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# **Effect of drainage and restoration on the ecology of peatlands in the Šumava Mountains**

Ph.D. Thesis

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### ■ **Annotation**

The effect of drainage and restoration on the ecology of different types of peatlands in the Šumava Mountains was investigated. The study was focused primarily on peat properties, vegetation dynamics, carbon gas fluxes and their linkages under the affected hydrological regimes.

### ■ **Declaration [in Czech]**

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Zuzana Urbanová

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## ■ List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

- I. Urbanová, Z.,** Píček, T., Bárta, J., 2011. Effect of peat re-wetting on carbon and nutrient fluxes, greenhouse gas production and diversity of methanogenic archaeal community. *Ecological Engineering* 37, 1017-1026 (IF = 3.106).  
*Zuzana Urbanová was responsible for field measurements, soil sampling, sample preparation, soil samples analysis, incubation experiment, data assembly, statistical analysis, and writing the manuscript.*
- II. Urbanová, Z.,** Píček, T., Hájek, T., Bufková, I., Tuittila, E.-S., (*in press*). Vegetation and carbon gas dynamics under a changed hydrological regime in central European peatlands. *Plant Ecology & Diversity*, DOI: 10.1080/17550874.2012.688069 (IF = 1.036).  
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- III. Urbanová, Z.,** Bárta, J., Píček, T., (*submitted manuscript*). Methane emissions and methanogenic Archaea on pristine, drained and restored mountain peatlands, Central Europe. *Ecosystems* (IF = 3.495).  
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- IV. Maanavilja, L., Urbanová, Z.,** Píček, T., Bárta, J., Laiho, R., Tuittila, E.-S., (*submitted manuscript*). Effect of long-term drainage and hydrological restoration on peat biogeochemistry in spruce swamp forests. *Soil Biology & Biochemistry* (IF = 3.504).  
*Zuzana Urbanová was responsible for vegetation monitoring on the Czech study sites, soil sampling of the Czech study sites, soil sample preparation and analysis, incubation experiment, DNA extraction, measurement of enzymes activity, data assembly, and revision of the manuscript.*

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## **ABBREVIATIONS**

BOG – bog

BOGD – drained bog

BOGR – restored bog

C – carbon

CH<sub>4</sub> – methane

CO<sub>2</sub> – carbon dioxide

DOC – dissolved organic carbon

DIN – dissolved inorganic nitrogen

DON – dissolved organic nitrogen

EC – electric conductivity

FEN – fen

FEND – drained fen

N – nitrogen

NEE – net ecosystem exchange

NH<sub>4</sub> – ammonium

NO<sub>3</sub> – nitrate

P – phosphorus

PAR – photosynthetically active radiation

POC – particulate organic carbon

P<sub>G</sub> – gross photosynthesis

R<sub>ECO</sub> – ecosystem respiration

S – sulphur

SRP – soluble reactive phosphorus

SSF – spruce swamp forest

T<sub>air</sub> – air temperature

T<sub>soil</sub> – soil temperature

VGA – vascular green area

WT – water table

# 1 INTRODUCTION

## 1.1 Background

Peatlands are wetland ecosystems sustained by high a water table level with specific vegetation where the accumulation of dead organic matter prevails over its decomposition. More than 90% of peatlands are located in the northern temperate and boreal regions and, although their area constitutes only about 3% of the Earth's land surface, they represent approximately one third of the carbon (C) stored in soils. This amount of C accumulated in northern peatlands is approximately equal to half of the C pool in the atmosphere (Gorham et al. 1991; Turunen et al. 2002). On the other hand, the high water level and anoxic conditions supporting C sequestration also enables methane (CH<sub>4</sub>) production and thus peatlands represent one of the natural sources of CH<sub>4</sub> to the atmosphere (Harriss et al. 1985). The massive peat deposits are evidence that peatlands have acted as sinks of atmospheric CO<sub>2</sub> for millennia, but also illustrate the potential for large CO<sub>2</sub> and CH<sub>4</sub> fluxes to the atmosphere at the global scale if peatlands are destabilized by climate and land use changes. Natural peatlands also have a high potential for nutrient retention and transport (Mitsch and Gosselink 2000) and at the landscape level they significantly contribute to biodiversity.

Based on their hydrology and nutrient status, peatlands can be classified into two main groups: (i) ombrotrophic peatlands (bogs) receive water and nutrients only from atmospheric deposition and are therefore acidic and poor in nutrients, (ii) minerotrophic peatlands (fens) receive water and nutrients from groundwater and tend to be more nutrient-rich (Clymo 1983). Differences in hydrology and nutrient status are also reflected in vegetation composition, primary production, organic matter decomposition and C gas fluxes. Hydrology is therefore considered to be a key factor in peatland functioning.

C fluxes are controlled by many interactions between biotic and abiotic factors including water table, temperature, nutrient status and plant community structure (Waddington and Roulet 2000; Riutta et al. 2007; Lund et al. 2010). Therefore a peatland ecosystem and its C sink function is very sensitive to changes in environmental conditions caused by climate or land use changes such as drainage and peat harvesting (Bubier et al. 2003; Holden et al. 2004; Aurela et al. 2007). Drainage has a profound effect on peatland biogeochemistry; it

induces vegetation changes which are reflected in changes to organic matter quality and decomposition rate. Thus peatlands may turn into a source of C into the atmosphere (Moore and Dalva 1993). However in some cases mild drainage can strengthen the C sink function (Minkkinen et al. 1999; 2000; Straková et al. 2012). The contrasting results of different studies may be explained by peatland type, climate and human activity (Minkkinen et al. 1999; Ojanen et al. 2010).

During the first decade of the 21<sup>st</sup> century, there has been an increasing focus on restoring disturbed peatlands and their functions (Vasander et al. 2003; Kimmel and Mander 2010). While peatlands restoration is primarily designed for biodiversity protection and to recover its characteristic hydrology, it can also play an important role in reducing C gas emissions. The restoration practices are based on an increase of the water table through ditch blocking and revegetation by original peatland vegetation. Currently, peatland restoration is also implemented in the Šumava Mountains, Czech Republic, where almost 70% of the peatland area have been affected by past drainage (Bufková 2009). The success of restoration is affected by many factors, especially by the state of degradation and type of peatland (Schumman and Joosten 2006). The time period necessary for successful restoration is still a matter of debate. Understanding the ecological mechanisms controlling peatland response to drainage and restoration is crucial for restoration planning and success.

## **1.2 Soil processes, vegetation and carbon dynamics on pristine peatlands**

Atmospheric CO<sub>2</sub> is fixed by plants through photosynthesis and most of it is released back to the atmosphere through plant respiration. The rest of C is bound into plant biomass or released in the form of root exudates into the soil. Senescent plants (litter) and root exudates are biochemically degraded by microorganisms in the surface oxic layer of the soil and released as CO<sub>2</sub> back to the atmosphere (acrotelm; Ingram 1978). Decomposition continues very slowly under anoxic conditions and C is released to the atmosphere in form of CO<sub>2</sub> and CH<sub>4</sub>.

CH<sub>4</sub> is produced only under anaerobic conditions by methanogenic Archaea and the CH<sub>4</sub> flux is controlled by several interacting factors. The most important factors are (i) the position of the water table, which determines the zones of CH<sub>4</sub> anaerobic production and aerobic oxidation (Dise et al. 1993; Sundh et al. 1995); (ii) soil temperature regulating the metabolic activity of CH<sub>4</sub> producers and



consumers (Yavitt et al. 1997); and (iii) plant community composition which affects CH<sub>4</sub> production through input of organic matter differing in quality and quantity and which also enables transport of oxygen from the atmosphere to the rhizosphere and CH<sub>4</sub> in the opposite direction (Whiting and Chanton 1992; Schimel 1995; Poop et al. 2000; Ström et al. 2003). In boreal mires, about 4-10% of the photosynthetically fixed C returns annually to the atmosphere as CH<sub>4</sub> (Alm et al. 1997) with annual emissions varying between -1 and 42 g C m<sup>-2</sup> a<sup>-1</sup> (Saarnio et al. 2007).

CO<sub>2</sub> and CH<sub>4</sub> emissions show high spatial and temporal variability and the rates of C fluxes are controlled by many interacting biotic and abiotic factors (Waddington and Roulet 2000; Riutta et al. 2007; Trinder et al. 2008; Lund et al. 2010; Maanavilja et al. 2011). Composition of the peatland plant community is considered as one of the most important factors controlling the rates of C fluxes through a peatland ecosystem. It affects the rates of photosynthesis, plant respiration, and the quality and quantity of litter, which is then reflected in the rates and character of microbial decomposition processes in the soil. Plant species composition has been considered to serve as a proxy for indicating and predicting greenhouse gas fluxes (Dias et al. 2010; Couwenberg et al. 2011). Plant community composition is a result of environmental conditions. Therefore, with a change in environmental conditions, caused, e.g., by climate or land-use, a shift in vegetation composition may result in shifts in C fluxes and balance.

In the long-term, there is an imbalance between net primary production and decomposition. Pristine peatlands act as long-term sinks of atmospheric C and approximately 2-16% of primary production accumulates in the form of peat (Päivänen and Vasander 1994; Clymo et al. 1998). The C accumulation rate mainly depends on the extent to which aerobic decay proceeds before the litter reach the anoxic layer. The long-term rate of C accumulation is estimated at 15-30 g C m<sup>-2</sup> a<sup>-1</sup>, but the variation within and between peatlands is large, between 2 – 89 g C m<sup>-2</sup> a<sup>-1</sup> (Gorham et al. 1991; Korhola et al. 1995; Turunen et al. 2001). Peat accumulation rate can vary according to peatland type and its age, climate and geographic position (Gorham 1991; Kayranli et al. 2010). The long-term peat accumulation rate is higher for bogs (21 g C m<sup>-2</sup> a<sup>-1</sup>) as compared to fens (17 g C m<sup>-2</sup> a<sup>-1</sup>) (Turunen et al. 2002). However, the net ecosystem C exchange can switch from positive to negative over short periods of time as a result of relatively small changes e.g. in climatic conditions between the years (Silvola et al. 1996; Bubier et al. 1999; Ward et al. 2009).

In addition to C gas emissions, some C and nutrients are lost from the ecosystem via leaching. Organic and inorganic C are transported by surface and subsurface water as POC, DOC and gaseous forms (CO<sub>2</sub>, CH<sub>4</sub>). Their fluxes are strongly related to catchment hydrology and exhibit great spatial and temporal variability (Roulet et al. 2007; Dinsmore et al. 2010). Evasion of gases from stream water can represent about 12% of C ecosystem uptake and DOC losses can represent up to 30% of C ecosystem uptake (Roulet et al. 2007; Dinsmore et al. 2010; Koehler et al. 2011). Therefore, this water-born flux is also an important part of the peatland C budget.

### **1.3 Effect of drainage on peatland functioning**

Peatlands have been subject to artificial drainage for centuries, mostly for forestry and mining, resulting in several environmental problems. Drainage changes the peatland ecosystem in such a way that many ecosystem services provided by pristine mires are lost. Water level drawdown initiated by drainage is followed by sometimes contradictory responses of the hydrological regime (Prevost et al. 1999; Price et al. 2003; Lundin and Bergquist 1990). Drained peatlands tend to subside rapidly due to the shrinkage and oxidation of peat above the water table. The surface peat layer is consequently compacted and its physical and hydraulic properties change, e.g. bulk density increases and hydraulic conductivity decreases (Schlotzhauer and Price 1999; Price et al. 2003). Denser degraded peat forces the water to fluctuate more relative to the surface and further enhances peat decay and densification (Whittington and Price 2006). Drainage also encourages DOC loss and peat erosion through drainage channels (Holden et al. 2004).

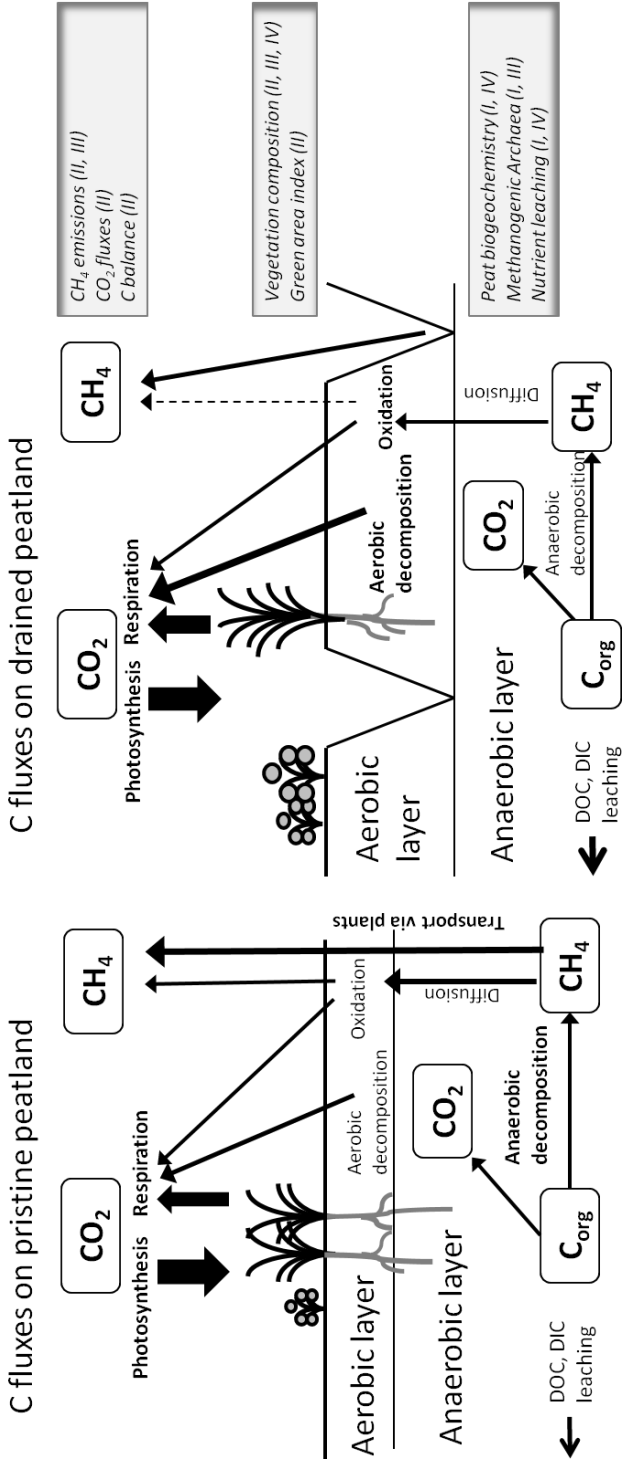
Drainage also brings about changes in the chemistry of the surface peat, which can have an impact on nutrient availability to plants (Laiho et al. 1999) and affects the quality of surface and runoff water (Lundin and Bergquist 1990; Prevost et al. 1999). Mineralization of nutrients is promoted due to increased aeration and microbial activity (Feeman et al. 1993). Mineralization and nitrification of organic N result in an increase of NO<sub>3</sub> concentrations in the pore water of drained peatlands (Olde Venterink et al. 2002; Holden et al., 2004), which can be easily leached out by runoff water (Tiemeyer et al. 2007). These processes are intensified by higher groundwater level fluctuation (Price et al. 2003). Increased leaching losses were also observed for K, Ca and Mg after drainage (Laiho et al. 1999). Phosphorus (P) is frequently sorbed to Fe- or Al-

hydroxides under aerobic conditions and becomes temporarily immobilized (Zak et al. 2004). Increased decomposition rate can be accompanied by decreases in pH and litter quality (Minkkinen et al. 1999).

Drainage causes simultaneous changes in vegetation and decomposition processes and hence affects the rates of C gas fluxes in the peatlands. Typical mire plant species are gradually replaced by forest or meadow vegetation; this proceeds much faster on fens as compared to bogs (Minkkinen et al. 1999; Minkkinen and Laine 2006). C losses from peat following water level drawdown essentially depend on peat quality; therefore a shift in vegetation composition may result in an overall shift in litter quality and decomposability (Hobbie et al. 2000; Straková et al. 2010). Litters with low concentrations of lignin or phenolics, and high nutrient concentrations, decompose relatively fast (e.g. graminoids and herbs). However, *Sphagnum* mosses and shrub litters decompose slowly due to the high content of phenolics and lignin (Bragazza et al. 2007; Laiho 2006).

Drained peatlands tend to emit more CO<sub>2</sub> (Moore and Dalva 1993; Silvola et al., 1996) while the emissions of CH<sub>4</sub> greatly decrease due to limited anaerobic conditions (Nykänen et al. 1995; Roulet and Moore, 1995; Minkkinen et al., 2002) (Figure 1). Furthermore, CH<sub>4</sub> production is reduced because the C input from plants is decomposed in the most upper peat layer and is not as available for methanogens in the deeper anaerobic peat horizons (Bergman et al. 1998; 2000; Basiliko 2003). Long-term drying also decreases the number of methanogens and their diversity because of oxygen toxicity (Yrjälä et al 2011). Lowering of the water table is followed by at least short-term C losses, when easily decomposable organic matter is decomposed (Moore and Dalva 1993; Blodau and Moore 2003). The increase in CO<sub>2</sub> emissions has mostly been seen only with lowering to a certain depth (30-40 cm). Only a negligible increase in CO<sub>2</sub> emissions was observed with a further lowering of the water table under this depth due to the lack of easily oxidized labile C in the deeper soil layers (Silvola et al. 1996).

Changes in the quantity and quality of the above- and below-ground litter may significantly affect the post-drainage C balance of a mire. The common hypotheses supposed that drainage results in increased C emissions and therefore increased radiative forcing of peatlands. However, in some cases, the peat C stores have been found to increase on sites drained for forestry due to increased primary production, especially of trees (Minkkinen et al. 1999, Straková et al. 2012).



**Figure 1:** Simplified scheme of carbon fluxes in pristine and drained peatland. This study focused on effect of peatland drainage and restoration on peat properties, vegetation and carbon gas fluxes (grey frames with Roman numerals refer to the particular papers).

## 1.4 Effect of restoration on peatland functioning

Restoration of disturbed peatlands attempts to re-establish the conditions that are essential for peat growth and restoration of natural ecosystem functions, foremost peat accumulation (Vasander et al. 2003; Kimmel and Mander 2010). The actual results of peatland restoration are encouraging, because they show a positive effect of re-wetting of both fen and bog sites in initiating vegetation succession and C balance development towards those of pristine mires. However, a systematic overview about the development of C gas dynamics, vegetation and peat properties in restored peatlands, especially over longer periods, is still not available.

Starting conditions and restoration techniques vary greatly from one site to other, therefore it is hard to apply existing results for different peatland types in different regions and predict post-restoration development. Most of the knowledge about peatland restoration comes from heavily disturbed sites previously used for peat mining (Tuittila et al. 2000; Rochefort et al. 2003; Marinier et al. 2004; Glatzel et al. 2004; Waddington and Day 2007; Kivimäki et al. 2008; Mahmood and Strack 2011) or for agriculture (Best and Jacobs 1997; Tiemeyer et al. 2005; Kieckbusch and Schrautzer 2007; Hahn-Schöfl et al. 2011). These studies demonstrated the importance of peatland vegetation succession for recovery of ecosystem functioning.

Restoration is followed by an increase of the water table to target level, but the range of water table fluctuation can remain larger because of the altered physical features of peat (Schantz and Price 2006). Rewetting of peatlands can present a risk of increased nutrient and DOC leaching, but this is strongly related to catchment hydrology and nutrient status of the peatland. It is expected that the hydrology will stabilize and the amplitude of variation in water table chemistry will decrease as the original structure of peat will begin to re-establish (Andersen et al. 2010). The water chemistry of restored sites can be still different from pristine sites especially during the first few years following restoration. Higher concentrations of nutrients (e.g. Ca, Mg, Na, Cl,  $\text{NH}_4$ ) were observed especially during the dry period when the water table reached the more decomposed peat (Andersen et al. 2010). Also, DOC concentrations and export can be higher on newly restored peatlands compared to pristine ones until a new moss layer develops (Waddington et al. 2008). On the contrary, a decrease in  $\text{NH}_4$  was observed following rewetting, being explained by uptake by microbes and plants (Andersen et al. 2010). In the case of nutrient richer sites, previously

used for agriculture, there is the risk of enhanced P mobilization due to the reduction of complexes under anaerobic soil conditions and low redox potential (Olde Venterink et al. 2002; Tiemeyer 2007).

Most of the studies of gas fluxes after restoration come from study sites abandoned after peat mining, thus mostly with bare peat on the surface. Rewetting of these sites is usually followed by decreased ecosystem respiration and higher incorporation of CO<sub>2</sub> into the system due to the developing plant cover (Tuittila et al. 2000; Waddington and Price 2000). However, higher ecosystem respiration after restoration was also observed in the case of straw mulch used for faster revegetation (Waddington et al. 2003). Also, restoration of vegetated sites can cause plant mortality and thus provide a fresh substrate for decomposition. CH<sub>4</sub> emissions usually increase after re-wetting, but still remain below levels typical of natural peatlands (Komulainen et al. 1998; Tuittila et al. 2000; Waddington and Day 2007), which can be caused by having a different vegetation composition from pristine peatlands, changed methanogenic community and changed peat properties after a few decades of drainage (Basiliko et al. 2004). On the contrary, extremely high CH<sub>4</sub> emissions were observed in flooded fen grasslands in Germany, because of increased availability of fresh organic matter (Hahn-Schöfl et al. 2011). Little if any research has been done on the effect of drainage and restoration on the methanogenic community (Jerman et al. 2009).

The C balance after re-wetting is strongly influenced by vegetation structure and the used restoration technique so that the carbon fluxes may change during post-restoration development (Komulainen et al. 1999; Waddington et al. 2003; Yli-Petäys et al. 2007; Kivimäki et al. 2008). The time period necessary to successfully restore a peatland is still a matter of debate and depends strongly on the stage of degradation and type of peatland (Schumann and Joosten 2006). Existing results of peatland restorations are ambiguous and therefore understanding ecosystem functioning and reaction to re-wetting requires consideration of both hydrology and soil processes together with vegetation structure, as well as their interactions. Understanding how vegetation change alters the C cycle and C mobilization seems to be crucial for ecosystem C balance estimation and restoration planning.

## 2 AIMS OF THE STUDY

The overall aim of this study was to evaluate the effect of drainage and hydrological restoration on the ecology of different types of peatlands (bog, fen, spruce swamp forest) in the Šumava Mountains, Central Europe. The thesis is focused on (i) the possible risk of increased nutrient leaching and methane emissions after rewetting, (ii) biotic and abiotic factors controlling the vegetation and C gas dynamics and (iii) evaluation of the success of restoration. The specific objectives of the thesis were:

- I** To simulate re-wetting of soils of different types of drained peatlands (bogs and fens) in Central Europe in a laboratory incubation experiment and evaluate its effect on microbial processes in soil, especially on nutrient mobilization and immobilization and CO<sub>2</sub> and CH<sub>4</sub> potential production.
- II** To quantify the variability and factors controlling vegetation and CO<sub>2</sub> gas dynamics in peatlands in the Šumava Mountains for the purpose of restoration planning. To quantify the potential of different peatland plant communities to fix and release C, estimate C gas fluxes for specific plant community types and evaluate the effect of drainage and restoration on ecosystem functioning.
- III** To determine the effect of long-term drainage (few decades) and hydrological restoration (3 years) of peatlands on CH<sub>4</sub> emissions, potential CH<sub>4</sub> production and on the methanogenic *Archaea* community on different types of peatlands under various hydrological regimes.
- IV** To describe and compare the functioning of spruce swamp forests (SSF) as one of the most endangered wetland ecosystems in Central Europe with SSF located in the boreal zone (Finland). To determine how several decades of drainage of SSF has changed their peat biogeochemistry, and if any effect of rewetting on peat biogeochemistry is observable within the first years after restoration.

## 3 DESCRIPTION OF STUDY SITES AND METHODS

### 3.1 Study sites

All field measurements, soil sampling and experiments described in this thesis were carried out on three ombrotrophic bogs (pristine, restored, drained) and two minerotrophic fens (pristine, drained). Later, the study sites were extended by six sites of spruce swamp forests (SSF; 2 pristine, 2 drained, 2 restored) to cover the variation in peatland types and different degree of anthropogenic alteration in the Šumava Mountains, Czech Republic. All of these study sites are situated in the Šumava National Park and are included under the long-term project of peatland restoration. Pristine and restored bogs (BOG, BOGR respectively) and SSF are situated on the upland plateau of the Šumava Mountains at an altitude of 1100 – 1200 m a.s.l. with the cold and humid climate. Mean annual temperature is 3.2 °C and annual precipitation around 1200 mm. The drained bog (BOGD), pristine fen (FEN) and drained fen (FEND) are located at an altitude of 900 m a.s.l. in the Kremelna River Valley which has a milder climate, with a mean annual temperature 4 °C and mean annual rainfall of 1000 mm. Three studies (**I**, **II**, **III**) were performed at the bog and fen sites and study **IV** in SSF. Together with the Czech SSF, 12 Finnish SSF in Southern Finland were also studied for comparison of boreal and temperate zones.

Peatlands in the area have generally been drained for forestry purposes, locally intensive drainage having been implemented during the last 50 years. Rewetting was achieved by blocking the drainage ditches with timber dams and also by filling ditches partially with organic material (branches, remains of timber, etc.). Rewetting of the bog site was undertaken in August 2008, one SSF site was restored in 2005-2006 and the second SSF site in 2009.

### 3.2 Field measurements

In order to study the effects of drainage and restoration on the ecology of peatlands many different approaches were used combining measurements in the field, laboratory experiments, and chemical and biological analysis including modern molecular methods. This study was carried out from 2007 to 2011. During this period basic environmental parameters such as water table (WT), pH, EC and pore water chemistry were regularly measured in plastic boreholes installed at each bog and fen site (**I-III**). The BOGR and FEND sites were



equipped with automatic meteorological stations measuring air temperature ( $T_{\text{air}}$ ), soil temperature ( $T_{\text{soil}}$ ), and precipitation (**I-III**).

The static closed chamber method was applied to quantify C gas fluxes and show their variability and dynamics (Alm et al. 2007) (**II, III**). Permanent sample plots for C gas flux measurements were established to represent variations in the vegetation structure typical of each site.  $\text{CO}_2$  exchange measurements were carried out at two- to three-week intervals during the 2009 (**II**) and 2010 (unpublished) growing seasons. Each measurement consisted of a couple of measurements of net  $\text{CO}_2$  ecosystem exchange (NEE) and total ecosystem respiration ( $R_{\text{ECO}}$ ) using a transparent chamber equipped with a cooling system and infrared gas analyser for  $\text{CO}_2$  concentration measurement.  $\text{CH}_4$  flux was measured using closed opaque chambers at two to three week intervals during the 2009-2011 growing seasons on the same sample plots as the  $\text{CO}_2$  exchange (**II, III**).

During gas flux measurements,  $T_{\text{air}}$ ,  $T_{\text{soil}}$  and WT were recorded (**II, III**). Photosynthetically active radiation (PAR) inside the chamber was measured simultaneously with the NEE measurement (**II**). Simultaneously, the vascular green area (VGA) was measured in each sample plot at two- or three-week intervals to relate the seasonal and spatial dynamics of the vegetation to the variation in  $\text{CO}_2$  and  $\text{CH}_4$  fluxes (**II, III**) (Wilson et al. 2007). In addition, the projected or top cover of mosses was estimated once during the growing season.

Process-based non-linear regression models for  $\text{CO}_2$  exchange were constructed and parameterised individually for each gas exchange sample plot according to Tuittila et al. (2004) and Laine et al. (2009) (**II**).

### **3.3 Soil sampling, laboratory experiments and analyses**

Soil sampling of the upper soil layer (300 mm) was done several times during the study period for laboratory analyses of total contents of basic elements (C, N, S, P) bulk density, dry weight, pH and soil microbial biomass C and N (Vance et al. 1987) (**I-IV**). Soil samples were used for aerobic and anaerobic laboratory incubations with the aim to assess nutrient mobilization and immobilization under aerobic and anaerobic conditions (**I, IV**), potential production of  $\text{CO}_2$  and  $\text{CH}_4$  (**I, III, IV**) and to determine the quantity and diversity of methanogens (Hales et al. 1996; Watanabe et al. 2004; Kim et al. 2008) (**I, III, IV**). Soil sampling and some analysis were done repeatedly before and after rewetting to note the changes caused by re-wetting (**III**). Microbial activity was characterized

by the activities of several extracellular enzymes involved in the degradation of cellulose and lignin (Ngo et al. 1980; Niku-Paavola et al. 1990; Hoppe 1993; Marx et al., 2001) (IV). Physico-chemical characteristics of peat and pore water are presented in Paper I (Table 1) and Paper IV (Table 1).

## 4 RESULTS AND DISCUSSION

The first part of the thesis deals with peat re-wetting and the possible risks of peatland water regime restoration, focusing on nutrient leaching and potential CO<sub>2</sub> and CH<sub>4</sub> production (I). Rewetting aims to reduce soil aeration and decrease N mineralisation, and hence to decrease N availability for wetland plants. Previous studies in this area had described an ambiguous effect of rewetting on nutrients mineralization and leaching. Peatlands can act as a source of DON, DOC and SRP in the first years after rewetting, but the mobile nutrient pool will probably decrease in the years following rewetting due to processes such as sedimentation and peat formation (Wallage et al. 2006; Kieckbusch and Schrautzer 2007; Olde Venterink et al. 2007). Rewetting can strongly stimulate denitrification, which can play an important role in the removal of N from restored peatlands (Silvan et al. 2002; Kieckbusch and Schrautzer 2007). However, N mineralisation need not necessarily decrease after rewetting (Olde Venterink et al. 2002). In our experiments, N mineralization was the same or lower under anaerobic conditions as compared to aerobic ones for all study sites (pristine and drained bogs and fens). A significant decrease of NO<sub>3</sub><sup>-</sup> concentration was observed in peat samples during anaerobic incubation which was result of either denitrification or nitrate reduction to ammonia. On the other hand, a much lower rate of nitrification was measured after rewetting and therefore denitrification will become a less important process in restored sites. In field conditions, a lower rate of denitrification can be expected after re-wetting because of assimilation of N by plants.

In our experiment, rewetting led to increased NH<sub>4</sub><sup>+</sup> and DON concentrations in the drained fen and DOC concentration increased both in the drained fen and degraded drained bog. On the contrary, rewetting did not affect P mobility in any studied soil. Based on these results, we can conclude that soils from minerotrophic mires reacted more dynamically to re-wetting compared to bogs, and therefore, leaching of some nutrients (especially nitrogen) and DOC may be expected from drained fens after their water regime is restored. We can suppose only a low risk of enhanced P leaching after rewetting in situ. Under aerobic conditions, more nutrients (N, P) were mobilized than under anaerobic conditions. Therefore less nutrients should be released from the studied soils after rewetting compared to the state before (drained conditions).

It is generally accepted that rewetting leads to decrease of soil organic matter mineralization, but CH<sub>4</sub> production can be supported. Also in our experiments,

CO<sub>2</sub> potential production decreased and CH<sub>4</sub> potential production increased in all peat samples after rewetting as has been shown by many previous studies (Komulainen et al. 1998; Tuittila et al. 2000; Waddington and Price 2000). The strong correlation between aerobic and anaerobic CO<sub>2</sub> and anaerobic CH<sub>4</sub> production rates suggests that in bogs and drained fens, methanogenic bacteria are limited by a lack of available organic substrate (Moore and Dalva 1997). In our study, a greater availability of substrate for soil microorganisms was indicated by the large potential CO<sub>2</sub> and CH<sub>4</sub> production rates in samples from the pristine sites (both fen and bog) compared to samples from drained sites. Traditionally, lowered water table with the consequent increase in oxygen availability in the surface soil was assumed to result in accelerated rates of decomposition, higher microbial and enzymatic activity, which lead to C losses from ecosystem (Alm et al. 1999; Laiho 2006). However, this concept is based on the observations of the short-term effect of drainage on peatlands. In the long-term perspective, changes on peatlands induced by drainage can have contradicting results in terms of C balance. In our case, few decades of drainage led to a considerable decrease of the peat decomposability and microbial activity (IV). It can be caused by decrease of pH and nutrient availability, increased content of recalcitrant organic material (old peat), and also by changes in the litter quality and quantity due to the changed vegetation composition on drained sites. Analogical results were observed by Minkkinen et al. (2002) and Straková et al. (2011; 2012), who found that peat C stores had even increased following drainage.

Our results showed that there is a potential for increased CH<sub>4</sub> production in drained peatlands after rewetting. Within a short period (three months) after rewetting, the number of methanogens increased by one or two orders of magnitude and the rate of methanogenesis increased by two or more orders of magnitude. However, CH<sub>4</sub> emissions in situ depend strongly on environmental factors and the actual activity of methanotrophs and methanogens, which can be limited by competition for substrate (Jerman et al. 2009). All of these parameters and CH<sub>4</sub> emissions in situ are strongly affected by vegetation composition which is described in paper III.

The results described above (I) indicated that the minerotrophic peatlands react more dynamically to changed hydrological regime than the ombrotrophic bogs and we can also expect their faster regeneration after rewetting. In further chapter (IV), minerotrophic spruce swamp forests (SSF) were studied and

restoration success was evaluated. We measured the surface peat biogeochemical properties in drained, restored and pristine SSF in the Šumava Mts. and in southern Finland. Restoration success is commonly monitored and evaluated as changes in vegetation. However, the recovery of the key soil processes could be slower than that of the vegetation and might take more than a century (Moreno-Mateos et al. 2012). Knowledge regarding the restoration succession of soil processes is lacking.

*Sphagnum* mosses tend to direct the post-restoration succession towards a self-maintaining state by changing the biogeochemical properties of the system (van Bremen et al. 1995). In our study sites, drainage led to decrease in *Sphagnum* cover and *Sphagnum* mosses survived only in ditches and wet patches, as observed also by Laine et al. (1995). Long-term drainage changed the peat physicochemical properties that affect microbial functioning (Laine et al. 1995). We observed lower pH, more compact and decomposed peat with significantly higher bulk density and lower C/N ratio in the drained sites compared to the pristine sites. Rewetting had been effective in providing better growth conditions for *Sphagnum* and its cover and thickness have increased towards the pristine reference level. After rewetting, the accumulating new organic matter decreased bulk density and increased C/N ratio. Also, pH started to change towards the pristine level.

The changed peat properties were reflected in microbial activity and microbial biomass, which were the lowest on the drained SSF sites and the highest on the pristine sites. Drainage had caused a decrease of ca. 40% in the surface peat layer microbial biomass in our sites, while Andersen et al. (2006) and Basiliko et al. (2007) observed a decrease of ca. 70% in soil microbial biomass caused by the total removal of the top 60 cm peat layer. It demonstrates the severe impact of peatland drainage for forestry on the peat microbial stock. After drainage, fast decomposition of the surface aerated layer and substantial changes in vegetation composition leading to the changed litter quality and quantity can have a large impact on the soil organic matter decomposition rate on peatlands (Straková et al. 2012). We found that CO<sub>2</sub> potential production, enzymatic activity, and microbial biomass were higher in the pristine SSF sites than in the drained and restored sites, and the analogous was observed in bogs and fens (**Paper I**). The pristine sites with extensive *Sphagnum* cover and sedges produced fresh surface peat continuously which supported high microbial activity. Higher CO<sub>2</sub> production was measured in rewetted sites than in the drained sites, although not statistically significant. The results from other studies

show that reaching the pristine level of microbial activity is possible with a 30 cm layer of new peat in the sites rewetted more than 30 years (Glatzel et al. 2004; Basiliko et al. 2007).

In conclusion, substantial change was observed in peat bulk density and C/N ratio in the rewetted sites, while other peat properties had not changed significantly. However, results from the principal component analysis, and the differences that were observed but remain under the significance limit suggest that peat microbial processes in these sites are in the process of directional change.

The **second** and **third paper** of the thesis summarise the results of direct field measurements of C gas fluxes and assess the effects of drainage and restoration on C gas dynamics, vegetation and ecosystem functioning. Direct measurements of CO<sub>2</sub> and CH<sub>4</sub> fluxes in the field using the static chamber method were done for subsequent modelling and estimation of the C balance of the studied ecosystems.

Our results in paper **II** highlighted the differences between pristine, drained and restored peatlands, their vegetation composition and C gas fluxes (gross photosynthesis, ecosystem respiration and CH<sub>4</sub> emissions). We hypothesised based on previous studies (Moore and Dalva 1993; Silvola et al., 1996) that drained peatlands are net sources of C. However, we found that drainage did not necessarily lead to a negative ecosystem C balance, similarly as was found for drained boreal peatlands by Minkkinen et al. (1999) and Strakova et al. (2012). In boreal peatlands, a positive C balance was explained by increased primary production due to forest development on drained peatlands and a shift in litter quality and quantity, whereas no or only a few trees were present at our study sites. Despite a significant change of plant species composition occurring on drained areas, all of our study sites acted as sinks of C during the growing season except the most drained areas near the drainage ditches, where a negative C balance was calculated (Table 1). These most heavily drained parts of the drained bog and fen had the most changed original vegetation structure, with either forest or meadow communities, while typical peatland plant species were not found on these plots. However, the areas with dense cover of *Molinia caerulea* acted as a strong C sink and formed an exception to this. Also, the C balance was positive for plant communities in the wetter parts of the drained sites, where the vegetation was less influenced compared to the more drained zones along the margins of ditches. Functionally, these communities were

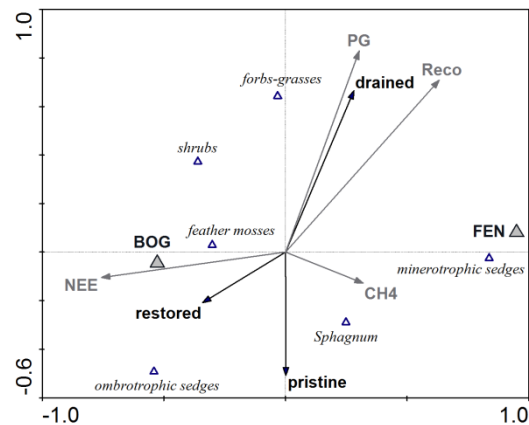
similar to those of pristine sites and their C sequestration was not or only slightly affected. For restoration purposes, the important feature of this slightly drained stage is that it continues to retain some of the original ecosystem functions and should facilitate future ecosystem restoration. C balance of the restored bog was still more similar to the drained bog than the pristine one. High C sequestration levels were found for *Trichophorum caespitosum* lawns and low dwarf shrubs with *Eriophorum vaginatum* on the pristine bog. On the contrary, the pristine fen did not accumulate C or was a weak sink during the two studied growing seasons, having much higher CH<sub>4</sub> emissions compared to the pristine bog. Based on these results, it appears that the plant communities present on a site significantly affected C fluxes and total C balance of the whole ecosystem. Therefore, the plant communities could be used as indicators of a positive or negative C balance as mentioned by Dias et al. (2010) and Couwenberg et al. (2011). When talking about the C balance of the whole ecosystem, then the aquatic C fluxes have to be taken into account too. In our study, we measured only the exchange of gaseous forms of C (CO<sub>2</sub>, CH<sub>4</sub>), but possible losses in the form of DOC, POC and DIC by surface and subsurface waters can contribute significantly to C losses from peatland system especially on drained sites (Holden et al. 2004; Dinsmore et al. 2010; Koehler et al. 2011).

**Table 1.** Estimated seasonal C balance (g m<sup>-2</sup> per growing season) for plant community groups during the 2009 and 2010 growing season (from May 20 to October 10). Positive values denote influx into the ecosystem and negative values denote efflux from the ecosystem. Net C balance is a result of integrated CO<sub>2</sub>-C and CH<sub>4</sub>-C fluxes. Plant community groups are described in **Paper II**.

Plant community group	C balance	
	2009	2010
FEN flex rostrata	-12,4	64,1
FEND girg-holcus	149,8	59,5
FEND sedge-grass	4,5	30,9
BOG trich lawn	210,7	222,9
BOG low shrub	172,9	334,6
BOGR trich lawn	129,0	102,4
BOGR high shrub	85,7	231,1
BOGD high shrub	-27,2	-16,6
BOGD inter shrub	154,3	170,8
BOGD molinia	237,9	321,6

The effect of drainage was clearly evident on the VGA, which was greater on drained sites compared to pristine ones. The increase in VGA was caused by

changes in plant species composition on the drained sites, where shrubs and grasses became dominant at the expense of minerotrophic and ombrotrophic sedges. The abundance of grasses and sedges appeared to be the key factor related to CO<sub>2</sub> fluxes. In drained sites, the effect of grasses cover was clearly reflected in gross CO<sub>2</sub> assimilation (P<sub>G</sub>) as well as ecosystem respiration (R<sub>ECO</sub>), which increased (Figure 2). The vegetation composition changed both on the drained bog and fen with the changes being much greater on the more nutrient-rich fen where the original mire species have almost vanished. This supports the hypothesis that vegetation succession is related to the nutrient status of a site (Laine et al. 1995; Minkkinen et al. 1999) and post-restoration development might also be related to nutrient status, as observed by Komulainen et al. (1999).



**Figure 2.** Ordination diagram of an RDA displaying the distribution of functional plant groups in relation to carbon exchange components (P<sub>G</sub>, R<sub>ECO</sub>, NEE, CH<sub>4</sub>) and state of study sites (pristine, restored, drained). Vascular green area (VGA) of functional plant groups was used as community data. The first two canonical axes together explained 45.8% of the variability.

CH<sub>4</sub> emissions dynamics were studied in the field in combination with molecular analysis to provide insights into the interactions between ecosystem processes and microbial community structure and functioning. CH<sub>4</sub> emissions varied between 0 and 90 g CH<sub>4</sub>-C m<sup>-2</sup> during the 2009, 2010 and 2011 growing seasons with the highest CH<sub>4</sub> emissions measured on the pristine fen (37-90 g CH<sub>4</sub>-C m<sup>-2</sup>) (III). The pristine fen was a much stronger CH<sub>4</sub> emitter than the pristine bog (8 – 10 g CH<sub>4</sub>-C m<sup>-2</sup>), this result is consistent with Saarnio et al. (2007). It is known that CH<sub>4</sub> emissions are the results of CH<sub>4</sub> production and consumption, and are influenced by many biotic and abiotic factors (temperature, pH, water table, plant species composition etc.) (Sundh et al. 1995;



Yavitt et al. 1997; Ström et al. 2003). If water table and peat temperature were almost similar on both the pristine bog and fen, CH<sub>4</sub> emissions would seem to depend on plant species and especially on the substrate quality and quantity they provide to microorganisms. Higher availability of organic substrate for microorganisms was detected in the pristine fen (I). In the frame of interannual variability, drought periods seemed to play an important role in seasonal CH<sub>4</sub> fluxes. It follows that the most important factors influencing CH<sub>4</sub> emissions were water regime together with plant species composition.

A few decades of lower water table led to decreased CH<sub>4</sub> emission, CH<sub>4</sub> potential production, abundance and diversity of methanogens on drained sites compared to pristine ones (III). These post-drainage changes were more obvious in fens than on bogs, which is consistent with our previous findings (I, II). The spatial variation of CH<sub>4</sub> emissions seemed to be influenced not only by WT level and its fluctuation, but also by the presence or absence of original peatland species and the quality of soil organic matter.

CH<sub>4</sub> emissions were still substantially lower in the restored bog than the pristine bog and none of the measured parameters (vegetation structure, number of methanogens and methanogenic community composition) showed significant changes three years after rewetting although the water table increased and its fluctuation was lower than before restoration. The reason may be that CH<sub>4</sub> emissions are strongly related to vegetation present on a site and not only to water table level. This theory is supported by studies dealing with the restoration of cutover peatlands, which reported significant increases of CH<sub>4</sub> emissions related to revegetation during the first post-restoration years (Tuittila et al. 2000; Waddington and Day 2007; Mahmood and Strack 2011). Therefore, it is likely that the time period necessary for regeneration of CH<sub>4</sub> emissions is a result of restoring all of the elementary factors, including water table, vegetation and methanogenic community, together.

## 5 CONCLUSIONS

The study demonstrates that drainage had a strong impact on plant community composition which changed towards a drier successional stage (on drained bogs) or forest or meadows plant communities (on drained SSF, fens and heavily drained bogs) (**II, IV**). Despite a decrease in the water table level and a significant change in species composition caused by drainage, the drained peatlands can still act as C sinks during the growing season except for the most drained areas (**II**). The findings in this study are in contradiction to the traditional concept that drainage leads to higher decomposition, microbial activity and C losses. In the long term (a few decades after drainage), biogeochemical changes to the peat and vegetation changes led to a considerable decrease in peat decomposability and microbial activity (**I, IV**). This suppression of microbial activities may be the reason for C accumulation occurring in the drained peatlands (**II**).

For restoration purposes, the important feature of less drained areas in drained sites is that they continue to retain some of the original ecosystem functions and should facilitate future ecosystem restoration (**II, III**).

Rewetting of drained peatlands is often linked with the possible risk of increased nutrient leaching and deterioration of water quality in the catchment. However, the laboratory study showed that there is only a very low risk of nutrient leaching in the case of nutrient poor mountains bogs and fens (**I**).

The study confirmed the traditional concept of faster post-drainage changes in minerotrophic fens compared to ombrotrophic bogs. Moreover, the results indicated a more dynamic reaction of minerotrophic mires to rewetting compared to bogs. Therefore, their faster regeneration after rewetting can be expected (**I, III, IV**). No significant changes were observed in vegetation structure, CH<sub>4</sub> emissions and the methanogenic community during the first three years after restoration in bog (**III**). However, in the case of SSF, the results showed that changes to peat biogeochemistry during the first few years after restoration are in the direction towards pristine conditions (**IV**). The time period necessary for regeneration of a functioning peatland is dependent upon the restoration of all of the elementary factors, including water table, vegetation and peat biogeochemistry, together.

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## **RESEARCH ARTICLES**



## Paper I

**Urbanová, Z.**, Pícek, T., Bárta, J., 2011. Effect of peat re-wetting on carbon and nutrient fluxes, greenhouse gas production and diversity of methanogenic archaeal community. *Ecological Engineering* 37, 1017-1026.



## **Abstract**

Many peatlands were affected by drainage in the past, and restoration of their water regime aims to bring back their original functions. The purpose of our study was to simulate re-wetting of soils of different types of drained peatlands (bogs and minerotrophic mires, located in the Sumava Mountains, Czech Republic) under laboratory conditions (incubation for 15 weeks) and to assess possible risks of peatland water regime restoration – especially nutrient leaching and the potentials for CO<sub>2</sub> and CH<sub>4</sub> production. After re-wetting of soils sampled from drained peatlands (simulated by anaerobic incubation) (i) phosphorus concentration (SRP) did not change in any soil, (ii) concentration of ammonium and dissolved organic nitrogen (DON) increased, but only in a drained fen, (iii) DOC increased significantly in the drained fen and degraded drained bog, (iv) CO<sub>2</sub> production decreased, (v) CH<sub>4</sub> production and the number of methanogens increased in all soils, and (vi) archaeal methanogenic community composition was also affected by rewetting; it differed significantly between drained and pristine fens, whereas it was more similar between drained and pristine bogs. Overall, the soils from fens reacted more dynamically to re-wetting than the bogs, and therefore, some nutrients (especially nitrogen) and DOC leaching may be expected from drained fens after their water regime restoration. However, if compared to their state before restoration, ammonium and phosphorus leaching should not increase and leaching of nitrates and DON should even decrease after restoration, especially during the vegetation season. Further, CO<sub>2</sub> production in soils of fens and bogs should decrease after their water regime restoration, whereas CH<sub>4</sub> production in soils should increase. However, we cannot derive any clear conclusions about CH<sub>4</sub> emissions from the ecosystems based on this study, as they depend strongly on environmental factors and on the actual activity of methanotrophs in situ.

## Abstrakt

Většina rašelinišť byla v minulosti ovlivněna odvodněním a revitalizace jejich vodního režimu by měla vést k obnově jejich původních funkcí. Cílem našeho výzkumu bylo simulovat zaplavení půdy různých typů odvodněných rašelinišť na Šumavě (vrchoviště, minerotrofní rašeliniště) v laboratorních podmínkách (inkubace 15 týdnů) a vyhodnotit případná rizika spojená s revitalizací vodního režimu rašelinišť – především vyplavování živin a potenciální produkci CO<sub>2</sub> a CH<sub>4</sub>. Po zaplavení půdy odvodněných rašelinišť (simulované anaerobní inkubací) (i) se koncentrace fosforu (SRP) nezměnila, (ii) koncentrace amonia a rozpuštěného organického dusíku (DON) vzrostla pouze v odvodněném minerotrofním rašeliništi, (iii) koncentrace rozpuštěného organického uhlíku (DOC) vzrostla průkazně ve vzorcích odvodněných minerotrofních rašelinišť a degradovaného odvodněného vrchoviště, (iv) produkce CO<sub>2</sub> poklesla (v) a naopak produkce CH<sub>4</sub> a počet metanogenních Archaea vzrostl ve všech půdách. (vi) Společenstvo metanogenních Archaea se lišilo významně mezi odvodněným a nenarušeným minerotrofním rašeliništěm, avšak společenstvo na odvodněném a nenarušeném vrchovišti si bylo více podobné. Celkově půdy minerotrofních rašelinišť reagovaly rychleji na zaplavení než půdy vrchovišť, a proto vyplavování některých živin po revitalizaci (především dusík) a DOC lze očekávat především z minerotrofních rašelinišť. Avšak, ve srovnání se stavem před zaplavením, vyplavování amonia a fosforu by nemělo vzrůst a vyplavování nitrátů a DON by se naopak mělo po revitalizaci snížit, především během vegetační sezóny. Produkce CO<sub>2</sub> by se měla snížit po revitalizaci jak na minerotrofních rašeliništích tak na vrchovištích, zatímco produkce CH<sub>4</sub> by měla narůstat. Jednoznačné závěry o emisích CH<sub>4</sub> z ekosystému na základě této studie nelze vyvodit, protože výsledné emise CH<sub>4</sub> jsou silně ovlivněny mnoha faktory prostředí a aktuální aktivitou metanotrofních bakterií *in situ*.

*Následující pasáž o rozsahu 20 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uložené na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.*

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## Paper II

**Urbanová, Z.**, Pícek, T., Hájek, T., Buřková, I., Tuittila, E.-S., (*in press*).  
Vegetation and carbon gas dynamics under a changed hydrological regime in  
central European peatlands. *Plant Ecology & Diversity*, DOI:  
10.1080/17550874.2012.688069.





## Abstract

Northern peatlands are known for having significant stocks of terrestrial soil carbon (C). However, little is known about how peatlands function under various land uses and what impacts land-use change has on their functioning in central Europe.

The objective of our study was to quantify the variability and controls of typical plant communities in terms of C gas dynamics on bogs and fens affected by a changed hydrological regime in the Bohemian Forest, Czech Republic.

Carbon dioxide (CO<sub>2</sub>) exchange and methane emissions (CH<sub>4</sub>) were measured in bogs (pristine, drained, restored) and in fens (pristine, drained) during the 2009 growing season. We applied cluster analysis to define plant communities and non-linear response models to quantify the variation in CO<sub>2</sub> dynamics among the communities.

Drainage had a strong impact on vegetation; forest and meadows species were dominant on drained peatland sites and the vascular green area was higher than on pristine sites. The net ecosystem CO<sub>2</sub> exchange (NEE) varied from -27 to 241 g CO<sub>2</sub>-C m<sup>-2</sup> per growing season on the bogs and from 27 to 153 g m<sup>-2</sup> on the fens. The most-drained parts of the bog and fen with the most changed vegetation structure acted as both net C sources and very weak C sinks; however, areas dominated by *Molinia caerulea* acted as a strong C sink. Plant communities on the wetter parts of drained sites had a positive seasonal NEE, comparable with NEE on pristine sites. Seasonal CH<sub>4</sub> emissions were relatively low (0–9 g CH<sub>4</sub>-C m<sup>-2</sup>) at all sites and did not influence net C balance, with the exception of pristine fen where CH<sub>4</sub> emissions with average 90 g C m<sup>-2</sup> led to a negative total growing season C balance. Water regime restoration caused neither a significant change in plant composition nor any major changes, such as plant die-back or increased CH<sub>4</sub> emissions during the first season after restoration.

Our results showed that C gas fluxes, and in turn the C balance of the whole ecosystem, were largely determined by plant community type. Drainage did not necessarily lead to a negative ecosystem C balance; however, a significant change of species composition occurred on most drained areas. The less-drained parts on drained sites, where original peatland species and original functions are preserved, could facilitate future ecosystem restoration.

## Abstrakt

Rašeliniště jsou z globálního hlediska významnými zásobárnami půdního uhlíku (C). Avšak stále není definováno, jaký vliv mají změny hydrologického režimu a využívání krajiny na fungování rašelinišť ve střední Evropě.

Cílem našeho studia bylo kvantifikovat variabilitu a faktory kontrolující typická rostlinná společenstva ve smyslu dynamiky plyných toků uhlíku na vrchovištích a minerotrofních rašeliništích s ovlivněným hydrologickým režimem na Šumavě, v České republice.

Výměna oxidu uhličitého (CO<sub>2</sub>) a emise metanu (CH<sub>4</sub>) byly měřeny na vrchovištích (přirozené, odvodněné, revitalizované) a na minerotrofních rašeliništích (přirozené, odvodněné) v průběhu vegetační sezóny 2009. Klastrová analýza byla použita k definování vegetačních skupin a nelineární regresní model byl použit ke stanovení variability toků CO<sub>2</sub> mezi vegetačními skupinami. Odvodnění mělo silný vliv na vegetaci; lesní a luční druhy byly dominantní na odvodněných rašeliništích a listová plocha (VGA) zde byla vyšší než na přirozených rašeliništích. Celková ekosystémová výměna CO<sub>2</sub> (NEE) byla v rozmezí od -27 po 241 g CO<sub>2</sub>-C m<sup>-2</sup> za vegetační sezónu na vrchovištích a od 27 po 153 g m<sup>-2</sup> na minerotrofních rašeliništích. Části nejvíce ovlivněné odvodněním s nejvíce pozměněnou vegetací na vrchovištích i na minerotrofních rašeliništích byly zdrojem nebo pouze slabou zásobárnou C. Výjimku představovaly porosty *Molinia caerulea*, které fungovaly jako silná zásobárna C. Rostlinná společenstva na vlhčích částech odvodněných rašelinišť měla pozitivní sezónní NEE srovnatelnou s NEE na přirozených rašeliništích. Sezónní emise CH<sub>4</sub> byly relativně nízké (0–9 g CH<sub>4</sub>-C m<sup>-2</sup>) na všech lokalitách a neovlivnily celkovou sezónní bilanci C. Výjimku představovalo přirozené minerotrofní rašeliniště s průměrnými sezónními emisemi CH<sub>4</sub> 90 g C m<sup>-2</sup>, které vedly k negativní celkové sezónní bilanci C. Revitalizace vodního režimu nezpůsobila žádné změny ve vegetační struktuře, ani nevedla k odumírání rostlin či nárůstu emisí CH<sub>4</sub> v prvním roce po revitalizaci.

Naše výsledky ukazují, že složení vegetace bylo nejdůležitějším faktorem určujícím celkovou bilanci C ekosystému. Odvodnění nemusí nutně vést k negativní C bilanci ekosystému, ačkoli změna druhového složení vegetace byla zřejmá na většině odvodněných lokalit. Části rašelinišť méně ovlivněné odvodněním, kde se stále vyskytují původní rašeliništní druhy a jsou zde zachovány původní funkce rašeliniště, mohou v budoucnu přispět k snazší revitalizaci ekosystému.

*Následující pasáž o rozsahu 24 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.*

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## Paper III

**Urbanová, Z., Bárta, J., Pícek, T.,** (*submitted manuscript*). Methane emissions and methanogenic Archaea on pristine, drained and restored mountain peatlands, Central Europe. *Ecosystems*.

III



## Abstract

Natural peatlands are known as an important source of methane ( $\text{CH}_4$ ). However, most peatlands in Central Europe were drained for forestry purposes in the past and some of them have been recently restored, both having a strong impact on  $\text{CH}_4$  emissions.

The main aim of our study was to determine the effect of long-term drainage (a few decades) and hydrological restoration (3 years) on  $\text{CH}_4$  emissions, potential  $\text{CH}_4$  production and on the methanogenic Archaea community in different types of peatlands under various hydrological regimes. For this purpose,  $\text{CH}_4$  emissions together with biotic and abiotic variables were measured over three growing seasons, in vitro potential  $\text{CH}_4$  production was determined, and qPCR and DGGE fingerprinting were used for methanogenic community description in three ombrotrophic bogs (pristine, drained, restored) and two fens (pristine, drained) located in the Šumava National Park within the Bohemian Forest, Czech Republic.

The highest  $\text{CH}_4$  emissions ( $37 - 91 \text{ CH}_4\text{-C g m}^{-2}$ ),  $\text{CH}_4$  potential production and the highest diversity of the methanogenic community were observed in the pristine fen and bog ( $8 - 10 \text{ CH}_4\text{-C g m}^{-2}$ ). In the frame of interannual variability, a drought period seemed to play an important role in seasonal  $\text{CH}_4$  fluxes. Plant species composition together with water table seemed to be the most important factors controlling  $\text{CH}_4$  emission. Drainage led to a significant decrease in  $\text{CH}_4$  emissions ( $0 - 7 \text{ CH}_4\text{-C g m}^{-2}$ ), potential  $\text{CH}_4$  production, and the abundance and diversity of methanogens as compared to pristine sites. These post-drainage changes were more obvious in the fen site than on bog sites. However, none of the measured parameters showed significant changes during the three years after rewetting. We assume that water table was not the main factor controlling  $\text{CH}_4$  emission and other factors such as vegetation composition and input of available substrate for methanogenic community were more important. Therefore it appears that the period necessary for regeneration of  $\text{CH}_4$  emissions is the result of restoring all of these elementary factors together.

## Abstrakt

Přirozená rašeliniště jsou známa jako důležité zdroje metanu ( $\text{CH}_4$ ). V minulosti byla většina rašelinišť ve střední Evropě odvodněna pro lesnické účely a v současné době se přistupuje k revitalizaci jejich vodního režimu. Obojí však může mít silný vliv na emise  $\text{CH}_4$ .

Hlavním cílem našeho výzkumu bylo stanovit vliv dlouhodobého odvodnění (několik desetiletí) a hydrologické revitalizace (3 roky) na emise  $\text{CH}_4$ , potenciální produkci  $\text{CH}_4$  a společenstvo metanogenních Archaea v různých typech rašelinišť s odlišným hydrologickým režimem. Pro tento účel byly měřeny emise  $\text{CH}_4$  společně s abiotickými a biotickými proměnnými prostředí během tří vegetačních sezón. Dále byla stanovena *in vitro* potenciální produkce  $\text{CH}_4$  a metody qPCR a DGGE fingerprinting byly použity pro popsání společenstva metanogenů na třech vrchovištích (přirozené, odvodněné, revitalizované) a na dvou minerotrofních rašeliništích (přirozené, odvodněné) na Šumavě, Česká republika.

Nejvyšší emise  $\text{CH}_4$  ( $37 - 91 \text{ CH}_4\text{-C g m}^{-2}$ ), produkce  $\text{CH}_4$  a nejrozmanitější společenstvo metanogenů bylo pozorováno na přirozeném minerotrofním rašeliništi a na přirozeném vrchovišti ( $8 - 10 \text{ CH}_4\text{-C g m}^{-2}$ ). V rámci meziroční variability toků  $\text{CH}_4$  hrály významnou roli období sucha. Hladina vody společně se složením vegetace se zdály být nejdůležitějšími faktory ovlivňujícími emise  $\text{CH}_4$ . Odvodnění vedlo k významnému poklesu emisí  $\text{CH}_4$  ( $0 - 7 \text{ CH}_4\text{-C g m}^{-2}$ ), potenciální produkce  $\text{CH}_4$  a početnosti a diverzity metanogenů ve srovnání s přirozenými lokalitami. Tyto změny po odvodnění byly ještě významnější na minerotrofním rašeliništi než na vrchovišti. Zatímco změny nebyly pozorovány ani v jednom ze sledovaných parametrů 3 roky po revitalizaci a revitalizované vrchoviště bylo stále velmi podobné odvodněnému vrchovišti. Emise  $\text{CH}_4$  byly nejnižší na nejvíce odvodněných částech rašelinišť, kde zcela chyběly původní rašeliništní druhy rostlin.

Přestože se hladina vody zvýšila po revitalizaci ostatní parametry jako například vegetační struktura a metanogenní společenstvo zůstaly nezměněny první tři roky po zaplavení vrchoviště. Z toho usuzujeme, že pro doba potřebná pro regeneraci emisí  $\text{CH}_4$  je výsledkem obnovy všech těchto základních faktorů dohromady.

*Následující pasáž o rozsahu 20 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.*

*Publikace byla odeslána do časopisu Ecosystems.*

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## Paper IV

Maanavilja, L., **Urbanová, Z.**, Pícek, T., Bárta, J., Laiho, R., Tuittila, E.-S., (*submitted manuscript*). Effect of long-term drainage and hydrological restoration on peat biogeochemistry in spruce swamp forests. Soil Biology & Biochemistry.

IV





## **Abstract**

Rewetting of peatlands drained for forestry is a growing practice that aims to restore threatened ecosystems, such as spruce swamp forests, improve water quality in intensively managed catchments or recreate carbon stores. To estimate restoration success and the ecosystem effects of rewetting, we measured surface peat (top 30 cm) biogeochemical properties in drained, restored and pristine spruce swamp forests in southern Finland (n=3+6+3) and the Šumava Mountains, Czech Republic (n=2+2+2). The sites had been drained to enhance tree growth 40 to 75 years prior to restoration. Rewetting was conducted in the years 1995 to 2008 by blocking or filling the ditches; sampling was conducted in 2010. Surface peat bulk density had increased substantially following drainage, but after rewetting it changed back towards pristine conditions. Microbial biomass and peat decomposability, measured as carbon dioxide production in aerobic and anaerobic incubations, were highest in the pristine sites. In the rewetted sites, a change towards pristine functioning was observed. In conclusion: accumulation of new organic matter changed surface peat bulk density relatively quickly, while microbial biomass and activity recovered more slowly.

## Abstrakt

Rašeliniště odvodněná pro lesnické účely (např. rašelinné smrčiny) jsou v posledních letech revitalizována s cílem obnovení ohrožených ekosystémů, zlepšení kvality vody v povodí nebo obnovy funkční zásobárny uhlíku. Ke stanovení úspěšnosti revitalizace a vlivu zaplavení na ekosystém jsme měřili biogeochemické vlastnosti svrchní vrstvy rašeliny (30 cm) v odvodněných, revitalizovaných a nenarušených rašelinných smrčinách v jižním Finsku ( $n=3+6+3$ ) a na Šumavě ( $n=2+2+2$ ). Lokality byly odvodněné za účelem zvýšení produkce dřeva před 40 až 75 lety. Revitalizace byla provedena v letech 1995 až 2008 přehrazením odvodňovacích rýh nebo jejich zaplněním. Odběr vzorků byl prováděn v roce 2010. Objemová hmotnost svrchní vrstvy rašeliny se značně zvýšila vlivem odvodnění, avšak po zaplavení se objemová hmotnost opět vracela k hodnotám nenarušených lokalit. Mikrobiální biomasa a rozložitelnost rašeliny, měřené jako produkce  $\text{CO}_2$  při aerobní a anaerobní inkubaci, byly nejvyšší v nenarušených lokalitách. Na revitalizovaných lokalitách byla pozorována změna sledovaných parametrů směrem k hodnotám nenarušených lokalit. Závěrem lze říci, že díky akumulaci nové organické hmoty dochází po zaplavení k relativně rychlé změně objemové hmotnosti povrchové vrstvy rašeliny, avšak mikrobiální biomasa a aktivita mikroorganismů regeneruje mnohem pomaleji.

*Následující pasáž o rozsahu 10 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uložené na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.*

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