y., Lee, S.H., Freeman, C., Fenner, N. & Kang, H. 2008. Comparative analysis of soil microbial communities and their responses to the short-term drought in bog, fen, and riparian wetlands. Soil Biology & Biochemistry 40: 2874-2880.

Knief, C., Lipski, A. & Dunfield, P.F. 2003. Diversity and activity of methanotrophic bacteria in different upland soils which oxidize atmospheric methane. Applied & Environmental Microbiology 69: 6703-6714.

Korkama-Rajala, T., Müller, M. & Pennanen, T. 2008. Decomposition and fungi of needle litter from slow- and fast-growing Norway spruce (*Picea abies*) clones. Microbial Ecology 56: 76-89.

Kraigher, B., Stres, B., Hacin, J., Ausec, L., Mahne, I., van Elsas, J. & Mandic-Mulec, I. 2006. Microbial activity and community structure in two drained fen soils in the Ljubljana Marsh. Soil Biology & Biochemistry 38: 2762-2771.

Kroppenstedt, R.M. 1985. Fatty acid and menaquinone analysis of actinomycetes and related organisms. In: Goodfellow, M. & Minnikin, D.E. (eds.). Chemical methods in bacterial systematics. Academic Press, London. p. 173-199.

Krumholz, L.R., Hollenback, J.L., Roskes, S.J. & Ringelberg, D.B. 1995. Methanogenesis and methanotrophy within a *Sphagnum* peatland. FEMS Microbiology Ecology 18: 215-224.

Kulichevskaya, I.S., Belova, S.E., Kevbrin, V.V., Dedysh, S.N. & Zavarin, G.A. 2007. Analysis of the bacterial community developing in the course of *Sphagnum* moss decomposition. Microbiology 76: 621-629.

Laiho, R. 2006. Decomposition in peatlands: reconciling seemingly contrasting results on the impacts of lowered water levels. Soil Biology & Biochemistry 38: 2011-2024.

—, Laine, J., Trettin, C.C. & Finér, L. 2004. Scots pine litter decomposition along soil moisture and nutrient gradients in peatland forests, and the effects of inter-annual weather variation. Soil Biology & Biochemistry 36: 1095-1109.

—, Vasander, H., Penttilä, T. & Laine, J. 2003. Dynamics of plant mediated organic matter and nutrient cycling following water level drawdown in boreal peatlands. Global Biogeochemical Cycles 17: 1053, doi: 10.1029/2002GB002015.

Laine, J. & Vasander, H. 2005. Suotyypit ja niiden tunnistaminen. Helsinki, Finland, Kustannusosakeyhtiö Metsälehti. 110 p.

—, Komulainen, V.-M., Laiho, R., Minkkinen, K., Rasinmäki, A., Sallantaus, T., Sarkkola, S., Silvan, N., Tolonen, K., Tuittila, E.-S., Vasander, H. & Päivänen, J. 2004. Lakkasuo – a guide to mire ecosystem. University of Helsinki Department of Forest Ecology Publications 31: 1-123.

—, Vasander, H. & Laiho, R. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. Journal of Applied Ecology, 32: 785-802.

Larkin, M.J., Kulakov, L.A. & Allen, C.C.R. 2005. Biodegradation and *Rhodococcus* - masters of catabolic versatility. Current Opinion in Biotechnology 16: 282-290.

Larmola, T., Tuittila, E.-T., Tiirola, M., Nykänen, N., Martikainen, P.J., Yrjälä, K., Tuomivirta, T. & Fritze, H. 2010. The role of *Sphagnum* mosses in the methane cycling of a boreal mire. Ecology doi: 10.1890/09-1343.

Lassey, K.R., Lowe, D.C. & Manning, M.R. 2000. The trend in atmospheric ^{13}C and implications for isotopic constrains on the global methane budget. Global Biogeochemical Cycles 14: 41-49.

Latter, P.M., Cragg, J.B. & Heal, O.W. 1967. Comparative studies on the microbiology of moorland soils in the northern Pennines. Journal of Ecology 55: 445-464.

Lepš, J. & Šmilauer, P. 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge,UK. 269 p.

Lesaulnier, C., Papamichail, D., McCorkle, S., Ollivier, B., Skiena, S., Taghavi, S., Zak, D. & van der Lelie, D. 2008. Elevated atmospheric CO_2 affects soil microbial diversity associated with trembling aspen. Environmental Microbiology 10: 926-941.

Lieffers, V.J. 1988. *Sphagnum* and cellulose decomposition in drained and natural areas of an Alberta peatland. Canadian Journal of Soil Science. 68: 755-761.

Lindahl, B. & Boberg, J. 2008. Distribution and function of litter basidiomycetes in coniferous forest. In: Boddy, L., Frankland, J.C. & van West, P. (eds.). Ecology of Saprotrophic Basidiomycetes. British Mycological Society Symposia Series. Academic press/Elsevier, Amsterdam/Boston. p. 183-196.

Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Högberg, P., Stenlid, J. & Findlay, R.D. 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytologist 173: 611-620.

Lodge, D.J. 1989. The influence of soil moisture and flooding on formation of VA-endo- and ectomycorrhizae in *Populus* and *Salix*. Plant & Soil 117: 243-253.

Ludwig, W., Strunk, O., Westram, R., Richter, L., Meier, H., Yadhukumar, Buchner, A., Lai, T., Steppi, S., Jobb, G., Förster, W., Brettske, I., Gerber, S., Ginhart, A.W., Gross, O., Grumann, S., Hermann, S., Jost, R., König, A., Liss, T., Lüßmann, R., May, M., Nonhoff, B., Reichel, B., Strehlow, R., Stamatakis, A., Stuckmann, N., Vilbig, A., Lenke, M., Ludwig,

T., Bode, A. & Schleifer, K.-H., 2004. ARB: a software environment for sequence data. Nucleic Acids Research 32: 1363-1371.

Lynch, M.D.J. & Thorn, R.G. 2006. Diversity of basidiomycetes in Michigan agricultural soils. Applied & Environmental Microbiology 72: 7050-7056.

Mäkiranta, R., Laiho, R., Fritze, H., Hytönen, J., Laine, J. & Minkkinen, K. 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. Soil biology & Biochemistry 41: 695-703.

Malmer, N., Horton, D.G. & Vitt, D. 1992. Element concentration in mosses and surface waters of western Canadian mires in relation to precipitation chemistry and hydrology. Ecography 15: 114-128.

Malmivaara-Lämsä, M., Hamberg, L., Haapamäki, E., Liski, J., Kotze, D.J., Lehvävirta, S & Fritze, H. 2008. Edge effects and trampling in boreal urban forest fragments – impacts on the soil microbial community. Soil Biology & Biochemistry 40: 1612-1621.

Männistö, M.K. & Häggblom, M.M. 2006. Characterization of psychrotolerant heterotrophic bacteria from Finnish Lapland. Systematic & Applied Microbiology 29: 229-243.

—, Tiirola, M. & Häggblom, M.M. 2007. Bacterial communities in Arctic fjelds of Finnish Lapland are stable but highly pH-dependent. FEMS Microbiology Ecology 59: 452-465.

McDonald, I.R., Hall, G.H., Pickup, R.W. & Murrell, J.C. 1996. Methane oxidation potential and preliminary analysis of methanotrophs in blanket bog peat using molecular ecology techniques. FEMS Microbiology Ecology 21: 197-211.

—, Miguez, C.B., Rogge, G., Bourque, D., Wendlandt, K.D., Groleau, D. & Murrell, J.C. 2006. Diversity of soluble methane monooxygenase-containing methanotrophs isolated from polluted environments. FEMS Microbiology Letters 255: 225-232.

—, Upton, M., Hall, G., Pickup, R.W., Edwards, C., Saunders, J.R. & Ritchie, D.A. 1999. Molecular ecological analysis of methanogens and methanotrophs in blanket bog peat. Microbial Ecology 38: 225-233.

McCarthy, A.J. 1987 Lignocellulose-degrading actinomycetes. FEMS Microbiological Reviews 46: 145-163.

Miller, A.N. & Huhndorf, S.M. 2004. Using phylogenetic species recognition to delimit species boundaries within *Lasiosphaeria*. Mycologia 96: 1106-1127.

Minkkinen, K., Korhonen, R., Savolainen, I. & Laine, J. 2002. Carbon balance and radiative forcing of Finnish peatlands in 1900–2100: impacts of drainage for forestry. Global Change Biology 8: 785-799.

—, Vasander, H., Jauhiainen, S., Karsisto, M. & Laine, J. 1999. Post-drainage changes in vegetation and carbon balance in Lakkasuo mire, Central Finland. Plant & Soil 207: 107-120.

Mitchell, E.A.D., Gilbert, D. Buttler, A. Amblard, C., Grosvenier, P. & Gobat, J.-M. 2003. Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. Microbial Ecology 46: 187-199.

Moore, T. & Dalva, M. 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. Journal of Soil Science 44: 651-664.

— & Dalva, M. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil Biology & Biochemistry 29: 1157-1164.

— & Knowles, R. 1989. The influence of water tables on methane and carbon dioxide emissions from peatland soils. Canadian Journal of Soil Science 69: 33-38.

Morales, S.E., Moluser, P.J., Ward, N., Hudman, S.P., Gotelli, N.J., Ross, D.S. & Lewis, T.A. 2006. Comparison of bacterial communities in New England *Sphagnum* bogs using

terminal restriction fragment length polymorphism (T-RFLP) Microbial Ecology 52: 34-44.

Morgenstern, I., Klopman, S. & Hibbett, D.S. 2008. Molecular evolution and diversity of lignin degrading heme peroxidases in the Agaricomycetes. Journal of Molecular Evolution 66: 243-257.

Morris, S.A., Radajewski, S., Willison, T.W., Murrell, J.C. 2002. Identification of the functionally active methanotroph population in a peat soil microcosm by stable-isotope probing. Applied & Environmental Microbiology 68: 1446-1453.

Murrell, J.C., Gilbert, B. & McDonald, I.R. 2000. Molecular biology and regulation of methane monooxygenase. Archives of Microbiology 173: 325-332.

Müller, M., Valjakka, R., Suokko, A. & Hantula, J. 2001. Diversity of endophytic fungi of single Norway spruce needles and their role as pioneer decomposers. Molecular Ecology 10: 1801-1810.

Nickel, A.M. 2000. Population dynamics of *Frankia* in soils. Chapter 5: Saprophytic growth of *Frankia*. Doctoral Dissertation. Swiss Federal Institute of Technology Zurich. p. 129-147.

Nilsson, M., & Rülcker, C. 1992. Seasonal variation of active fungal mycelium in an oligotrophic Sphagnum mire, northern Sweden. Soil Biology & Biochemistry 24: 795-804.

—, Bååth, E. & Söderström, B. 1992. The microfungal communities of a mixed mire in northern Sweden. Canadian Journal of Botany 70: 272-276.

Nykänen, H., Alm, J., Silvola, J., Tolonen, K. & Martikainen, P.J. 1998. Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochemical Cycles 12: 53-69.

Økland, R.H., Økland, T. & Rydgren, K. 2001. A Scandinavian perspective on ecological gradients in north-west European mires: reply to Wheeler and Proctor. Journal of Ecology 89: 481-486.

Osono, T. 2003. Effects of prior decomposition of beech litter by phyllosphere fungi on substrate utilization by fungal decomposers. Mycoscience 44: 41-45.

—, Hirose, D. & Fujimaki, R. 2006. Fungal colonization as affected by litter depth and decomposition stage of needle litter. Soil Biology & Biochemistry 38: 2743–2752.

Paarlahti, K. & Vartiovaara, U. 1958. Havaintoja luonnontilaisten ja metsäojitettujen soiden pieneliöstöstä. Summary in English: Observations concerning the microbial populations in virgin and drained bogs. Communicationes Instituti Forestalis Fenniae 50. 38 p.

Päivänen, J. & Vasander, H. 1994. Carbon balance in mire ecosystems. World Resource Review 6: 102-111.

Pankratov, T.A., Dedysh, S.N. & Zavarzin, G.A. 2006. The leading role of actinobacteria in aerobic cellulose degradation in *Sphagnum* peat bogs. Doklady Biological Sciences 410: 428-430.

Pennanen, T., Caul, S., Daniell, T.J., Griffiths, B.S., Ritz, K. & Wheatley, R.E. 2004. Community-level responses of metabolically-active soil microorganisms to the quantity and quality of substrate inputs. Soil Biology & Biochemistry 36: 841-848.

—, Liski, J., Bååth, E., Kitunen, V., Uotila, J., Westman, C.J. & Fritze, H. 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. Microbial Ecology 38: 168-179.

—, Paavolainen, L. & Hantula, J. 2001. Rapid PCR-based method for the direct analysis of fungal communities in complex environmental samples. Soil Biology & Biochemistry 33: 697-699.

Piercey, M.M., Thormann, M.N. & Currah, R.S. 2002. Saprobic characteristics of three fungal taxa from ericalean roots and their association with the roots of *Rhododendron groenlandicum* and *Picea mariana* in culture. Mycorrhiza 12: 175-180.

Pind, A., Freeman, C. & Lock, M.A. 1994. Enzymic degradation of phenolics materials in peatlands—measurement of phenol oxidase activity. Plant & Soil 159: 227-231.

Pol, A., Heijmans, K., Harhangi, H.R., Tedesco, D., Jetten, M.S.M. & Op den Camp, H.J.M. 2007. Methanotrophy below pH 1 by a new Verrucomicrobia species. Nature 450: 874-878.

Popp, T.J., Chanton, J.P., Whiting, G.J. & Grant, N. 2000. Evaluation of methane oxidation in the rhizosphere of a *Carex* dominated fen in north central Alberta. Biogeochemistry 51: 259-281.

Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., Rijpstra, W.I.C., Wolters-Arts, M., Derksen, J., Jetten, M.S.M.., Schouten, S., Sinninghe Damsté, J.S., Lamers, L.P.M., Roelofs, J.G.M., Op den Camp, H.J.M. & Strous, M. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436: 1153-1156.

Ramette, A. 2007. Multivariate analyses in microbial ecology. FEMS Microbiology Ecology 62: 142-160.

Rasbash, J., Browne, W., Goldstein, H., Yang, M., Plewis, I., Healy, M.,Woodhouse, G., Draper, D., Langford, I. & Lewis, T. 2000. A user's guide to MlwiN. Version 2.1c. Centre for Multilevel Modelling, Institute of Education, University of London. 256 p.

Read, D.J. & Perez-Moreno, J. 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance. New Phytologist 157: 475-492.

—, Leake, J.R. & Perez-Moreno, J. 2004. Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Canadian Journal of Botany 82: 1243-1263.

Rheims, H., Felske, A., Seufert, S. & Stackebrandt, E. 1999. Molecular monitoring of an uncultured group of the class Actinobacteria in two terrestrial environments. Journal of Microbiological Methods 36: 65-75.

— , Spröer, C., Rainey, F.A. & Stackebrandt, E. 1996. Molecular biological evidence for the occurrence of uncultured members of the actinomycete line of descent in different environments and geographical locations. Microbiology 142: 2863-2870.

Roulet, N., Moore, T., Bubier, J. & Lafleur, P. 1992. Northern fens: methane flux and climatic change. Tellus 44B: 100-105.

Ruggiero, P. & Radogna, V.M. 1984. Properties of laccase in humus-enzyme complexes. Soil Science 138: 74-87.

Rydin, H. & Jeglum, J. 2006. The biology of peatlands. The biology of habitats series. Oxford University Press, UK. 343 p.

Saarinen, T. 1996. Biomass and production of two vascular plants in a borealmesotrophic fen. Canadian Journal of Botany 74: 934-938.

Safo-Sampah, S. & Torrey, J.G. 1988. Polysaccharide-hydrolyzing enzymes of *Frankia* (Actinomycetales). Plant & Soil 112: 89-97.

Sallantaus, T. 1992. Leaching in the material balance of peatlands - preliminary results. Suo 43: 253-358.

— & Kaipainen, H. 1996. Water-carried elements balances of peatlands. In: Laiho, R., Laine, J. and Vasander, H. (eds.). Northern peatlands in global climatic change. Publications of the Academy of Finland. Edita, Helsinki. p. 197-203

Salminen, J., Hernesmaa, A., Karjalainen, H., Fritze, H. & Romantschuk, M. 2010. Activity of nematodes and enchytraeids, bacterial community composition, and functional redundancy in coniferous forest soil. Biology & Fertility of Soils 46: 113-126.

Salo, K. 1993. The composition and structure of macrofungus communities in boreal upland type forests and peatlands in North Karelia, Finland. Karstenia. 33: 61-99.

Salonen, V. & Saari, V. 1990. Generic composition of macrofungus communities on virgin mire site types in Central Finland. Annales Botanici Fennici 27: 33-38.

Scheffer, R.A., van Logtestijn, R.S.P. & Verhoeven, J.T.A. 2001. Decomposition of *Carex* and *Sphagnum* litter in two mesotrophic fens differing in dominant plant species. Oikos 92: 44-54.

Schrempf, H. 2001. Recognition and degradation of chitin by streptomycetes. Antonie van Leeuwenhoek 79: 285-289.

Shannon, C.E. & Weaver, W. 1963. The mathematical theory of communication. University of Illinois Press, Urbana, IL. 117 p.

Shephard, S.K., Beckmann, M. & Lloyd, D. 2007. The effect of temperature on methane dynamics in soil and peat cores: calculations from membrane inlet mass spectrometry. Canadian Journal of Soil Science 87: 11-22.

Silvola, J. 1986. Carbon dioxide dynamics in mires reclaimed for forestry in eastern Finland. Annales Botanici Fennici 23: 59-67.

— , Alm, J., Ahlholm, U., Nykänen, H. and Martikainen, P.J. 1996. CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. Journal of Ecology, 84: 219-228.

Smolander, A. & Sundman, V. 1987. *Frankia* in acid soils of forests devoid of actinorhizal plants. Physiology of Plant 70: 297–303.

Smolander, A., Van Dijk, C. & Sundman, V. 1988. Survival of *Frankia* strains introduced into soil. Plant & Soil 106: 65–72.

Stach, J.E.M., Maldonado, L.A., Ward, A.C., Goodfellow, M. & Bull, A.T. 2003. New primers for the class *Actinobacteria*: application to marine and terrestrial environments. Environmental Microbiology 5: 828-841.

Strack, M., Waddington, J.M, Bourbonniere, R.A., Buckton, E.L., Shaw, K., Whittington, P. & Price, J.S. 2008. Effect of water table drawdown on peatland dissolved organic carbon export and dynamics, Hydrological Processes 22: 3373-3385.

Sundh, I., Borgå, P., Nilsson, M. & Svensson, B.H. 1995. Estimation of cell numbers of methanotrophic bacteria in boreal peatlands based on analysis of specific phospholipid fatty acids. FEMS Microbiology Ecology 18: 103-112.

—, Nilsson, M. & Borgå, P. 1997. Variation in microbial community structure in two boreal peatlands as determined by analysis of phospholipid fatty acid profiles. Applied & Environmental Microbiology, 63: 1476-1482.

—, Nilsson, M., Granberg, G. & Svensson, B.H. 1994. Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. Microbial Ecology 27: 253-265.

Thormann, M.N., 2006a. Diversity and function of fungi in peatlands: a carbon cycling perspective. Canadian Journal of Microbiology 86: 281-293.

—, 2006b. The role of fungi in boreal peatlands. In: Wieder, R.F & Vitt, D.H. (eds.). Ecological Studies. Boreal Peatland Ecosystems. Vol. 88. Springer-Verlag, Berlin, Germany. p. 101-123.

—, Currah, R.S. & Bayley, S.E. 1999. The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta, Canada. Wetlands 19: 438-450.

—, Currah, R.S. & Bayley, S.E. 2001. Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. Bryologist 104: 548-559.

—, Currah, R.S. & Bayley, S.E. 2002. The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. Canadian Journal of Microbiology 48: 204-211.
—, Currah, R.S. & Bayley, S.E. 2003. Succession of microfungal assemblages in decomposing peatland plants. Plant & Soil 250: 323-333.
—, Currah, R.S. & Bayley, S.E. 2004a. Microcosm tests of the effects of temperature and micorbial species number on the decomposition of *Carex aquatilis* and *Sphagnum fuscum* litter from southern boreal peatlands. Canadian Journal of Microbiology 50: 793-802.
—, Currah, R.S. & Bayley, S.E. 2004b. Patterns of distribution of microfungi in decomposing bog and fen plants. Canadian Journal of Botany 82: 710-720.
—, Rice, A.V. & Beilman, D.W. 2007. Yeasts in peatlands: A review of richness and roles in peat decomposition. Wetlands 27: 761-773.
Toberman, H., Evans, C., Freeman, S., Fenner, N., White, M., Emmett, B.A. & Artz, R.R.E. 2008. Summer drought effects upon soil and litter extracellular phenol oxidase activity and soluble carbon release in an upland *Calluna* heathland. Soil Biology & Biochemistry 40: 1519-1532.
Torkko, P., Suomalainen, S., Iivanainen, E., Suutari, M., Tortoli, E., Paulin, L. & Katila, M.L. 2000. *Mycobacterium xenopi* and related organisms isolated from stream waters in Finland and description of *Mycobacterium botniense* sp. nov. Internation Journal of Systematic and Evolutionary Microbiology 50: 283-289.
Tortoli, E. 2003. Impact of genotypic studies on mycobacterial taxonomy: the new Mycobacteria of the 1990s. Clinical Microbiological Reviews 16: 319-354.
Trinder, C.J., Johnson, D. & Artz, R.R.E. 2008. Interactions between fungal community structure, litter decomposition and depth of water-table in a cutover peatland. FEMS Microbiology Ecology 64: 433-448.
Tuomivirta, T., Yrjälä, K. & Fritze, H. 2009. Quantitative PCR of *pmoA* using a novel reverse primer with potential methane oxidation in Finnish fen. Research in Microbiology 160: 751-756.
Turenne, C.Y., Tschetter, L., Wolfe, J. & Kabani, A. 2001. Necessity of Quality-Controlled 16S rRNA Gene Sequence Databases: Identifying Nontuberculous *Mycobacterium* Species. Journal of Clinical Microbiology. 39: 3637-3648.
Turner, S.D., Amon, J.P., Schneble, R.M. & Friese, C.F. 2000. Mycorrhizal fungi associated with plants in ground-water fed wetlands. Wetlands 20: 200-204.
Urban, N.R., Bayley, S.E. & Eisenreich, S.J. 1989. Export of dissolved organic carbon and acidity from peatlands. Water Resources Research 25: 1619-1628.
Vainio, E.J. & Hantula, J. 2000. Direct analysis of wood-inhabiting fungi using denaturing gradient gel electrophoresis of amplified ribosomal DNA. Mycological Research 104: 927-936.
Valášková, V., Šnajdra, J., Bittner, B., Cajthaml, T., Merhautová, V., Hofrichter, M. & Baldrian, P. 2007. Production of lignocellulose-degrading enzymes and degradation of leaf litter by saprotrophic basidiomycetes isolated from a *Quercus petraea* forest. Soil Biology & Biochemistry 39: 2651-2660.
van der Geize, R. & Dijkhuizen, L., 2004. Harnessing the catabolic diversity of rhodococci for environmental and biotechnological applications. Microbiology 7: 255-261.
Vasander, H., Laiho, R. & Laine, J. 1997. Changes in species diversity in peatlands drained for forestry. In: Trettin, C.C., Jurgensen, M.F., Grigal, D.F., Gale, M.R. & Jeglum, J.K. (eds.). Northern Forested Wetlands: Ecology and Management. CRC Press, Lewis Publishers, Boca Raton, Fla, USA. p. 109-119.

Vuorenmaa, A. 2005 Pohjaveden pinnanlaskun vaikutus suon mikrobiyhteisöjen aktiivisuuteen ja rakenteeseen. Master's Thesis. The Department of Biological and Environmental Science. University of Jyväskylä. 77 p.

Wang, Z. 2006. Evolution of helotialean fungi (Leotiomycetes, Pezizomycotina): A nuclear rDNA phylogeny. Molecular Phylogenetics & Evolution 41: 295-312.

Wang, Q, Garrity, G.M, Tiedje, J.M. & Cole, J.R. 2007. Naïve Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Applied & Environmental Microbiology 73: 5261-7.

Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J. & Harth, C. 2003. Potential effects of warming and drying on peatland plant community composition. Global Change Biology 9: 141-151.

—, Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K. & Chapin, C.T. 2000. Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81: 3464-3478.

Wheatley, R.E., Greaves, M.P. & Inkson, R.H.E., 1996. The aerobic bacterial flora of a raised bog. Soil Biology & Biochemistry. 8: 453-460.

Wheeler, B.D. & Proctor, M.C.F. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. Journal of Ecology 88: 187-203.

White, T.J., Bruns, T., Lee, S. &Taylor, J. 1990. Analysis of phylogenetic relationships by amplification and direct sequencing of ribosomal RNA genes. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.). PCR Protocols: A Guide to Methods and Applications. Academic Press, New York, USA. p. 315-322.

White, J.R., Shannon, R.D., Weltzin, J.F. & Pastor, J. 2008. Effects of soil warming and drying on methane cycling in a northern peatland mesocosm study. Journal of Geophysical Research. 113: G00A06, doi:10.1029/2007JG000609.

Wilkinson, S.G. 1988. Gram-negative bacteria. In: Ratledge C. & Wilkinson S.G. (eds.). Microbial lipids, vol. 1. Academic press, London. p. 299-488.

Williams, R.T. & Crawford, R.L. 1983. Microbial diversity of Minnesota peatlands. Microbial Ecology 9: 201-214.

Wise, M.G., McArthur, J.V. & Shimkets, L.J. 1999. Methanotroph diversity in landfill soil: isolation of novel type I and type II methanotrophs whose presence was suggested by culture-independent 16S ribosomal DNA analysis. Applied & Environmental Microbiology 65: 4887-4897.

Woese, C.R., 1987. Bacterial evolution. Microbiological Reviews 51: 221-271.

—, 1998. Default taxonomy: Ernst Mayr's view of the microbial world. Proceedings of the National Academy of Science 95: 11043-11046.

Wolfe, D., Mummey, D.L., Rillig, M.C. & Klironomos, J.N., 2007. Small-scale spatial heterogeneity of arbuscular mycorrhizal fungal abundace and community composition in a wetland plant community. Mycorrhiza 17: 175-183.

Yavit, J.B. & Lang, G.E. 1987. Aerobic methane oxidation in the surface peat from a mass-dominated wetland in West Virginia. Abstr Reports, 193rd ACS National Meeting, Symposium on Atmospheric Methane, Denver, CO, April 5–10, 1987.

Appendix A. The best known representatives for actinobacterial sequences from papers I, IV and V according to Ribosomal Database Project (RDP) classifier. Numbers after the taxa are confidence values (%). Hierarchy is based on a naïve Bayesian rRNA classifier (Wang et al. 2007)

Paper	GeneBank Accession	Sequence	Suborder	Family	Genus	Classification
II	EU527074	rj1A-B3	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	EU527072	rj1A-B5	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	EU527067	rj1A-A3	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	EU527057	rj1A-A2	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	EU527062	rj1A-A16	Corynebacterineae	Nocardiaceae	Rhodococcus	
	EU527069	rj1A-B22	Streptosporangineae 84	Thermonosporaceae 84	Actinoallomurus 63	unclassified Thermomonosporaceae
	EU527066	rj1A-B15	Streptosporangineae 84	Thermonosporaceae	Actinoallomurus 46	unclassified Actinomycetales
	EU527056	rj1A-B18	Streptosporangineae 88	Thermonosporaceae 87	Actinoallomurus 66	unclassified Thermomonosporaceae
	EU527058	rj1A-B23	Streptosporangineae 74	Thermonosporaceae 65	Thermomonospora 37	unclassified Actinomycetales
	EU527054	rj1A-B26	Streptosporangineae 97	Thermonosporaceae 88	Thermomonospora 31	unclassified Thermomonosporaceae
	EU527053	rj1A-B25	Streptosporangineae 94	Thermonosporaceae 90	Thermomonospora 39	unclassified Thermomonosporaceae
	EU527052	rj1A-B24	Streptosporangineae 75	Thermonosporaceae 63	Thermomonospora 39	unclassified Actinomycetales
	EU527068	rj1A-B17	Frankineae 80	Acidothermaceae 67	Acidothermus 67	unclassified Actinomycetales
	EU527071	rj1A-A21	“Acidimicrobineae”	Iamiaceae 86	Iamia 86	
	EU527070	rj1A-A20	“Acidimicrobineae”	Iamiaceae 91	Iamia 91	
	EU527065	rj1A-B16	“Acidimicrobineae”	Iamiaceae 98	Iamia 98	
	EU527064	rj1A-A18	“Acidimicrobineae”	Iamiaceae 94	Iamia 94	
	EU527063	rj1A-B12	“Acidimicrobineae” 82	Iamiaceae 41	Iamia 41	unclassified “Acidimicrobineae”
	EU527073	rj1A-B9	“Acidimicrobineae” 99	Acidimicrobiaceae 77	Ferrimicrobium 43	unclassified “Acidimicrobineae”
	EU527061	rj1A-A13	“Acidimicrobineae” 87	Acidimicrobiaceae 73	Ferrimicrobium 44	unclassified “Acidimicrobineae”
	EU527060	rj1A-A9	“Acidimicrobineae” 74	Acidimicrobiaceae 53	Ferrimicrobium 32	unclassified Acidimicrobidae
	EU527055	rj1A-A7	“Acidimicrobineae” 73	Acidimicrobiaceae 62	Ferrimicrobium 35	unclassified Actinobacteria
	EU527051	rj1A-B14	“Acidimicrobineae” 92	Acidimicrobiaceae 55	Ferrimicrobium 37	unclassified “Acidimicrobineae”
	EU527059	rj1A-A8	Micrococcineae	Intrasporangiaceae	Knoellia 75	unclassified Intrasporangiaceae
IV	EF570496	SnsA-d	Corynebacterineae	Mycobacteriaceae 98	Mycobacterium 98	
	EF570493	SnsA-b	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	EF570492	SnsA-m	Streptosporangineae 64	Thermomonosporaceae 64	Actinoallomurus 35	unclassified Actinomycetales

Paper	GeneBank Accession	Sequence	Suborder	Family	Genus	Classification
	EF570490	SnsA-n1	Streptosporangineae 83	Thermomonosporaceae 83	Actinoallomurus 61	unclassified Thermomonosporaceae
	EF570489	SnsA-p	Streptosporangineae 99	Thermomonosporaceae 99	Actinoallomurus 92	
	EF570488	SnsA-j	Streptosporangineae 84	Thermomonosporaceae 80	Actinoallomurus 65	unclassified Thermomonosporaceae
	EF570487	SnsA-q	Streptosporangineae 95	Thermomonosporaceae 95	Actinoallomurus 85	unclassified Thermomonosporaceae
	EF570486	SnsA-o	Streptosporangineae 91	Thermomonosporaceae 91	Actinoallomurus 81	unclassified Thermomonosporaceae
	EF570491	SnsA-h1	Streptosporangineae 84	Thermomonosporaceae 70	Spirillospora 25	unclassified Streptosporangineae
	EF570498	SnsA-t	Streptosporangineae 96	Thermomonosporaceae 94	Actinocorallia 86	
	EF570495	SnsA-l	Frankinae 79	Acidothermaceae 72	Acidothermus 72	unclassified Frankinae
	EF570494	SnsA-j1	Frankinae 81	Acidothermaceae 72	Acidothermus 72	unclassified Frankinae
	EF570497	SnsA-i	“Acidimicrobineae” 76	Iamiaceae 39	Iamia 39	unclassified “Acidimicrobineae”
	EF570485	SnsA-f1	“Acidimicrobineae” 91	Iamiaceae 75	Iamia 75	unclassified “Acidimicrobineae”
V	GU557022	pta1A-38	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	GU557043	pta2A-43	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	GU557048	pta12A-14	Corynebacterineae	Mycobacteriaceae	Mycobacterium	
	GU557038	pta2A-28	Streptosporangineae 80	Thermonosporaceae 80	Actinoallomurus 61	unclassified Actinomycetales
	GU557039	pta2A-29	Streptosporangineae 89	Thermonosporaceae 89	Actinoallomurus 66	unclassified Thermomonosporaceae
	GU557045	pta2A-50	Streptosporangineae 86	Thermonosporaceae 84	Actinoallomurus 62	unclassified Thermomonosporaceae
	GU557019	pta1A-17	Streptosporangineae 77	Thermonosporaceae 75	Spirillospora 48	unclassified Thermomonosporaceae
	GU557044	pta2A-48	Streptosporangineae 90	Thermonosporaceae 81	Spirillospora 34	unclassified Thermomonosporaceae
	GU557017	pta1A-9	Streptosporangineae 95	Thermonosporaceae 89	Thermomonospora 47	unclassified Thermomonosporaceae
	GU557051	pta12A-29	Streptosporangineae 72	Thermonosporaceae 66	Thermomonospora 28	
	GU557021	pta1A-33	Frankineae 81	Acidothermaceae 67	Acidothermus 67	unclassified Frankinae
	GU557015	pta1A-7	Frankineae 44	Geodermatophilaceae 33	Blastococcus 33	unclassified Actinomycetales
	GU557023	pta1A-47	Frankineae 60	Geodermatophilaceae 49	Blastococcus 47	unclassified Actinomycetales
	GU557035	pta2A-10	Frankineae 56	Geodermatophilaceae 40	Blastococcus 14	unclassified Actinomycetales
	GU557040	pta2A-31	Frankineae 36	Geodermatophilaceae 25	Blastococcus 20	unclassified Actinomycetales
	GU557031	pta1A-67	Frankineae 82	Geodermatophilaceae 59	Blastococcus 54	unclassified Frankinae
	GU557030	pta1A-66	Frankineae 38	Sporichthyaceae 33	Sporichthya 33	unclassified Actinomycetales
	GU557018	pta1A-12	“Acidimicrobineae” 99	Iamiaceae 44	Iamia 44	unclassified “Acidimicrobineae”
	GU557020	pta1A-23	“Acidimicrobineae” 89	Iamiaceae 66	Iamia 66	unclassified “Acidimicrobineae”

Paper	GeneBank Accession	Sequence	Suborder	Family	Genus	Classification
V	GU557034	pta2A-5	“Acidimicrobineae”	Iamiaceae 41	Iamia 41	unclassified “Acidimicrobineae”
	GU557037	pta2A-27	“Acidimicrobineae” 99	Iamiaceae 81	Iamia 81	
	GU557047	pta2A-55	“Acidimicrobineae” 97	Iamiaceae 74	Iamia 74	unclassified “Acidimicrobineae”
	GU557049	pta12A-15	“Acidimicrobineae” 81	Iamiaceae 39	Iamia 39	unclassified “Acidimicrobineae”
	GU557032	pta1A-70	“Acidimicrobineae” 96	Acidimicrobiaceae 87	Ferrimicrobium 45	unclassified “Acidimicrobineae”
	GU557033	pta2A-4	“Acidimicrobineae”	Acidimicrobiaceae 63	Ferrimicrobium 41	unclassified “Acidimicrobineae”
	GU557036	pta2A-19	“Acidimicrobineae” 91	Acidimicrobiaceae 78	Ferrithrix 51	unclassified “Acidimicrobineae”
	GU557014	pta1A-5	Micromonosporineae 61	Micromonosporaceae 61	Pilimelia 33	unclassified Actinomycetales
	GU557016	pta1A-8	Micromonosporineae 46	Micromonosporaceae 61	Pilimelia 33	unclassified Actinomycetales
	GU557024	pta1A-50	Micromonosporineae 47	Micromonosporaceae 47	Pilimelia 38	unclassified Actinomycetales
	GU557025	pta1A-53	Micromonosporineae 76	Micromonosporaceae 76	Pilimelia 53	unclassified Actinomycetales
	GU557026	pta1A-58	Micromonosporineae 67	Micromonosporaceae 67	Pilimelia 43	unclassified Actinomycetales
	GU557027	pta1A-59	Micromonosporineae 61	Micromonosporaceae 61	Pilimelia 42	unclassified Actinomycetales
	GU557029	pta1A-63	Micromonosporineae 60	Micromonosporaceae 60	Pilimelia 38	unclassified Actinomycetales
	GU557041	pta2A-34	Micromonosporineae 68	Micromonosporaceae 68	Pilimelia 43	unclassified Actinomycetales
	GU557042	pta2A-36	Micromonosporineae 49	Micromonosporaceae 49	Pilimelia 39	unclassified Actinomycetales
	GU557053	pta12A-51	Micromonosporineae 54	Micromonosporaceae 54	Pilimelia 38	
	GU557046	pta2A-52	Micromonosporineae	Micromonosporaceae	Actinoplanes 84	
	GU557054	pta12A-57	Micromonosporineae 50	Micromonosporaceae 50	Asanoa 21	
	GU557013	pta1A-1	Pseudonoocardineae 70	Pseudonoocardiaceae 33	Crossiella 26	unclassified Actinomycetales
	GU557050	pta12A-28	Pseudonoocardineae 46	Pseudonoocardiaceae 45	Crossiella 41	unclassified Actinomycetales
	GU557052	pta12A-32	Pseudonoocardineae 29	Pseudonoocardiaceae 20	Crossiella 17	unclassified Actinomycetales
	GU557028	pta1A-60	Kineosporiineae 28	Kineosporiaceae 28	Kineococcus 27	unclassified Actinomycetales