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NOORA RÄSÄNEN

MICROBIAL ACTIVITY IN RUNOFF WATERS OF RESTORED BOREAL MIRES

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ABSTRACT

Boreal peatlands are widely drained for agricultural, forestry or peat mining purposes. Draining for forestry in Finland during the 1960s and 1970s has shrunk the original mire area by ca. half. Some of these drainings were unsuccessful in improving tree growth and the area of some natural mire types shrank. Since the 1990s the restoration of drained peatlands has been implemented. In the boreal zone, the impact of restoration on runoff from forestry drained mires have been measured mainly in terms of nutrient (nitrogen (N), phosphorus (P) or carbon (C)) load (kg ha^{-1}).

The purpose of my study was to evaluate mire restoration induced changes in the quantity and quality of dissolved organic matter (DOM), and the impact of dissolved organic carbon (DOC), N and P on microbial activity (bacterial production (BP) and respiration (R)) in mire runoff waters. The measurements were done during three years at seven different mire sites, representing two different types of mire (Spruce swamps and *Sphagnum* bogs) located in south-central Finland. Four of the forestry-drained mires were restored during the study, one remained drained and two were natural reference sites.

The concentrations of DOC, N and P, especially in the runoff waters from a nutrient- rich spruce swamp and *Sphagnum* bogs, were raised after restoration. The increase in DOC concentrations lasted one to five years and the N and P elevation in the runoffs lasted for three to five years. The higher N and P concentrations enhanced BP and bacterial growth efficiency after restoration, but not R or the proportion of decomposed DOC per day. Under experimental conditions, elevated pH alone, and with phosphate addition, increased R but did not have an effect on BP. Mixing *Sphagnum* bog runoff water with humic, oligotrophic lake water did not increase microbial activity. The lake water rather diluted the bog runoff waters and, thus, the microbial activity was decreased. The pH of runoff waters did not change and DOC quality was not more utilizable after restoration. The microbial activity, even in the most nutrient rich mire site, was very low compared to other aquatic environments. In recipient headwater lakes the recalcitrant mire-originating DOC may cause browning, and after mire restoration the higher nutrient concentrations may temporarily increase the risk of eutrophication.

Universal Decimal Classification: 551.312.2, 551.438.22, 579.68, 626.871

CAB Thesaurus: wetlands; peatlands; swamps; bogs; drainage; ecological restoration; runoff water; microbial activities; soil bacteria; biomass production; growth; respiration; organic carbon; nitrogen; phosphorus; pH; eutrophication

Yleinen suomalainen asiasanasto: suot; ojitus; ennallistaminen; valumavesi; bakteerit; hiili; typpi; fosfori; pH; rehevöityminen

I dedicate this thesis to the memory of my beloved father. We all miss you.

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The laboratory work of this study was conducted at the Joensuu campus in the Department of Environmental and Biological Sciences; most of the writing I have done at home in Kurjala. I am very thankful to all my supervisors: Jarkko Akkanen, Teemu Tahvanainen, Paula Kankaala and Sanna Saarnio for making the arrangement possible. I know that I have not been the easiest PhD student partly because of the distance between us and also with the prolonged studies. I am very grateful to you all for making my studies possible, and for having the persistence to explain and teach me the issues. Especially Sanna and Paula, thank you for the active work and support during this study.

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Kurjala, 20th October 2017
Noora Räsänen

LIST OF ABBREVIATIONS

BGE	Bacterial growth efficiency
BP	Bacterial production
CH_4	Methane
CO_2	Carbon dioxide
DeDOC	Decayed dissolved organic carbon
DIP	Dissolved inorganic phosphorus
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
DON	Dissolved organic nitrogen
DOP	Dissolved organic phosphorus
N	Nitrogen
NH_4	Ammonium
NO_2-N	Nitrite
NO_3-N	Nitrate
P	Phosphorus
PO_4-P	Phosphate
R	Respiration
$SUVA_{254}$	Specific UV absorbance
TN	Total nitrogen
TOC	Total organic carbon
TP	Total phosphorus
WT	Water table

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman Numerals I-III.

I Räsänen N, Kankaala P, Tahvanainen T, Akkanen J and Saarnio S. (2014). Short-term effects of phosphorus addition and pH rise on bacteria utilization and biodegradation of dissolved organic carbon (DOC) from boreal mires. *Aquatic Ecology*, 48: 435-446.

II Räsänen N, Kankaala P, Tahvanainen T, Akkanen J and Saarnio S. (2016). Effect of mire-originated dissolved organic carbon, nitrogen and phosphorus on microbial activity in boreal headwaters. *Inland Waters*, 6:65-76.

III Räsänen N, Kankaala P, Tahvanainen T, Akkanen J and Saarnio S. (Accepted with minor revision). Changes in dissolved organic matter and microbial activity in runoff waters of boreal mires after restoration. *Aquatic Sciences*

The above publications have been included at the end of this thesis with their copyright holders' permission.

AUTRHOR'S CONTRIBUTION

I) Noora Räsänen did the laboratory analyses, contributed to the data analysis and was mainly responsible for writing the paper. The study was desinged together with the supervisors, Paula Kankaala, Teemu Tahvanainen, Jarkko Akkanen and Sanna Saarnio. The supervisors instructed me on all laboratory methods as well as data analysis, they contributed to the writing of the manuscript and data-analysis.

II) Noora Räsänen did the laboratory analyses, contributed to data analysis and writing the paper. The study was planned together with the supervisors, they participated in the data analysis and writing.

III) The study was designed by the supervisors, Noora Räsänen did the laboratory experiments and data analyses and was mainly responsible for writing the paper. The supervisors of the thesis contributed to the writing and data analysis of their special fields, and designed the statistical analyses (especially time-series and PCA analysis) of the data.

CONTENTS

1 INTRODUCTION

1.1 NATURAL MIRES

Peat forming ecosystems are found all over the world (Ingram 1978). About 6-7% (820 – 1010 Mha) of the land surface area of the Earth (not including Antarctica and glaciated Greenland) is covered by peatlands (Lehner & Döll 2004). Northern peatlands are the biggest reservoir of carbon of all the peatlands in the world; they hold ca. 90% (547 Gt C) of the total peatland carbon (Yu 2011). In Finland, one third of the total land area is covered by peatlands (10.3 Mha, Vasander 1998). The large amount of paludification in Finland is due to cool climatic conditions with a high moisture surplus. Those conditions cause low evapotranspiration, and combined with flat topography and impermeable soil, lead to the formation of water-saturated soils. In water-saturated soils, the rate of litter formation is higher than that of decomposition and leads to peat accumulation. The status of the poor-rich gradient of natural mires depends on the source of water, which also influences water pH and alkalinity (Tahvanainen et al. 2002). In ombrotrophic mires, water mainly originates from precipitation, whereas minerotrophic mires are also in contact with water flowing from mineral soil or with groundwater (Eurola et al. 1984, Bridgham et al. 1998, Lindholm & Heikkilä 2005, Hill et al. 2014). The origin of water affects the vegetation in mires (Sjörs 1952, Vitt et al. 1995). The minerotrophic mires can be classified as oligotrophic, mesotrophic or eutrophic types in accordance with their richness in different plant species (Pakarinen 1995). The wet conditions and nutrient-poor environment is challenging for vegetation and requires specialization (Charman 2002). For example, *Sphagnum* mosses and many sedge species are adapted to those conditions (Gorham 1991, Charman 2002).

1.1.1 Carbon

Peatlands are the largest reservoir of carbon in Finland (Kauppi et al. 1997). The low decomposition rate of plant litter is the main driver of peat formation. The accumulation rate varies between different kinds of peatland; in Finland the long-term rate of carbon accumulation in undrained peatlands is approximately 17-19 g C m^{-2} $year^{-1}$ (Turunen et al. 2002). The carbon is released from mires either in gaseous form (CO_2, CH_4; Nykänen et al. 1998, Saarnio et al. 2007, Koskinen et al. 2016) or via runoff as dissolved organic carbon (DOC; Mattsson et al. 2005). The decomposition rate of organic matter is higher in oxic layers than in the anoxic peat layers (Schlesinger 1997, Rochefort & Lode 2006). This so called diplotelmic structure with two functionally different layers of peat, the oxic acrotelm and the deeper anoxic catotelm, is typical to boreal mires (Ingram 1978, Laitinen et al. 2007). The acrotelm typically has clearly higher hydraulic conductivity and porous structure, while the catotelm peat is denser and has poor hydraulic conductivity (Rochefort & Lode 2006). In recent years a triplotelimic model has also been introduced (Clymo & Bryant 2008) where the mesotelm layer between the acrotelm and catotelm create its own environment where oxic and anoxic conditions are contiguous (McAnallen et al. 2017).

Peat layers have low pH, which is caused by accumulation of organic acids that are the end products of anoxic microbial activity (fermentation). Mosses, shrubs and sedges are the dominant plant groups in mires, and decompose very slowly in anoxic peat layers and the lack of oxygen favors CH_4 production (Fig 1). Certain by-products from incomplete decomposition of mosses effectively inhibit microbial growth due to recalcitrant, and even antimicrobial, characteristics (Verhoeven & Liefvield 1997, Klavina et al. 2015). Low temperatures and lack of nutrients (N,P) further retard the decomposition rate in northern peatlands. Peat organic material can have high aromatic content with phenolic and organic acids (Schlesinger 1997). The portion of DOM and CO_2 as degradation products depends on conditions in soil (Moore & Dalva 2001, Fisk et al. 2003). In peat soils, anoxia favors DOM production and less of the carbon is disengaged in the inorganic form (Moore & Dalva 2001). Aromatic DOM is accumulated in the organic matter and remains in the catotelm. For this same reason, nutrients (N, P) are not available for decomposers and a small amount of the nutrients are reserved in the peat (Schlesinger 1997). This nutrient poor environment limits the microbial activity, most often due to availability of N or P, alongside labile carbon substrates and low pH (Schlesinger 1997, Bååth 1998, Andersson & Nilsson 2001, Ye et al. 2012, Lin et al. 2014, Wyatt & Turetsky 2015).

1.1.2 Nitrogen and phosphorus

In ombrotrophic mires, atmospheric dry and wet deposition are the most significant sources of nitrogen, while in minerotrophic mires the sources are surface water or groundwater (Limpers et al. 2003). The role of biological nitrogen fixation is minor in natural mires and in cool temperatures, the rate of N mineralization is low (MacDonald et al. 1995). Nitrogen has diverse oxidation rates in natural reactions, from 3- (NH_4) to 5+ (NO_3); hence, it has multiple routes between organic and inorganic forms (Kirchman 2012). When organic material is decomposed by microbes, a high proportion of organic nitrogen is bound to poorly bioavailable humic and fulvic acids (Schulten & Schnitzer 1995, Kelley & Stevenson 1995). While the organic nitrogen is released into the soil water, or mineralized as NH_4 (ammonification), most of the ammonium is immobilized back to organic forms by microbes and vegetation, or fixed into soil material (Fig 1; Schlesinger & Bernhardt 2013). Some of the available ammonium is fixed by microbes, which oxidize NH_4 to inorganic nitrogen, such as nitrate (NO_3, nitrification). Nitrate is also easily utilized by vegetation and microbes, but it is easily leached with water. In anoxic conditions, the nitrate (NO_3) is quickly reduced to NO_2, NO, N_2O or N_2 (denitrification), but mires typically have low nitrate concentrations and in acidic conditions the denitrification rate is low (Verry & Timmons 1982, Limpens et al. 2003).

In natural environments, the most important source of P is weathering of apatite rock (Schlesinger 1997). Phosphorus also originates from atmospheric sources, as a dry or wet deposit, similar to nitrogen (Walbridge & Navaratnam 2006). The phosphorus cycle in nature is much simpler than the nitrogen cycle, because P can be incorporated into organic compounds or occur as inorganic phosphate (PO_4-P). The phosphorus in mires is usually bound to the peat profile. The peat may accumulate in mires so that the peat profile raises and is no longer connected to the mineral water; the minerotrophic mire turns to ombrotrophic and so the accumulated peat can be a source of P for microbes and vegetation. P is bound in the humic matter by metals, for example by iron and aluminum. Anoxic conditions in peat, for example

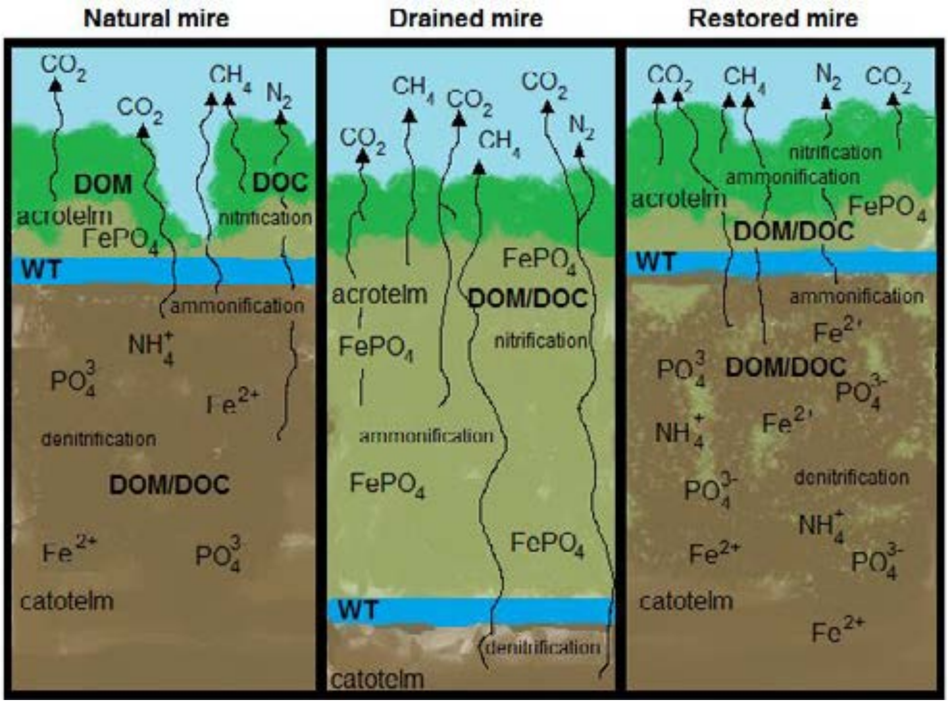

Figure 1. Carbon and nutrient cycle components of natural, drained and restored mire peat profiles. Carbon is respired by microbes and released as either CO_2 or CH_4, depending on the availability of oxygen and activity of methanogens and methanotrophic bacteria. In anaerobic peat (dark brown, natural and restored mire) denitrification produces N_2 and ammonification NH_4, phosphorus can be found as free phosphate. In aerobic peat profiles (green and light brown, drained mire) there may be easy leaching of nitrite or nitrate as a result of nitrification, but phosphate is bound with iron or other metals. In restored mires, the concentrations of DOC, dissolved N and P can be higher than in natural mires, because of higher mineralization rates during drainage and release of P by re-established anoxia. Picture modified from Vasander 1998 and Päivänen 2007.

during inundation, lead to reduction of ferric iron and release of dissolved inorganic phosphorus (DIP, PO_4-P) to the water (Fig 1; Correll 1998, Zak et al. 2010). Global warming and/or mire draining may enhance decomposition of organic matter during drought, leading to increased leaching of P (Walbridge & Navaratnam 2006). The free P in mire pore water is rapidly bound by microbes; over 90% of free DIP is immobilized by microbes (Walbridge 1991, Williams & Silcock 2001), but in high concentrations the immobilization is weaker (Walbridge 1991). In studies of peat buffer zones, P was found to be mainly bound to vegetation or peat, rather than microbes (Väänänen et al. 2008). When the residence time of water is low, the peat retention capacity of DIP is weak and the concentration of P in runoff increases (Väänänen et al. 2008).

1.2 DRAINED MIRES

The drainage of peatlands aims to increase the depth of the oxic peat layer by lowering the water table to enable oxygen diffusion. A large proportion of the peatlands of northern Europe have been drained for use (Joosten & Clarke 2002, Vasander et al. 2003, Holden et al. 2004). Peatland draining has been done most intensively in Finland, Netherlands, Lithuania, UK, Ireland, Estonia and Denmark (Joosten & Clarke 2002). The proportion of natural mires varies between countries, for example, in Denmark the proportion of natural mires is only 8%, whereas in Norway the natural mire proportion is 80% (Maljanen et al. 2010). In Sweden more than half of the mire area is undrained (Joosten & Clarke 2002). In Canada, peatland utilization is not as intensive as in Europe (Cleary et al. 2005). In many countries, such as Ireland and UK most of the drained mires have been taken for agricultural use (Holden et al. 2004). In Finland, over half of the original mire area has been drained for forestry (5.7 Mha) and to a lesser extent for agricultural (0.7 Mha) or peat mining purposes (0.05 Mha; Vasander et al. 2003).

In drained mires soil respiration rates are higher than in natural mires (Jaatinen et al. 2008, Ojanen et al. 2010, Mustamo et al. 2016). Overall, the rate of soil C and nutrient cycling is enhanced in drained peatlands due to water level drawdown increasing the rate of aerobic decomposition. In addition to increased availability of oxygen, carbon and nutrient availability generally increase due to extra litter production by trees and increased peat decomposition after drainage (Minkkinen & Laine 1998a). Carbon is respired as CO_2 to the atmosphere or lost in runoff water as DOC. Concentrations of DOC after drainage are higher than in undrained, natural mires (Laine et al. 2014, Evans et al. 2014, Hulatt et al. 2014). Due to enhanced decomposition, the release of phosphorus and organic matter (Walbridge & Navaratnam 2006) and efflux of N_2O have been shown to increase after drainage, especially at very nutrient rich sites (Martikainen et al. 1993, Mustamo et al. 2016). The peat profiles in drained peatlands collapse and become denser and less porous (Mäkilä 2011, Tahvanainen & Haapalehto 2014) and the diplotelmic system of natural mires is lost (Ingram 1978, Landry and Rochefort 2012). The peat accumulation slows down or ceases (Tahvanainen & Haapalehto 2014, Kareksela et al. 2015), but the total carbon accumulation may increase due to growth of tree stands after drainage (Minkkinen & Laine 1998b).

1.3 MIRE RESTORATION

Today peatlands are being restored around the world to ensure the continued existence of these long-term carbon accumulating ecosystems, which have unique structure and functions as biodiversity services (Rochefort & Lode 2006, Minayeva et al. 2017). Peatland restorations have already been made in e.g. Germany, Belarus, Canada, U.S.A. and Finland (Joosten & Clarke 2002). In Finland, restoration plans are in place for ca. 15 000 ha of disturbed mires and approximately one third of that area has already been restored (Penttinen 2015) with the earliest restoration cases dating back to the 1990's (Lindholm & Heikkilä 2005, Penttinen 2015). Restoration is done mainly in national parks and other conservation areas for improving their natural state, and in a few cases at sites where drainage has been unsuccessful. There are a few cases of privately-owned peatlands having been restored (Lindholm & Heikkilä 2005).

The primary aim of restoration is to return the hydrological properties so that biological and physico-chemical structures such as vegetation and natural acrotelm-catotelm peat layering are revived and peat will again begin to accumulate. The return of hydrological properties is implemented by blocking the ditches with the aim of recovering the amount and quality of water in the mire (Fig 2; Aapala et al. 2005). The high water table (WT) and natural fluctuation range should also return (Aapala et al. 2005). In addition, some peat ridges may be built on former ditches to spread water flow over sites from the ditches. If the mire was originally an open mire, trees are usually logged before ditch blocking. The WT usually rises immediately after ditch blocking and will remain high if the restoration was successful (Fig 2; Koskinen et al. 2011, Haapalehto et al. 2011, Laine et al. 2011, Ronkanen et al. 2016).

After restoration the vegetation starts to develop towards a community, which requires wetter conditions (Haapalehto et al. 2011). The formation of typical mire vegetation at the restored sites takes many years, even decades (Jauhiainen et al. 2002, Haapalehto et al. 2011, Kozlov et al. 2016). Certain changes in the quality of runoff waters are well known, including elevated concentrations of DOC, N and P that are often observed a few years after restoration (Glatzel et al. 2003, Höll et al. 2009, Zak et al. 2010, Haapalehto et al. 2014, Koskinen et al. 2017). The main reason for higher nutrient (N and P) concentrations after restoration is the elevated WT changing the peat oxidation status, which is quickly lowered after restoration because of inundation and microbial activity. There are also some studies showing that microbial processes and communities at restored peatlands start to develop towards the communities found in natural mires (Andersen et al. 2006). However, like in the development of vegetation, the microbial communtity may not have recovered similar to that in pristine mires (Elliott at al. 2015).

Figure 2. The view of an old ditch after blocking using an excavator at site ResB1.

1.4 PEATLAND-ORIGIN ORGANIC MATTER IN AQUATIC ECOSYSTEMS

The concentration of total organic carbon (TOC) in boreal runoff waters from catchments with a high proportion of mires is usually high (10 - 60 mg L^{-1}) (Mulholland 2003, Kortelainen et al. 2004 & 2006). More than 90% of TOC consists of dissolved forms (Mattsson et al. 2005). By comparison, organic carbon concentration in ground water is approximately 0.5 mg L^{-1}, in seawater from 0.5 to 3.0 mg L^{-1} (Mulholland 2003) and in boreal lake water generally ranging between 5.1 and 21 mg L^{-1} (Mattsson et al. 2005). Increased DOC export from soils is causing brownification of northern hemisphere freshwaters (Roulet & Moore 2006). Brownification has been connected to climate warming, increased precipitation and runoff, changes in soil frost period and moisture conditions, and decreased acidic deposition (Monteith et al. 2007, Jennings et al 2010, Larsen et al. 2011, Lepistö & Kortelainen 2011, Pumpanen et al. 2014).

A major proportion (50 to 75 %) of DOC is comprised of humic substances such as polymeric organic acids, with functional carboxylic, phenolic and hydrocylic groups (Thurman 1985, Mattsson et al. 1998, Wershaw 2004). These substances are aromatic and can be separated as humic or fulvic acids (Thurman 1985, Pettit 2004). The humic substances give the water a light to dark brown color, which affects the light penetration and UV-light absorption properties (Jones 1992, Vähätalo et al. 2000). The amount of dissolved organic nitrogen (DON) is connected to the amount of DOC and both are rich in mire runoff waters (Kortelainen et al. 2006). Inorganic P is rarely free in the surface waters because the DIP is rapidly used by microbes, vegetation or bound in complexes of organic compounds and metals in the soils and sediments (Correll 1998, Kellogg & Bridgham 2003). That is the reason why P is the limiting nutrient in lakes and other fresh water bodies (Schindler 1978, Correll 1998).

Heterotrophic bacteria are the most important link between carbon derived from soils and peatlands (allochthonous carbon) and higher trophic levels in the aquatic environments, especially in the humic lakes (Tranvik & Höfle 1987, Hessen 1992, Jones 1992, Karlsson et al. 2012). In streams and lakes, DOC from peatlands may lose aromaticity and become more available to bacteria due to photo-oxidation after exposure to UV light (Wetzel et al. 1995, Vähätalo et al. 2003, Olefeld et al. 2013). We may assume that restoration has an effect on the microbial activity (production and respiration) in mire runoff water, because elevated nutrient concentrations are generally known to increase microbial activity in boreal streams and rivers (Berggren et al. 2010a, Asmala et al. 2014) and lakes (Tulonen et al. 1992, Karlsson et al. 2001, Jansson et al. 2006).

Microbial activity in acidic conditions is rather low and rising pH conditions may increase the activity, even in mire waters (Rousk et al. 2009, Andersson & Nilsson 2001, Ye et al. 2012). In receiving water bodies in Finland the median pH is 6.3 (range 4.1-8.0, Kortelainen 1999), which is generally higher than that in boreal mires. For example, in *Sphagnum* bog and spruce swamp waters pH is in the range of around 4 to 6, depending on the trophic conditions of the mire (Tahvanainen & Tuomaala 2003). Lake water pH is more favorable for microbes and also contains autochthonous, algae-originating carbon. It has been hypothesized that easily utilized autochthonous carbon could promote utilization of recalcitrant terrestrial DOC (Guenet et al. 2010). The phenomenon is known as a 'priming effect'. In mineral soils the microbial diversity and interactions between living organisms and detritus are complex, but the priming effect has been proven to exist (Kuzyakov 2010, Mau et al. 2015). In peatlands, however, the priming effect hypothesis was not supported (Linkosalmi et al. 2015).

The scale of implemented restoration in mires is quite small – in Finland for example, approximately 15 000 ha of mires need restoration (Penttinen 2015). However, the restoration effects may be comparable to those expected to be caused by climate change and other peatland management operations. Increases in temperature, precipitation and frequency of extreme weather events probably promote alternation between dry and soaked peat, which may elevate the concentrations of C and N in the runoff waters, (Austnes et al. 2010, Kaila et al. 2016) and possibly to a lesser extent increase organic P leaching from the mires (Arvola et al. 2006, Kaila et al. 2016). In addition, temperature increase directly promotes peat degradation (Ojanen et al. 2010) and increased precipitation, especially in winter time

(Kivinen et al. 2017), flushes recalcitrant DOM into recipient waters. High concentrations of DOC and DON can also be found in runoff waters of peatland forests, especially after forestry management operations, such as clear-cutting (Nieminen 2004, Nieminen et al. 2015). Terrestrial mire-originated DOM causes water browning, which together with increased nutrient load may have various effects on lake food webs (Solomon et al. 2015, Taipale et al. 2016).

1.5 AIMS OF THE STUDY

The main goal of this study is to clarify how restoration of drained mires affects quantity and quality of dissolved organic carbon (DOC) leaching and how efficiently aquatic microbes can utilize these carbon compounds in different nutrient conditions. It is hypothesised that the quality of DOC would change after restoration and that due to higher nitrogen and phosphorus concentrations microbial activity would increase in mire runoff water. Microbial activity may also rise in recipient waters due to higher pH conditions and autochthonous carbon availability. The more specific hypotheses are:

1. High availability of inorganic phosphorus and increases in pH of mire runoff improves microbial utilization of leached organic carbon compounds (I)

2. Biodegradation of dissolved organic carbon originating from differently managed *Sphagnum* bogs will be enhanced in recipient lakes due to the 'priming effect' of lake-originating DOC (II)

3. Restoration changes the concentrations and quality of DOC, N and P in mire runoff water and, hence, increases the microbial activity in runoff water (III)

2 MATERIALS AND METHODS

2.1 STUDY SITES

The Natural Heritage Services of Finland started the monitoring project of different types of natural, drained and restored peatlands in Finland. The sites were monitored to evaluate the recovery of hydrological properties and vegetation at the restored sites. For this study, seven monitoring sites were selected (Table 1, Fig 3).

Table 1. The main features of the study sites. The numbers after study site names refer to site identification in Ronkanen et al. 2016.

Study site name, the monitoring ID	Lat Lon	Vegetation type	Fertility	Catchment area (ha)	State of site during study (2010-2015)
ResSp, 7	61 59.8 23 53.0	*Vacc. myrtillus* spruce swamp	meso	9.1	restored 2010
NatSp, 17	61 51.4 24 14.2	*Vacc. myrtillus* spruce swamp	meso	5.7	natural
ResB1, 86	62 01.7 23 55.3	Low sedge bog	ombro	23.5	restored 2010
ResB2, 85	61 59.8 23 52.8	Low sedge bog	ombro	34	restored 2010
ResB3, 103/1	61 59.7 23 56.5	Tall sedge bog	oligo	34.8	restored 2011
NatB, 94	62 00.1 23 56.5	Low sedge bog	ombro	10.6	natural
DrB, 103/2	61 59.8 23 56.2	Tall sedge bog	oligo	17.8	drained

The study sites consisted of drained mires and pristine reference sites in natural mires of the respective vegetation types. A drained spruce swamp and five bog sites are located near to each other, within a distance of approximately 6 km in the Helvetinjärvi National park, Ruovesi, southern Finland. The second of the two spruce swamp sites is a natural reference site located in Susimäki, near the Hyytiälä Forestry Field Station. The restoration of four sites was implemented during this study, so we could measure bacterial activity already before restoration. This study was focussed on the restoration impacts on DOC, N and P concentrations and the bioavailability of the mire originating carbon.

2.2 METHODS

Water chemistry of the study sites has been monitored since 2008 by the Natural Heritage Services of Finland. The samples for the measurement of pH, electrical conductivity, suspended solids, alkalinity, DOC, absorbance (254 nm), N, P, PO_4-P,

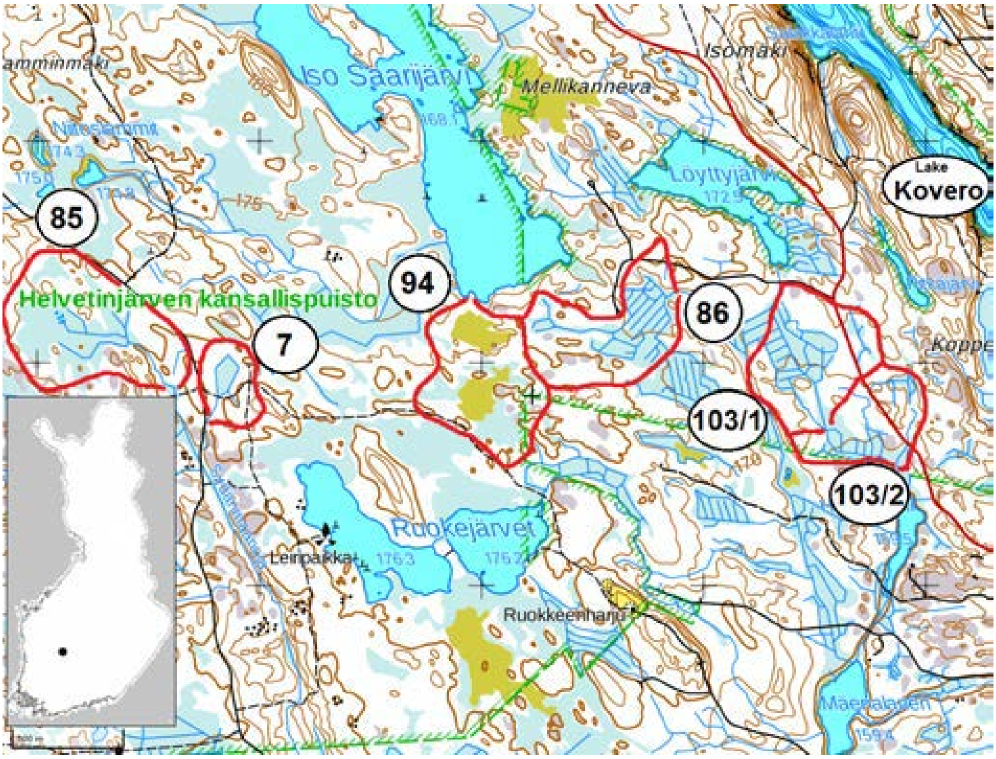

Figure 3. The map of study sites in Helvetinjärvi National park. Red lines are the catchment areas of mires: 85 ResB2, 7 ResSp, 94 NatB, 86 ResB1, 103/1 ResB3, 103/2 DrB and Lake Kovero. The gap in the red line shows the weir location (next to numbers). The catchment area drawings are imitated from Teemu Tahvanainen 27.3.2012 drawing to the map from karttapaikka database. https://asiointi.maanmittauslaitos.fi/karttapaikka/?lang=fi

NH_4-N, NO_3-N, NO_2-N, Fe, Ca, Mg, K and Na were taken from outflow weirs (Fig 4) once per month, during the frost-free season, from April to November. The DOC quality evaluation was done by measuring different absorbance ratios and specific UV absorption at 254 nm ($SUVA_{254}$) (Weishaar et al. 2003, Peacock et al. 2014). Relative differences in the size distribution of DOC molecules was measured with HPSEC (High Performance Size Exclusion Chromatography; Akkanen et al. 2004). During the years 2010-2012, collected water was also used for microbial activity measurements (III). In addition, two short experiments (I, II) were done with the runoff waters. Methods are only described here in brief and more detailed descriptions can be found from the method section of the original articles I, II and III.

In the first study (I), the effects of better availability of inorganic phosphorus and increased pH on microbial utilization of mire-originating DOC were assessed. The main idea behind this short experiment was that peat rewetting usually increases leaching of nutrients, especially that of P in runoff, and acidic and P-rich runoff eventually ends up in recipient watercourses and less acidic conditions. In this study, pH in mire runoff waters was artificially raised by adding NaOH. The phosphorus addition was made with KH_2PO_4 at four different concentrations (10, 20, 50 and 100 µg L^{-1}) and the combined effect of P addition and pH increase was done using a P concentration of 10 µg PO_4-P L^{-1}, which caused the greatest increase in bacterial activity. In the second experiment, the 'priming effect' hypothesis was tested by mixing lake water with mire water (II). We included runoff waters from three study sites: pristine (NatB), restored (ResB1) and at that moment, drained (ResB2) *Sphagnum* bog, which was restored during the second study year (Fig 3, 5). The study lake (Kovero) represented a typical humic lake in Finland (Fig 3).

Figure 4. The weir of the outflow ditch. The water samples were collected from the V-notch.

The lake water and runoff waters from each type of *Sphagnum* bog were mixed together (1/1; Fig 5). Measurements were also made solely with lake water and runoff water from each mire site. The experiment was made twice, first in the year 2011 and repeated in the year 2012. The measurements were done at the end of summer to ensure the highest possible concentration of autochtonous carbon in the lake water.

Microbial activity measurements in the runoff waters were made about once per month during the open water season 2010-2012, before and after mire restorations as

Figure 5. The lake and mire runoff water samples in 20 mL glass bottles, in the lake water mixing experiment (II). From left to right the bottles contain: milli-Q water, lake water sample (Kovero), mire and lake water mixture samples, mire runoff water NatB, ResB3 and ResB1 samples (respectively).

well as at the reference sites (III). The measurements were made as short-term (6 days) laboratory incubations. Quality measurements (aromaticity, molecular size distribution) were used to evaluate whether possible differences in DOC quality affect bacterial activity. In this study we obtained general information on bacterial activity in runoff waters of differently managed mires. The results of these measurements were tested using appropriate statistical tests (Table 2).

Table 2. The statistical methods of the studies.

Statistical methods	Paper (I)	Paper (II)	Paper (III)
The one-way analysis of variance (ANOVA)	X		x
Tukey's post-hoc test	X		x
a paired t-test	X	x	
Bivariate correlations		x	x
Linear regressions		x	x
a principal components analysis (PCA)			x
a time-series of expected value ranges (95% Confidence Interval (CI))			x

Net bacterial production (BP) is a measure of the bacterial biomass formation, microbial respiration (R) is a measure of the CO_2-formation, and bacterial growth efficiency (BGE) reveals the total proportion of carbon required for the new bacterial biomass production and that consumed in respiration (del Giorgio & Cole 1998). BGE% was calculated using the formula: BGE% = BP / (BP+R) x 100. We measured the BP in one hour incubations during the days 0, 3, and 6 of the experiment. Bacterial production was determined by the ^{14}C-leucine method (Kirchman et al. 1985, Tulonen 1993), where the ^{14}C-labelled leucine is taken up by bacteria for protein synthesis and measured with a scintillation counter. The rate of microbial respiration (CO_2) was determined by measuring the accumulation of CO_2 in gas-tight bottles during 6 day incubations. The CO_2 gas concentration was determined using a system with a head-space sampler and gas chromatograph equipped with a PlotQ capillary column, methanizer and flame ionization (FID) detector (Karvinen et al. 2015).

3 RESULTS AND DISCUSSION

3.1 RESTORATION IMPACTS ON DOC, N AND P IN MIRE RUNOFF WATERS

The impact of restoration was already observed in the runoff waters of our study sites during the first summer after restoration (II, III). The increased WT after ditch blocking in the restored study sites indicated that the restoration process had started (Ronkanen et al. 2016, Koskinen et al. 2017). Concentrations of DOC, TN and TP in the runoff waters from restored mires were higher than those during the years before restoration (Figs 7 & 8, according to monitoring data acquired since 2008, II, III). These results support earlier studies of restored mires (Glatzel et al. 2003, Zak et al. 2010, Koskinen et al. 2011).

3.1.1 DOC quantity and quality in mire originated runoff

DOC concentration increased significantly in most of the restored sites (ResSp, ResB1 and ResB2) during the first summer after restoration and decreased in the second year to near the levels observed before restoration (Fig. 6, III, Koskinen et al. 2017). The increase in DOC concentration was more pronounced in minerotrophic and nutrient rich sites. Similar observations have been made in earlier studies where runoff DOC concentrations were around 50 mg L^{-1} but after restoration can be as high as 150-250 mg L^{-1} (Glatzel et al. 2003, Koskinen et al. 2011, Strack et al. 2015, Herzsprung et al. 2017). DOC concentrations eventually return to similar levels as in natural mires (Höll et al. 2009). One possible explanation for the short DOC peak after restoration could be the blocking of ditches by the excavator, which released additional DOC from tilled peat layers (Fig 2). Hulatt et al. (2014) showed that older DOC is released into the runoff from agricultural and peat extraction sites at greater concentrations than from natural and drained peatland reference sites; i.e. the tillage of peat releases DOC from the deeper and older peat matrix into the runoffs.

A minor increase in DOC concentration was also seen in unmanaged NatB, during the rainy years 2008 and 2012 (Fig. 6, III). The alternation between dry and wet conditions in the peat layers increases the degradation rates in peat and causes higher DOC in runoff during wet years than drier years (Kortelainen et al. 1997, Arvola et al. 2006). Therefore, increased DOC runoff is also seen in natural mires. Floods after dry periods have also been observed to promote increases in DOC concentration in the runoff waters of natural and restored mires (Höll et al. 2009, Laine et al. 2014).

The pH affects the molecular composition of organic matter; in low pH (4-5), for example, larger DOM molecules were observed in waters from the Yensei river and

German forest soils (Roth et al. 2015). In this study, the quality of DOM and pH (average 4.3, SE ±0.02, III, Ronkanen et al. 2016) was quite stable at all study sites. DOM originating from the study sites mostly had large size variations (63-91%), which is in accordance with earlier results from acidic waters originating from bogs or drained peatlands in the boreal zone (Roth et al. 2013, Kiikkilä et al. 2014). In the restored and drained sites there was some temporal variation in aromaticity (absorbance 254 nm, $SUVA_{254}$) and in molecular size distribution, but similar variation was also detected in the natural and drained counterparts (III). This finding supports the results of Glatzel et al. (2003) and Strack et al. (2015), who found that the quality of DOM did not change after restoration in Canadian boreal bog complexes.

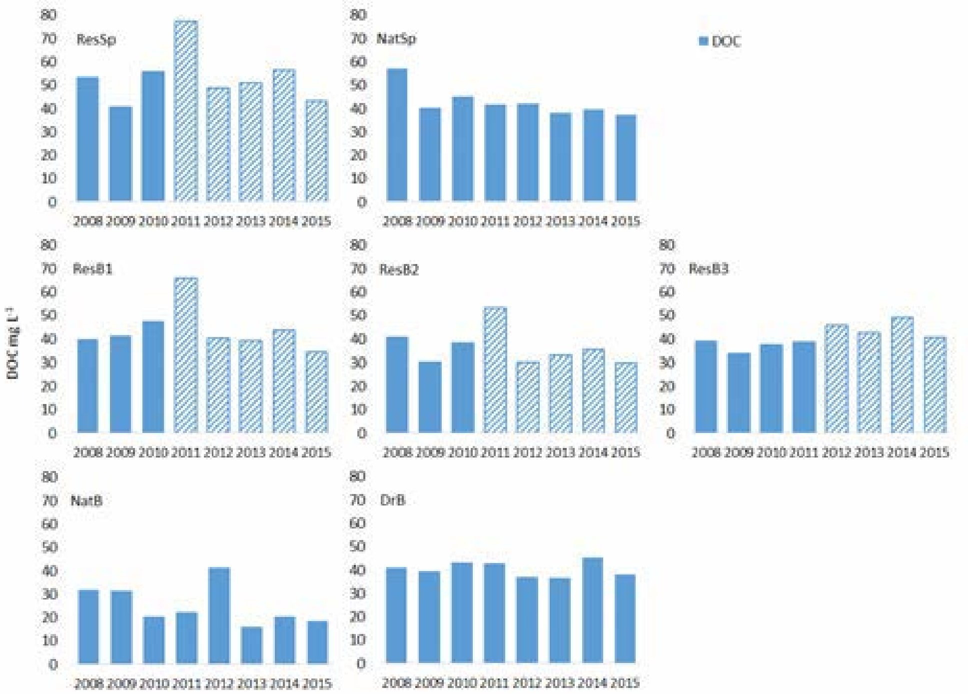

Figure 6. Mean of dissolved organic carbon (DOC) concentrations (mg L^{-1}) in study site runoffs 2008-2015. The striped columns show the DOC of runoffs after restoration (implemented in the years 2010 and 2011).

3.1.2 N and P concentrations increase after restoration

The concentration of nitrogen increased in the runoffs after restoration and remained at higher levels for three to five years. The increase in TN concentrations was 1.3 to 1.7-fold after restoration and most of the nitrogen was leached in organic form (III, Fig 7). Only a minor part of the TN was in inorganic form (2-12% of TN). The amount of DIN was ten-fold after restoration of a nutrient rich site (ResSp) and only one- to two-fold in bog sites. Higher ammonium concentrations have also been detected from other boreal, forestry drained spruce swamps and bogs after restoration, especially in the runoff water of nutrient rich spruce swamp where the concentrations ranged between 85 and 265 μg L^{-1} six years after restoration (background level 14-17 μg L^{-1}; Koskinen et al. 2011). The elevated concentrations of DON in runoffs lasted longer than elevated DOC (III). The possible explanation for long-lasting DON leach is the lowered microbial activity in anoxic peat after restoration. In general, high DON leach has been measured from drained and natural mires during heavy rain events or spring and autumn floods (Arvola et al. 2006, Mattsson et al. 2015, Tattari et al. 2017).

The amount of released phosphorus from different peatlands depends on their nutrient status and the concentration of P binding metals (Al, Fe) in the peat (Kaila et al. 2016). In the studied natural and drained mires, the leached P was mainly in the form of dissolved organic phosphorus (DOP); in natural sites a little over 50 % and in drained sites 60-70% of total P consisted of DOP. TP concentrations increased by 1.5-fold, or even seven-fold (ResSp and ResB1) after restoration (III). In the altered oxygen conditions P was released (39-92%) as dissolved inorganic phosphorus (DIP). The elevated DIP concentrations were highest in the first summer after restoration in *Sphagnum* bog sites. In the spruce swamp site, the highest P leaching took place during the second year after restoration and DIP concentrations were at higher levels (15-fold higher) for two to three years (III, Fig 8). According to Koerselman et al. (1993), *Sphagnum* peat releases more P and ammonium than *Carex* peat. After restoration, the anoxic conditions contribute to the release of iron bound phosphorus in the runoffs (Fig 2; Sinha 1971, Patrick & Khalid 1974, Kaila et al. 2016).

Annual variation in precipitation may also affect leaching of P. In this study, the years 2008 and 2012 were rainier than the long-term average and P concentrations in runoff water were higher in those years at all study sites, especially in the natural sites (Fig 8). Similar elevation in the portion of DIP from TP was seen at the NatSp site and in the ResSp site after restoration: DIP concentration was at its highest in the second year after a rainy year or restoration (Fig 8). However, the increase in P leaching after heavy rainfall or inundation of soil was moderate compared to the increases in C and N leaching observed by Nieminen (2004).

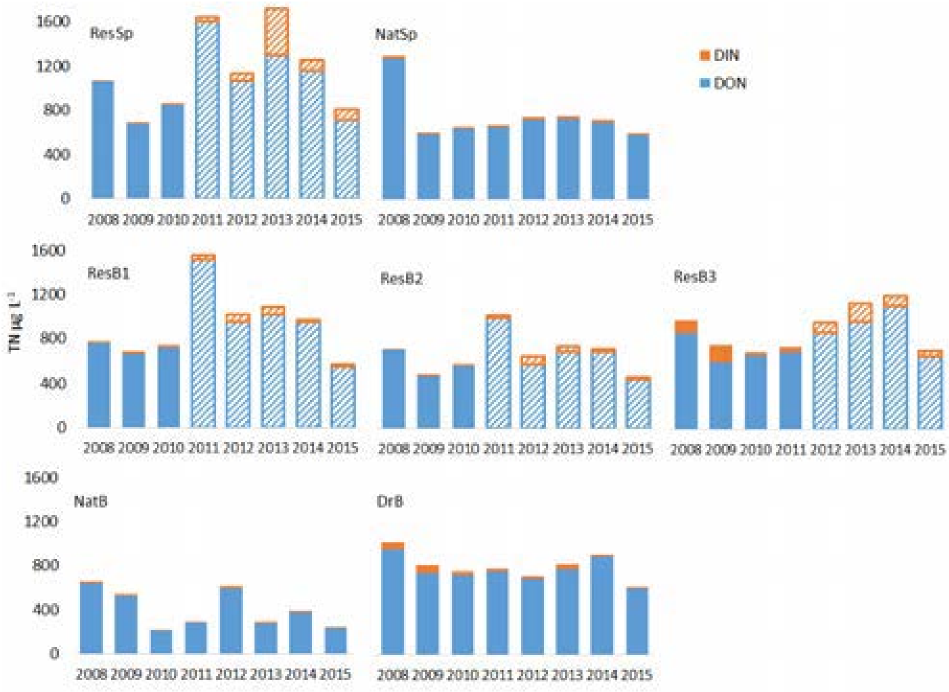

Figure 7. Mean dissolved inorganic nitrogen (DIN) and dissolved organic nitrogen (DON) concentrations (µg L^{-1}) in study site runoffs 2008-2015. The DIN include NH_4-N, NO_2-N and NO_3-N concentrations. The striped columns show runoffs after restoration (implemented in the years 2010 and 2011).

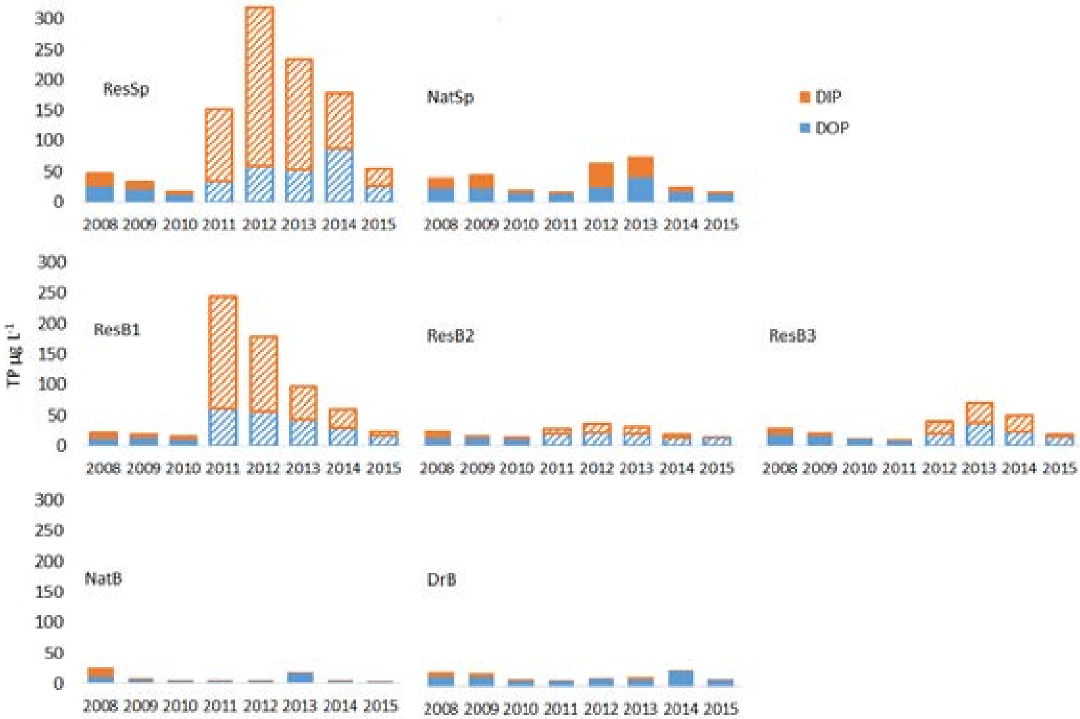

Figure 8. Mean dissolved inorganic phosphorus (DIP) and dissolved organic phosphorus (DOP) concentrations (µg L^{-1}) in the study sites 2008-2015. The DIP is PO_4-P form phosphate. The striped columns are the runoffs after restoration.

3.2 MICROBIAL ACTIVITY IN MIRE ORIGINATED RUNOFF WATERS

Microbial activity (BP, R) levels in the boreal mire runoffs were low (Fig 9, III) compared to other freshwaters, such as lakes or rivers in the boreal zone (Tulonen 1993, Jansson et al. 2006, Berggren et al. 2007, Asmala et al. 2013). The recalcitrant nature of mire originating DOC and poor nutrient availability are probably the main reasons for the low activity in the mire runoffs. In oligotrophic environments with low nutrient (N, P) availability, microbes mainly use organic carbon for respiration and less for biomass production (Jansson et al. 2006).

In drained, ombrotrophic bog sites, the microbial BP and R in runoff was higher than in the natural counterpart, which can be explained by higher nutrient and DOC concentrations measured from the drained site runoffs (II, III, Fig 9). A similar difference was not observed for the spruce swamp sites.

The effect of restoration on microbial activity was seen during the first summer after restoration. Restoration did increase BP and BGE% in most of the restored sites. BGE% remained at higher levels in the second year after restoration of the studied sites, while BP already started to decrease (Fig 9). The rate of respiration was not as sensitive to the changes as BP, with only slight shift towards higher rates detected after restoration (III). Only at the site ResB1 were the respiration rates elevated during the first summer after restoration, whereas at the other sites no significant rise was observed. However, when comparing the study sites, the respiration rates were the highest in the most nutrient rich sites (Fig 8), which was also seen in significant correlation of R with DOC, TN and TP concentrations.

Experimentally elevated pH significantly increased respiration in the studied runoff waters (I), but did not affect the BP (I). Higher nutrient or carbon concentrations did not significantly change respiration rates in our sites. Increased respiration rates were also measured from boreal river and bog waters in elevated pH conditions, and from core samples of bog and fen peat where higher pH mainly promoted the fermentative process (Andersson & Nilsson 2001, Ye et al. 2012). Increasing pH has been shown to promote bacterial activity in low pH soils (Grybos et al. 2009, Rousk et al. 2009). The increased respiration at elevated pH may be a result of changed DOC solubility, dissociation of acid functional groups and molecular composition (Brunner and Blaser 1989, Andersson et al. 2000, Roth et al. 2015). In the study sites, pH was not affected by restoration, and thus, microbial respiration and the proportion of decomposed DOC (DeDOC% d^{-1}) were not affected.

3.2.1 DOC quality do not favor microbial activity

The poor availability and recalcitrance of mire originating DOC has been well established earlier (Tranvik 1990, Wetzel et al. 1995, Eiler et al. 2003, Jansson et al. 2006, Asmala et al. 2013). In our study, the proportion of decomposed DOC per day in the mire runoffs was also very low (0.17-0.36 %, Fig 9, III). The incubation of water samples in the dark might have further decreased the decomposition rate in our study as in nature the photochemical breakdown of DOC may provide molecules that are more assimilable for bacteria (Anesio et al. 2005, Wetzel et al. 1995, Vähätalo et al. 2003, Olefeld et al. 2013). The photochemical breakdown of DOC might become weaker while higher concentrations of brown colored water prevents light penetration in deeper layers of recipient waters. As in the study of Glatzel et al. (2003) on Canadian mires, we did not detect any signs of increased release of easily degradable C after restoration. The measurements of carbon quality instead indicated greater aromatic C release from some of the restored sites (ResSp, ResB2) after restoration, but the changes cannot be generalized to all restored sites. The aquatic microbes cannot utilize mire originating carbon compounds effectively and thus waters rich in mire originating C usually have lower microbial activity than waters with organic carbon mainly originating from lakes or rivers (Tulonen 1993, Moran & Hodson 1990, Berggren et al. 2007, 2009 & 2010b, Asmala et al. 2013, Broder et al. 2017). The amount of utilizable carbon might be the limiting factor in boreal mire runoff even after restoration, which is due to the elevated DOC concentration decreasing faster than the N or P leachates after restoration (III, Wyatt & Turetsky 2015). The increased C, N and P availability after restoration may temporarily increase microbial activity in the recipient lakes, but according to our study the lake originated DOC will not stimulate the decomposition of mire originated DOC (II). Our results do not support the 'priming effect' hypothesis, suggested by Guenet et al. (2010) to occur in various terrestrial, marine and lake ecosystems. In contrast, the rates of bacterial production and respiration declined in mixtures of lake and mire runoff water compared to those in mere mire runoff water, which is due to the lake water diluting the mire runoff waters (II). In freshwater systems the importance of the priming effect is not as clear as in soils (Catalán et al. 2015).

3.2.2 Short-term increases in N and P concentrations after restoration have an effect on microbial activity

The higher N and P concentrations in mire runoff after restoration significantly increased bacterial production in all restored sites (II, III, Fig 8). In a short-term experiment, small phosphorus addition (10 $\mu g\ L^{-1}$) raised the rate of BP in runoff from the study sites (I). The increase in BP was significant in sites in which the C:P ratio was the highest (ranging between 11,000 and 24,000). In sites where the C:P ratio was lower (under 10,000), either the pH elevation or phosphate addition did not change the rate of BP (I). The ratio in runoffs of carbon to P, and also N in this study is very high, which is typical of highly humic waters. The high C:P and C:N ratios indicate poor availability of DOC in mire runoff production (Solomon et al. 2015). The increased availability of nutrients was used for biomass growth of heterotrophic bacterial cells, which has also been detected in earlier studies (Jansson et al. 2006, Kirchman 2012). In the most P rich sites, bacterial growth efficiency (BGE%) increased from 4-6% to 8-11% after restoration (III). Although BGE% doubled, it was still low compared to the BGE% generally measured in lakes and estuaries (20-50%) and even in rivers and oceans (5-30%) (del Giorgio & Cole 1998), thus indicating that in mire waters a greater proportion of C is used for respiration than for biomass production. When nutrient availability increases the productivity usually increases, and it becomes the turn of carbon to be the limiting factor in microbial production (Eiler et al. 2003, Kirchman 2012). The low microbial activity in these mire runoff waters, even with higher N and P concentrations, might be due to the recalcitrant, humic material.

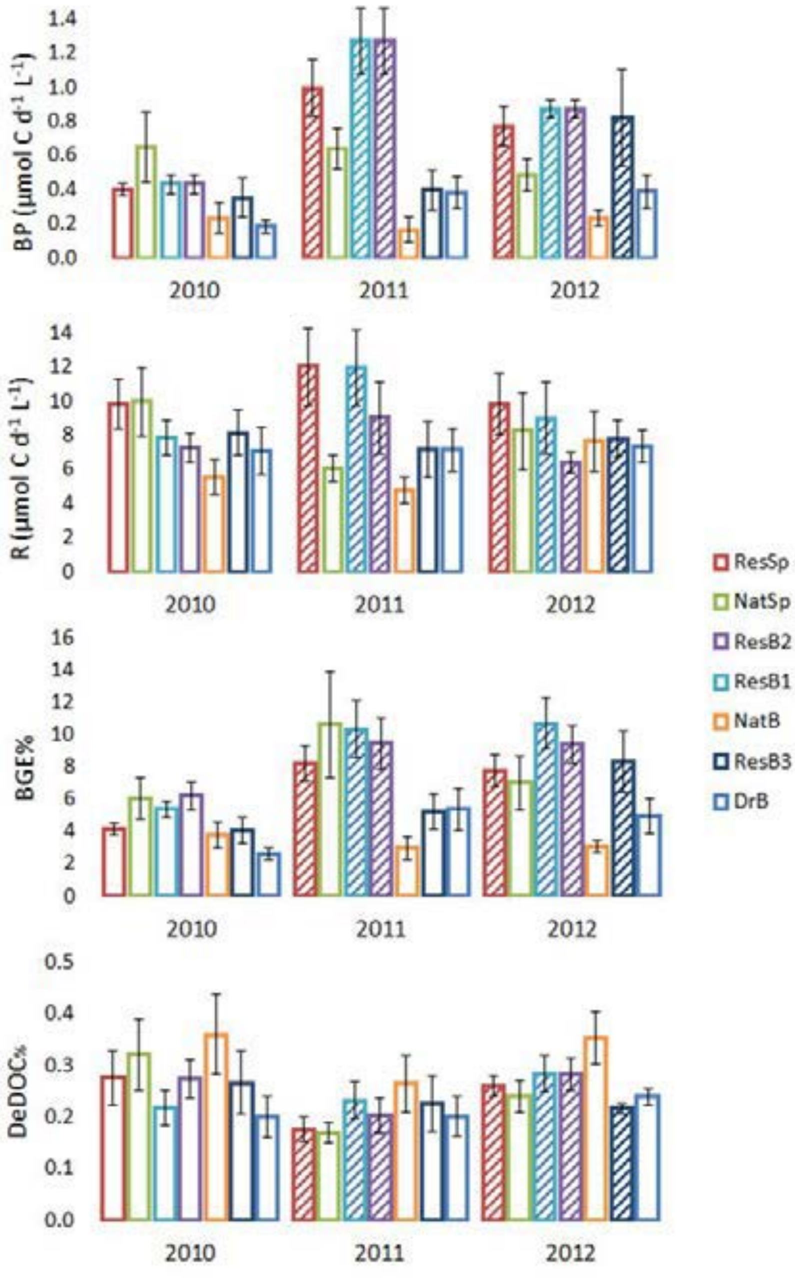

Figure 9. Mean (±SE) bacterial production (BP, µmol C L^{-1} d^{-1}), respiration (R, µmol C L^{-1} d^{-1}), bacterial growth efficiency % (BGE%) and decayed DOC % d^{-1}(DeDOC%) at all study sites during the years 2010-2012. The striped columns are activities after restoration.

3.3 EFFETS ON AQUATIC ECOSYSTEMS – FUTURE PERSPECTIVES

Concentrations of organic carbon and nutrients (N, P) tend to increase in runoff waters after mire restoration for a few years (III). Mire restoration does not change DOM quality, but increases the amount of large, aromatic and recalcitrant carbon compounds in the runoff. The increased DOM load enhances browning of boreal headwaters, which has many ecological consequences, e.g. via changing light penetration and thermal dynamics of the lakes (e.g. Solomon et al. 2015, Williamson et al. 2015). Exposure to UV-light presumably accelerates degradation of mire-originating DOM in the recipient lakes and streams, but only in the topmost surface layers due to reduced light penetration (Vähätalo et al. 1999, Hernes and Benner 2003). Bacterial production will be slightly stimulated by increased availability of N and P (II, III). The decomposition of DOM as well as microbial cycling of nutrients, e.g. nitrification of ammonium leached after restoration (II, III), may contribute to oxygen depletion in recipient lakes (Quirós 2003, Camargo & Alonso 2006) and effluxes of greenhouse gases (CO_2, CH_4 and N_2O) to the atmosphere (e.g. Juutinen et al. 2009, Miettinen et al. 2015). The increased nutrient load, especially inorganic P, from restored mires may promote primary production and together with other nutrient sources may increase risk of eutrophication in the recipient watercourses (Schindler 1978, Correll 1998). On the other hand, the reduced penetration by visible light tends to diminish primary production in the water column, which may have negative consequences on aquatic food webs (Rask et al. 2014, Solomon et al. 2015, Taipale et al. 2016). Water browning also sets demands for better purification of surface waters that are utilized as drinking water.

In Finland, it is unlikely that the restoration of mires alone would lead to the wide-scale consequences described above, as restorations are implemented in less than 1% (15000 ha) of the area drained for forestry. Actively managed peatland forests, however, cover nearly 5 Mha and forestry management operations, e.g. ditch maintenance and harvesting, may lead to similar increases in DOM and nutrient load to watercourses (Joensuu et al. 2002, Nieminen et al. 2010, 2015). In addition, c. 800000 ha of the forestry drained peatlands in active use or undergoing restoration will be outside of ditch network maintenance programmes and those sites will be gradually paludified again. It would be interesting to compare the quality of runoff waters from overgrown ditches of those naturally restoring sites to those from other peatland utilization types. Long-term monitoring is also needed, which is emphasized by a recent study of drained boreal peatlands by Nieminen et al. (2017) showing that N and P export declined after drainage to a level typical of natural mires within the first 20-30 years, but later increased again presumably due to erosion of highly degraded peat soil. Climate change may further increase consequences in watercourses, for example, by increasing the runoff of C, N and P compounds from peatlands due to increasing precipitation (Kivinen et al. 2017).

4 CONCLUSIONS

In the boreal zone, the impacts of restoration on the runoff from forestry drained mires have mainly been measured in terms of nutrient or carbon load (kg ha^{-1}). In this study, the focus was to understand how the quality of carbon or leached nutrients affect the microbial activity in runoff waters from restored mires.

Impacts on water quality were evident after restoration, with impacts lasting longer in nutrient rich peatlands such as spruce swamps than nutrient poor bogs. Restoration temporally increased concentrations of DOC, N and P in mire runoff waters. Nitrogen was leached mainly in organic form, and phosphorus in inorganic form. The mire originating DOC consisted of large and highly aromatic molecules which dominated in the runoffs making the DOC recalcitrant. The quality of DOC did not alter after restoration.

The net bacterial production and bacterial growth efficiency % (BGE%) increased after restoration. This indicates that BP is limited by nutrient availability in boreal mire runoffs. The increased P availability, both artificially elevated and elevated as a result of restoration, increased bacterial production in mire runoff waters. Respiration rates were only slightly increased after restoration, but the elevated pH conditions increased the respiration rates significantly in laboratory experiments. Changes in the proportion of decomposed DOC per day were not detected after restoration. The bacterial activity was generally low in the studied mire runoffs. The low activities are related to recalcitrant DOC in runoff water, which keeps the microbial activity at low levels compared to other aquatic environments.

DOC from an oligotrophic lake did not enhance DOM biodegradation in runoff waters of boreal *Sphagnum* bogs. The situation may be different in lakes in which primary production is higher and autochthonous carbon availability is higher than in the studied Kovero lake.

The higher carbon and nutrient concentrations after restoration increased the microbial activity, even though these mire runoffs consist mainly of recalcitrant organic matter. In the future, the microbial activity in recipient waters should also be monitored after mire restoration to clarify how far the changes in runoff waters extend. More studies with recipient waters, including estuaries, should be done to find out the fate of mire originating DOC, N and P. In addition, longer studies than three year are needed in order to see whether the microbial activity declines along with declining nutrient (N and P) concentrations and if the poorly utilized carbon compounds from mires enhance browning of lake waters.

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NOORA RÄSÄNEN

The main goal of this study was to evaluate effects of restoration on bacterial production and respiration in mire runoff waters during three years at seven different mire sites locating in south-central Finland. Restoration of forestry drained mires increased concentrations of dissolved organic carbon, N and P for 1-5 years in the mire runoffs, which enhanced bacterial production. Experimentally increased pH alone and together with increased P availability supported bacterial respiration. Mixing oligotrophic lake water with mire runoff water did not stimulate microbial activity indicating no priming effect of lake-origin DOC. Further studies are needed to evaluate long-term effects of restoration in recipient waters.

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