Dissertationes Forestales 191

Restoration of ecosystem structure and function in boreal spruce swamp forests

Liisa Maanavilja

Department of Forest Sciences
Faculty of Agriculture and Forestry
University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in lecture room B2, B-building (Viikki Campus, Latokartanonkaari 7, Helsinki) on May 8th 2015, at 12 o'clock noon.

Title of dissertation:
Restoration of ecosystem structure and function in boreal spruce swamp forests

Author: Liisa Maanavilja

Dissertationes Forestales 191

http://dx.doi.org/10.14214/df.191

Thesis supervisor:
Dr. Eeva-Stiina Tuittila
School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

Pre-examiners:
Dr. Tapio Lindholm
Finnish Environment Institute, Helsinki, Finland
Dr. Roxane Andersen
Environmental Research Institute, Thurso, UK

Opponent:
Assistant Professor, Dr. Juul Limpens
Department of Nature Conservation and Plant Ecology, Wageningen University,
The Netherlands

ISSN 1795-7389 (online)
ISBN 978-951-651-471-3 (pdf)
ISSN 2323-9220 (print)
ISBN 978-951-651-472-0 (paperback)

2015

Publishers:
Finnish Society of Forest Science
Natural Resources Institute Finland
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial office:
The Finnish Society of Forest Science
P.O. Box 18, FI-01301 Vantaa, Finland
http://www.metla.fi/dissertationes

Maanavilja, L. 2015. Restoration of ecosystem structure and function in boreal spruce swamp forests. Dissertationes Forestales 191. 31 p.
http://dx.doi.org/10.14214/df.191

Drainage to increase timber production has drastically decreased the area of undrained spruce swamp forests in northern Europe. In restoration by rewetting, drainage ditches are blocked to restore the original hydrology and, ultimately, the structure, function and ecosystem services of undrained boreal spruce swamp forests. This study quantifies the restoration success of rewetting regarding plant community composition, moss community carbon assimilation potential, *Sphagnum* biomass production and surface peat biogeochemistry, and aims to determine the main controls of success. The study sites comprised 18 rewetted, nine undrained and nine drained spruce swamp forests in southern Finland, complemented by sites in the Šumava Mountains, Czech Republic. Drainage had taken place decades prior; the rewetted sites varied in their rewetting age from 1 to 15 years.

The results show that rewetting has to raise the water table above a threshold to initiate any changes in the drained ecosystem. If the threshold is crossed, the changes that occur will be rapid. Two strands of development emerged throughout the different components of the ecosystem: development towards the undrained reference state and development towards a new direction, different from both the undrained and the drained state. Rewetting created favourable conditions for *Sphagnum* photosynthesis. *Sphagnum* mosses recovered in cover and biomass production rapidly. The new growth started the accumulation of the porous surface organic matter layer characteristic of mires, which increased microbial decomposition activity in the surface organic layer towards undrained levels. Meanwhile, rewetting applied on the compacted, physicochemically altered peat created wet, unstable hydrological conditions, which increased the cover of opportunistic plant species in the understory and caused high NH_4 mobilization and CH_4 production in the surface organic layer. Demanding spruce swamp forest species were lacking at the rewetted sites, but rewetting was successful in restoring the common species and directing the ecosystem towards mire-like functioning.

Keywords: peatland forest, vegetation, *Sphagnum*, moss photosynthesis, biomass production, biogeochemistry

ACKNOWLEDGEMENTS

This thesis is a result of the efforts of the many people who gave their time and expertise to the research project. Thank you for accompanying me on this venture. First, I want to express my gratitude to my supervisor Eeva-Stiina Tuittila. Thank you for your insightful thinking and persistent support. To my co-authors, thank you for your contribution. It has been a privilege to work with so many intelligent, creative and generous people. Your knowledge, skills and enthusiasm, be it in peatland restoration, plant ecophysiology, statistics or soil biogeochemistry, made this work happen. To my pre-examiners Dr. Tapio Lindholm and Dr. Roxane Andersen, thank you for your constructive comments on the thesis manuscript. To Prof. Harri Vasander, thank you for guiding me through the thesis process.

I thank Parks and Wildlife Finland, Metsähallitus Forestry, and the Administration of the Šumava National Park for providing the study sites for this thesis. Thank you Seppo Kallonen, Tuomas Haapalehto, Pekka Vesterinen and others at Parks and Wildlife Finland, as well as Antti Maukonen (Metsähallitus Forestry), Sakari Sarkkola, Timo Penttilä (Natural Resources Institute Finland) and Kari Minkkinen (University of Helsinki) for helping me to establish the study site network. Many thanks to Kaisu Aapala and Harri Tukia from the Finnish Environment Institute for your support during the construction of this project and onwards. I also want to thank Kimmo Syrjänen (Finnish Environment Institute) for opening the world of mosses and liverworts for me.

I am deeply grateful to the research assistants for their contribution to the field and laboratory work: Annukka Närhi, Noora Ilola, Janne Sormunen, Salli Uljas, Henna Mäkinen, Anssi Venho, Kirsi Kurki-Miettinen, Maija Aarva, Jérôme Le Ster and Mita Nagarkar − this work would not have been possible without you. I thank Daniel Vaněk, Terezia Říhová and Marjut Wallner for their help in the laboratory, Lauri Mehtätalo and Jarkko Isotalo for statistical advice, and David Wilson for checking the language of the manuscripts.

This thesis was made possible by funding from the Finnish Cultural Foundation, the Graduate School in Forest Sciences (GSForest) and the University of Helsinki. The work was mainly carried out in the Department of Forest Sciences at the University of Helsinki. Department of Ecosystem Biology at the University of South Bohemia, Lammi Biological Station and Hyytiälä Forestry Field Station provided excellent facilities for the field and laboratory work. All these institutions are greatly acknowledged. Thanks are due to all staff members at the Department of Forest Sciences, and to Peatlanders in particular, for the warm, supportive and friendly working environment during these years.

To my friends and family, thank you for all the fun and support.

LIST OF ORIGINAL ARTICLES

This dissertation is based on the following articles, which are referred to by their Roman numerals. The articles **I** and **II** are reprinted with kind permission of the publishers, while articles **III** and **IV** are author versions of the submitted manuscripts.

I Maanavilja L., Aapala K., Haapalehto T., Kotiaho J. S., Tuittila E.-S. (2014). Impact of drainage and hydrological restoration on vegetation structure in boreal spruce swamp forests. Forest Ecology and Management 330: 115–125. http://dx.doi.org/10.1016/j.foreco.2014.07.004

II Kangas L., Maanavilja L., Hájek T., Juurola E., Chimner R. A., Mehtätalo L., Tuittila E.-S. (2014). Photosynthetic traits of *Sphagnum* and feather moss species in undrained, drained and rewetted boreal spruce swamp forests. Ecology and Evolution 4: 381–396. http://dx.doi.org/10.1002/ece3.939

III Maanavilja L., Kangas L., Mehtätalo L., Tuittila E.-S. Rewetting of drained boreal spruce swamp forests results in rapid recovery of *Sphagnum* production. Submitted manuscript.

IV Maanavilja L., Urbanová Z., Bárta J., Picek T., Laiho R., Tuittila E.-S. Restoration of peatland soil functioning: responses of peat soil biogeochemistry to drainage and rewetting of spruce swamp forests. Submitted manuscript.

Liisa Maanavilja is fully responsible for the summary of this doctoral thesis.

I	L. Maanavilja planned the study together with the other authors. She conducted the vegetation survey, was responsible for the data analysis, and served as the main author and reviser of the manuscript.
II	L. Maanavilja participated in the planning of the study, conducted a part of the statistical analysis, interpreted the results in cooperation with the other authors, and served as the main author together with L. Kangas, bringing the manuscript to its final form and serving as the reviser of the manuscript.
III	L. Maanavilja participated in the planning of the study and in organizing the field and laboratory work. She conducted the statistical analyses, interpreted the results in cooperation with the other authors, and served as the main author of the manuscript.
IV	L. Maanavilja participated in the planning of the study, and was responsible for the field and laboratory work regarding the peat samples from the sites in Finland. She conducted the statistical analysis, interpreted the results together with the other authors, and served as the main author of the manuscript.

TABLE OF CONTENTS

INTRODUCTION

Human land use has reshaped the landscape of the earth: ca. 80% of the terrestrial biologically productive land has been altered for human use (Hannah et al. 1994, Sanderson et al. 2002), which has resulted in a massive loss of biodiversity and ecosystem services (Millennium Ecosystem Assessment 2005). In international policymaking, restoration of degraded ecosystems is perceived as one of the prime means to combat the losses (Convention on Biological Diversity 2010). Peatlands are a priority for action because of their special value as carbon storage and natural water filters (Joosten et al. 2012). In the second commitment period of the Kyoto Protocol (2013-2020) countries can voluntarily elect to include carbon emissions and removals from peatland rewetting in their carbon accounting (Blain et al. 2014). As a consequence of the international policy and changing attitudes within societies, restoration of peatlands is on the rise.

In northern Europe, drainage by ditching to increase timber production is a major cause of peatland degradation (Joosten and Clarke 2002). Although vegetation and surface peat layer are not directly removed or manipulated, drainage alters the peatland ecosystem in such fundamental ways that many ecosystem services provided by pristine mires are lost. After water-level drawdown, *Sphagnum* mosses recede to drainage ditches and moist patches (Laine et al. 1995). The microclimate of the site is altered: enhanced tree growth increases shading, while lower water table position decreases air humidity. Input waters are channeled to the ditches, which changes the hydrological regime of the catchment and may lead to leaching of nutrients and organic matter, (Sallantaus 1992, Dinsmore 2011). This decreases the availability of nutrients for microbes and plants at the site, but contributes to potentially harmful effects in receiving water bodies.

Peat subsidence and compaction take place, at first through physical collapse and compression and later through advancing decomposition, which is likely to affect peat hydrological (Weiss et al. 1998) and microbial properties. Drainage increases the depth of the aerobic surface layer, which favors decomposition (Jaatinen et al. 2008). In nutrient-rich boreal peatlands, such as spruce swamp forests, decomposing drained peat can be a substantial source of carbon into the atmosphere (Ojanen et al. 2013).

Due to their large timber production potential, spruce swamp forests are among the peatland types most commonly altered by drainage (Päivänen and Hånell 2012). In Finland, the area of undrained spruce swamp forests in south- and mid-boreal vegetation zones has declined by 73% since 1950s, from 1 200 000 to 300 000 hectares (Kaakinen et al. 2008), and they are consequently classified as threatened habitats (Kaakinen et al. 2008, 2012). Undrained spruce swamp forests sustain high biodiversity (Hörnberg et al. 1998), store carbon, and filter catchment waters before they enter the watercourses (Nieminen et al. 2005b). Due to degradation by drainage, these services are lost.

Restoration of spruce swamp forests by rewetting began in Finland in the 1990s with the aim of improving habitat quality in national parks and other conservation areas (Aapala and Tukia 2008). At present, spruce swamp forests are also restored in protected areas on private land and in commercial forests (Government of Finland 2008). Concurrently, spruce swamp forests have been experimentally rewetted to be used as buffer zones for runoff waters from areas of intensive forestry to reduce concentrations of organic matter, nitrogen and phosphorus (Nieminen et al. 2005ab, Väänänen et al. 2008, Vikman et al. 2010).

While high expectations are set for restoration of peatlands, we still need research on to what extent it is possible to restore the ecosystem services lost as a result of drainage. The different components of the ecosystem structure and function produce the ecosystem services that deliver the desired benefits (Fig. 4 in de Groot et al. 2010). The underlying principle of ecological restoration is that by changing the main environmental drivers, structure and function change back to a pristine-like state (Dobson et al. 1997). However, different components of ecosystem structure and function may recover at different pace, or some may show no notable recovery at all. For instance, recovery of the key soil processes might be slower than that of the vegetation (Andersen et al. 2006) and take more than a century (Moreno-Mateos et al. 2012). Or, on the contrary, key functions, such as carbon dioxide (CO_2) sink function, may recover faster than vegetation structure (Tuittila 2000). Quantification of the restoration success of different ecosystem components is important for assessing the effectiveness of restoration measures in fulfilling the policy targets.

Benefits desired from spruce swamp forest restoration can be classified into three groups: aesthetic benefits, biodiversity benefits, and functional benefits. Ecological restoration aims to benefits similar to those provided by pristine ecosystems rather than maximal benefits (SERI 2004).

Aesthetic benefits concern the human experience of our landscape surroundings (Gobster et al. 2007). In conservation areas, an important restoration target is, for intrinsic and recreational values, to restore the perceived landscape and site naturalness: a pristine-like landscape structure and the feel of a spruce swamp forest. These depend on the basic structure of the ecosystem: in spruce swamp forests on the formation of a *Sphagnum* carpet, created by *Sphagnum* colonization and height growth that build the characteristic soft moss surface, and on pristine-like water table position and uneven tree stand structure.

Biodiversity is one of the main motivations for ecological restoration (Bullock et al. 2011). Biodiversity refers to site-level species occurrence and abundance structure, or to landscape-level biodiversity to which the restored site is expected to contribute. The concept of boreal spruce swamp forests encompasses a wide spectrum of biotopes that vary in their structural and biodiversity properties (Kaakinen et al. 2012, Kutenkov 2012). Undrained spruce swamp forests, especially those that exhibit high diversity of different surfaces relative to water table, sustain high site biodiversity (Hörnberg et al. 1998, Økland et al. 2008). In the landscape scale, pristine spruce swamp forests with abundant dead wood provide habitats for specialized old-growth forest species that have become threatened in intensively managed forest landscapes (Ohlson et al. 1997, Syrjänen et al. 2010). Thus spruce swamp forest rewetting, in order to promote biodiversity, should create new wet microhabitats and dead-wood microhabitats.

Functional benefits from spruce swamp forests comprise carbon sequestration and storage and water filtration functions. Accumulation of new *Sphagnum* biomass could be expected to contribute to carbon sequestration, but the peat accumulation process is poorly known even for undrained boreal spruce swamp forests, as it has not been a priority for research. High water table could be expected to decrease decomposition by decreasing the depth of aerobic layer. If rewetting ceases the high CO_2 emissions from old peat measured in drained sites (Ojanen et al. 2013), significant carbon benefits are expected – but only if the decreased CO_2 emissions are not counteracted by increased CH_4 emissions from the blocked ditches and other new wet habitats (Cooper et al. 2014, Koskinen et al. 2012). Spruce swamp forests rewetted as buffer zones for runoff waters have functioned as efficient sinks for dissolved organic matter (Nieminen et al. 2005b) and, after more than six years after rewetting, for phosphorus (Väänänen et al. 2008) and nitrogen (Vikman et al. 2010). During the first (seven) years after rewetting though, rewetting of spruce swamp forest may increase leaching of phosphorus, nitrogen and total organic carbon (Nieminen et al. 2005a, Koskinen et al. 2011). Carbon sink and water filtration functions are considered to depend on a successful water table rise, formation of a new acrotelm (the porous aerobic layer typical of pristine peatlands) from new *Sphagnum* growth (Lucchese et al. 2010), and from development of pristine-like biogeochemical functioning.

The aim of this thesis is to quantify restoration success of spruce swamp forests following rewetting and to determine the main controls of the success. The work addresses the recovery of four key components of the ecosystem structure and function: **I** plant community composition of the understory **II** moss community carbon assimilation potential, **III** *Sphagnum* biomass production, and **IV** surface peat biogeochemistry to a pristine-like state.

The research subject comprises rewetted spruce swamp forests of varying number of years since rewetting. Restoration success is approached using undrained spruce swamp forests to represent the restoration target and drained sites to represent the starting point for restoration. Restoration is considered to be successful if, ultimately, the rewetted sites were situated within the range of variation of the undrained reference ecosystems in the region regarding the measured properties. The study on peat biogeochemistry **II** comprised additional rewetted, drained and undrained spruce swamp forests in the Šumava Mountains, Czech Republic.

The work is a first comprehensive study on restoration of boreal spruce swamp forest, activity that is growing in magnitude and could potentially be used for multiple ecosystem services.

MATERIAL AND METHODS

Study sites

The main set of study sites in Finland comprised 9 undrained, 9 drained and 18 rewetted spruce swamp forests in southern Finland (Fig. 1a). The same number of undrained, drained and rewetted sites was sampled in each pre-defined sampling region (Fig. 1a). The number of rewetted sites was higher than the number of each set of reference sites: due to the effect of time since rewetting and larger variation in environmental conditions, the rewetted sites were expected to show more variation in the measured variables than the reference sites. The sampling was designed to represent the prevailing restoration practice in southern Finland. Accordingly, also insufficiently rewetted sites were included in the sample: this enabled the estimation of the limit conditions for successful restoration.

The sites were selected to represent the same original (before drainage) site type, *Vaccinium myrtillus* spruce (*Picea abies*) mires (Laine et al. 2012). This spruce swamp forest type is the most common in southern Finland (Kaakinen et al. 2012): it does not harbor the largest number of species (Kutenkov 2012), but of this habitat type it was possible to obtain a reasonably large, representative sample without introducing too much variation due to variable ecohydrological status. Two sites (**I,** Appendices A, B), where the understory vegetation was surveyed, were found to represent a more nutrient-rich site type: they were not included in study on plant community composition (**I**), but were used as supplementary cases in the multivariate analysis. All sites had peat depths >80 cm. Ditches were dug in the drained and rewetted sites between 1900 and 1980 (**I**, Appendix A).

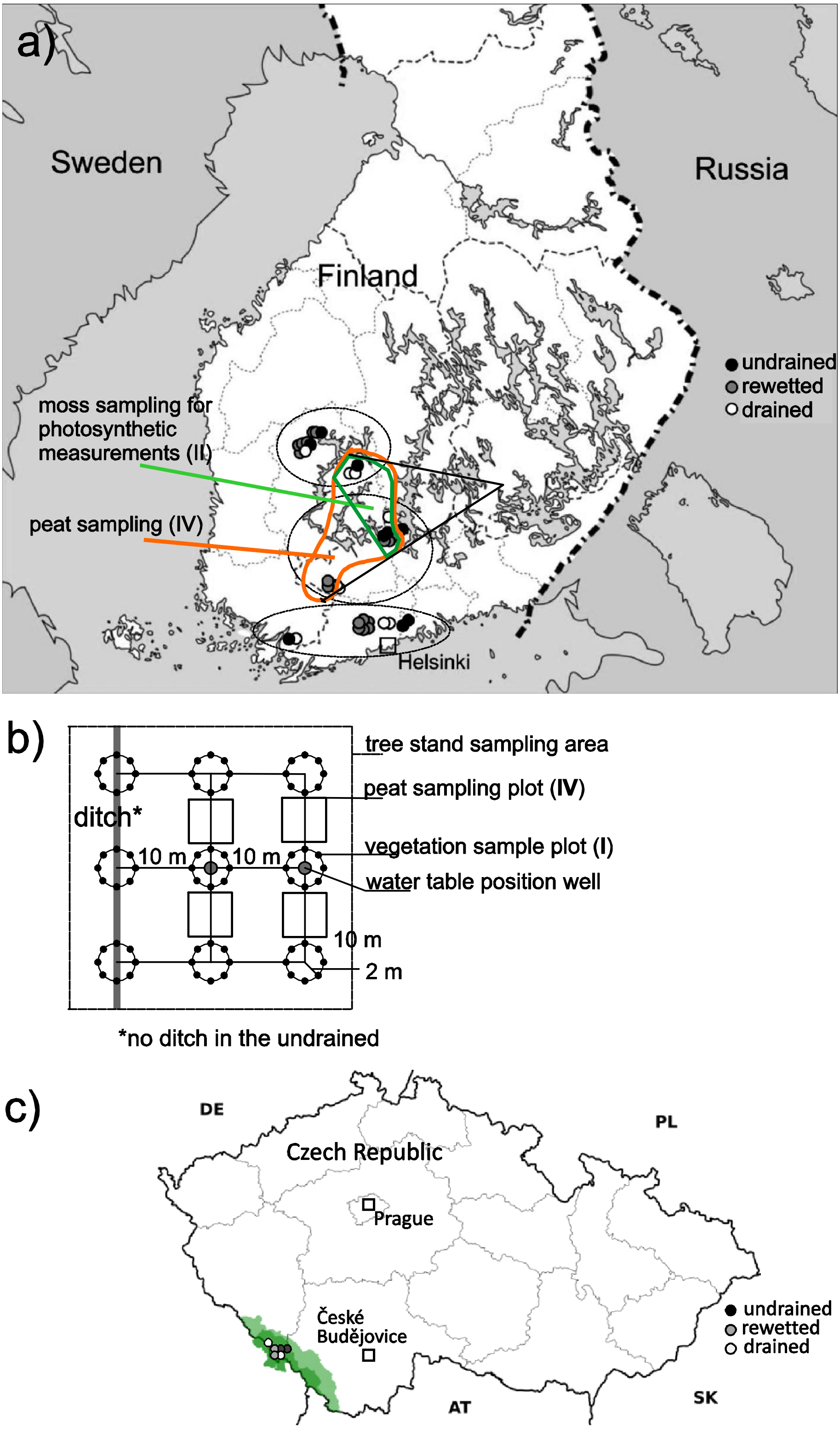

a)
Sweden
Russia
Finland
moss sampling for photosynthetic measurements (II)
peat sampling (IV)
Helsinki
● undrained
● rewetted
○ drained
b)
tree stand sampling area
peat sampling plot (IV)
vegetation sample plot (I)
water table position well
ditch*
10 m
10 m
10 m
2 m
*no ditch in the undrained
c)
DE
PL
Czech Republic
Prague
České Budějovice
AT
SK
● undrained
● rewetted
○ drained

Figure 1. (facing page) Study sites and sampling: a) location of the study sites in Southern Finland b) sampling grid, and c) location of the peat sampling sites (II) in the Šumava Mountains, Central Europe. In a), each sampling region (dashed circles), comprised 3 undrained, 3 drained and 6 rewetted sites. For the studies on moss photosynthetic traits (II) and peat biogeochemistry (IV), subsamples of the sites were used (solid lines in a). Moss growth nets (III) were situated by the vegetation sample plots in b).

Rewetting was conducted by Metsähallitus, Natural Heritage Services unit (presently Parks and Wildlife Finland), a public agency that forms part of the state-run enterprise Metsähallitus, during the years 1995 to 2008 (**I**, Appendix A): the ditches were filled with peat or blocked with wooden or peat dams (Vesterinen et al. 2013).

In **III**, this set of study sites was used in its entirety. In **I**, two outlier sites showing features of a more fertile site type (**I**, Appendices A and B) were used only as supplementary variables in the ordination analysis on plant community structure and not used for the calculation of the biodiversity measures. In **II**, photosynthetic measurements were conducted for mosses sampled at three undrained, three drained and three rewetted sites, but moss cover data from all the 36 sites was used also. In **IV**, peat was sampled at three undrained, three drained and five rewetted spruce swamp forests in southern Finland, and two undrained, two drained and two rewetted spruce swamp forests in the Šumava Mountains, southwestern Czech Republic (Fig. 1c). The sites were selected to be typical of each geographical area and similar in their estimated initial nutrient level within each area, based on their site type. Because of a more humid climate and higher atmospheric N deposition, the sites in the Šumava Mountains represented a wetter and more nutrient-rich site type than the ones in Southern Finland. The drained and rewetted sites in the Šumava Mountains were originally drained in the 1970s. Rewetting was conducted by the Administration of the Šumava National Park in 2005 and 2008 by ditch blocking.

Water table position and tree stand measurements

Water table position was measured manually in two perforated tubes (at the rewetted sites also in one tube at the filled ditch) five times at each site: in July-August 2009, May-June 2010, May 2011, September 2011 and May 2012. Height and diameter of the living trees at breast height were measured, and volume calculated for each tree species (Norway spruce *Picea abies* (L.) H. Karst and downy birch *Betula pubescens* Ehrh.) in a 30 x 30 m square that enclosed the sample plots (Fig. 1b) in May-June 2010.

Plant community structure (I)

At each site, in total 72 circular sample plots, 30 cm in diameter, were placed in a clustered design (Fig. 1b). The cover of mosses, hepatics and vascular plants, and the cover of different microhabitats (ditch, ditch bank, lawn, hummock, depression, tree base, tree root, stump, log) were estimated for each plot. *Sphagnum girgensohnii* Russow and *Sphagnum russowii* Warnst were treated as one species unit, since they could not be visually identified from each other without extensive effort.

To evaluate restoration success, the similarity of the understory plant community composition of the rewetted sites to the undrained and drained communities was quantified. A redundancy analysis (RDA) was performed on the undrained and drained communities, with the undrained and drained states as predictors and sampling region (Fig. 1a) as a covariate. The RDA analysis was performed on log-transformed, centered plant species data using Canoco 5 (ter Braak and Šmilauer 2012). The rewetted communities were added to this ordination space as supplementary variables: their scores on the constrained ordination axis indicated their position on the undrained-drained gradient. The distance of the rewetted communities as a group to the drained and undrained communities was analyzed using ANOVA on site scores; the interactive effects of time since rewetting and water table position on similarity to undrained was analyzed using a linear model in R version 2.13.1 (R core team 2012).

To examine how environmental variables shape plant community composition in the studied spruce swamp forest ecosystems, a hierarchical variation partitioning analysis was performed. The aim was to detect the most influential predictor variables from many correlated variables, comprising the management categories (undrained, drained, rewetted), sampling region (three levels), water table position, spruce volume, birch volume, total tree stand volume and cover of different microhabitats. The analyses were conducted on log-transformed, centered plant species data using Canoco 5 (ter Braak and Šmilauer 2012).

Species richness, evenness and diversity of the understory plant community were calculated for each site using the measures and terminology defined by Tuomisto (2010, 2012). Richness S is the number of species present in an area. Evenness ^1E describes the proportional abundances of the species in the site (Tuomisto 2012). Diversity ^1D is the product of richness and evenness: the number of equally-abundant species needed to obtain the same mean proportional species abundance as observed (Tuomisto 2010). ^1D is equal to the exponential function of Shannon entropy. Differences in richness, evenness and diversity across the management categories were analyzed using linear models and linear mixed-effect models (package lme4, Bates et al. 2012) in R.

Moss community carbon assimilation potential (II)

For assessing changes in the carbon assimilation potential of the spruce swamp forest moss communities following drainage and rewetting, the plant cover data (**I**) was re-analyzed by acknowledging the marked spatial variation related to the presence of the ditch. The vegetation sample plots were classified into habitats: undrained, drained main site, ditch of drained site, rewetted main site, ditch of rewetted site. To quantify the effect of habitat on moss community composition in the 36 sites of the vegetation survey, a redundancy analysis (RDA) was applied on centered, non-transformed moss species data using the program Canoco 5 (ter Braak and Šmilauer 2012).

Photosynthetic properties of *Sphagnum* and feather mosses were measured monthly during the summer of 2011 from mosses collected at three undrained, three drained and three rewetted sites in southern Finland. Dominant moss species in each site (3–4 species, except for the first sample date 4–6) were collected from where they were the most abundant. *Sphagnum girgensohnii* and *Pleurozium schreberi* (Brid.) Mitt., which were common to all sites, were always collected regardless of dominance. In the drained and rewetted sites, note was taken whether the moss sample was collected from near the ditch or away from the ditch.

Photosynthetic CO_2 exchange and chlorophyll fluorescence were measured in the laboratory using a portable gas exchange fluorescence system GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany). Measurements on CO_2 exchange provide information on the photosynthetic efficiency and light responses of the mosses, while chlorophyll fluorescence measures levels of plant stress due to water limitations, light intensity, and/or nutrient supply (Maxwell and Johnson 2000). Five photosynthetic properties, estimated from the measured data, were in the focus: 1) the maximum rate of light-saturated gross photosynthesis (*PMAX*) showing the photosynthetic capacity, 2) dark respiration (*R*), 3) light compensation point of net photosynthesis ($PPFD_c$,): a measure of photosynthetic light use efficiency at low light, 4) actual quantum yield of photosystem II in high light (Φ_{PSII}) showing the efficiency of the photosynthetic machinery, and 5) maximum potential quantum yield of photosystem II (F_v/F_m): an indicator of plant physiological state.

To explore the main trends in the variation of moss photosynthetic traits, we used principal component analysis (PCA) on measured photosynthetic properties. To determine the effects of habitat and species on the photosynthetic properties, a partial RDA analysis in Canoco 5 (ter Braak and Šmilauer 2012) and linear and non-linear mixed-effect models in the package nlme of R (Pinheiro et al. 2012) were performed.

***Sphagnum* height and biomass increment (III)**

Sphagnum height and biomass increment was measured using grow-through nets located in undrained, drained and rewetted spruce swamp forests: in 18 nets at each of the 36 sites, altogether 648 nets. *Sphagnum* was allowed to grow through the nets during the summer season (May-Sept, nine nets each site) or during one year (nine nets each site). Growth increment was quantified at two spatial levels. Firstly, growth increment in height (cm) and dry biomass (g m^{-2}) was measured at the *Sphagnum* patch level and the effects of water table position and *Sphagnum* species on it were quantified using linear mixed-effect models in the lme4 (Bates et al. 2012) and nlme (Pinheiro et al. 2012) packages of R. Secondly, ecosystem *Sphagnum* biomass production (g m^{-1} yr^{-1}) was estimated based on the moss cover data (**I**). The sensitivity of the ecosystem *Sphagnum* biomass production to variation in water table position, species composition and ditch area was evaluated using the linear mixed-effect models (**III**).

Peat biogeochemistry (IV)

Surface peat (top 30 cm) biogeochemical properties were studied from samples collected at undrained, drained and rewetted spruce swamp forest sites in Southern Finland (site n=3+3+5, respectively) and in the Šumava Mountains, Czech Republic (site n=2+2+2, respectively). Four samples (Fig. 1b) were taken at each site (Fig. 1ac), altogether 76 samples; each was composite of three 1–2 dm^3 sub-samples. The measured properties comprised 1) peat physicochemical properties: bulk density, peat C/N and pH, 2) microbial biomass: microbial C and C/N, 3) microbial decomposition activity: CO_2 production under aerobic and anaerobic conditions, CH_4 production under anaerobic conditions, and activities of decomposing enzymes betaglucosidase, oxidases, phenoloxidases and Mn-peroxidase, and 4) microbial transformations of C and N: immobilization or mobilization of soluble organic carbon (SOC), total organic nitrogen (TON), ammonium (NH_4-N) and nitrate (NO_3-N) under aerobic and anaerobic conditions.

The responses of peat biogeochemistry as an assemblage of diverse biogeochemical properties were analyzed using multivariate methods (ter Braak and Šmilauer 2012) on centered and standardized peat variable data. The effects of management category and geographical area were separated and analyzed using partial RDAs. The effects of water table position and plant community composition on peat properties were quantified using a hierarchical variation partitioning analysis. After these overall analyses, the behavior of individual peat properties were studied using linear mixed-effects models in the lme4 package of R (Bates et al. 2012).

RESULTS

Water table position and tree stand structure (I)

Water table position was higher in the undrained and rewetted groups than in the drained group (Fig.2a). The undrained and the rewetted group did not differ from each other in their water table position (Fig. 2a). However, among the rewetted sites the variation in water table position was higher (Fig. 2a). Mean water table position (±standard error of the mean) relative to the moss surface was −19 ±4 cm in the undrained sites, −42 ±5 cm in the drained sites, and −16 ±4 in the rewetted sites. These values are from the main dataset of 36 spruce swamp forests; the values in the substudies **II** and **IV**, which use a smaller number of sites, are slightly different, but the pattern is the same. Temporal variation of the measurements did not differ between the management categories, p=0.92. Ditch microhabitats had substantially higher water table positions than the main sites (Fig. 2a).

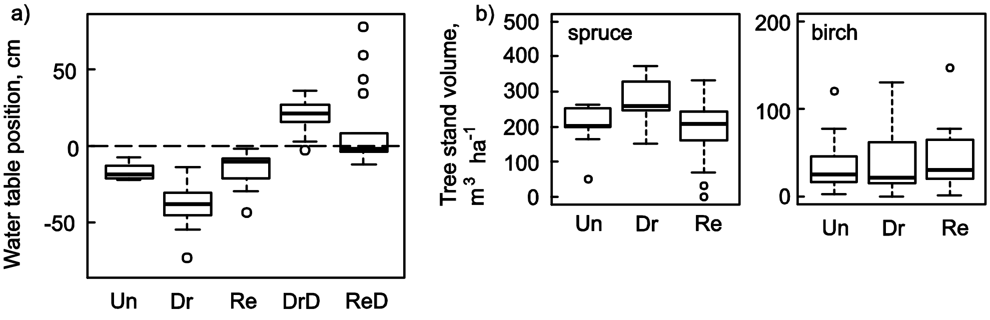


Figure 2. a) Water table position relative to moss surface or ditch bottom, by habitat. Boxes show quartiles of site water table position for undrained (Un) drained (Dr) and rewetted (Re) spruce swamp forest sites and for ditch line of drained (DrD) and rewetted (ReD) sites.
b) Tree stand volume by tree species and management category. Boxes show quartiles of spruce and birch volume for undrained (Un) drained (Dr) and rewetted (Re) spruce swamp forest sites.
Bars represent the most extreme data points that do not extend more than 1.5 times the nearest interquartile range from the box.

Total tree stand volume was higher at the drained sites than at the undrained and rewetted sites: 332 ±42 m^3/ha, 243 ±29 m^3/ha and 238 ±36 m^3/ha, respectively, but only the difference between the drained and the rewetted sites was statistically significant. The values are from the dataset of 36 sites. Birch volume did not differ between the management categories (Fig. 2b), and neither were the differences in spruce volume (Fig. 2b) statistically significant. However, the differences in total tree stand volume tended to result from differences in spruce rather than birch volumes (Fig. 2b).

Plant community structure (I)

When compared to the undrained communities, the communities of the drained sites were characterized by an increased abundance of feather mosses (*Pleurozium schreberi*, *Hylocomium splendens* (Hedw.) Schimp.), spruce seedlings and saplings (*Picea abies*), and *Sciurohypnum spp.*, *Plagiothecium spp.*, and *Lophocolea heterophylla* (Schrad.) Dum.: small bryophytes growing on litter and wood (Fig. 3a). The undrained communities were characterized by a high abundance of the *Sphagnum* mosses: *Sphagnum girgensohnii/russowii*, *S. angustifolium* (Warnst.) C.E.O. Jensen and *S. magellanicum* Brid., and the evergreen dwarf shrub *Vaccinium vitis-idaea* L. (Fig. 3a). Regarding their plant community composition, the rewetted sites were situated half-way between the drained and the undrained sites along the drained-undrained ordination axis (Fig. 3b). The rewetted communities differed significantly from both the undrained ($p<0.001$) and the drained communities ($p<0.01$) (Fig. 3b).

Higher water table position significantly correlated with increasing similarity of the rewetted communities to the undrained reference communities ($p=0.017$, Fig. 3c), similarity measured as position along the drained-undrained ordination axis. Time since rewetting did not show an effect on the position of the rewetted communities along the axis, and no significant interaction effect existed between time since rewetting and water table position ($p=0.12$). After a few years since rewetting, some rewetted communities of high water table position sites were already situated within the variation of the undrained communities (Fig. 3c). Water table position at the successfully rewetted sites was, on average, higher than at the undrained sites: the water table position required for a pristine-like community composition, calculated from the linear model on the effect of water table position on RDA site scores was -13 cm (Figure 3c), range based on parameter standard errors: -4 to -22 cm). This is higher than the undrained water level mean, −19 ±3 cm, and markedly higher than the water level at the driest undrained site, −28 cm.

In the hierarchical variation partitioning, undrained state, i.e. the division to undrained and other (drained or rewetted) sites was the most important variable explaining plant community composition. The division explained 12% of the variation in plant species composition, $p=0.01$. It was followed by the mean water table position (10%, $p=0.005$), birch volume (8%, $p=0.005$) and sampling region (7%, $p=0.005$). The rewetted state as such showed no significant impact on the plant community composition, nor did the cover of any microhabitat.

Species diversity ${}^1D$ was significantly lower in the communities of the undrained sites than in the drained and rewetted communities (Table 1 in **I**). The components of diversity, species richness (S) and evenness (${}^1E$), showed no significant differences, but pairwise comparisons suggest that evenness was higher in the rewetted and drained communities than in the undrained communities (Table 1in **I**). Thus, the differences in diversity were mostly due to differences in species evenness, not richness. Only one of the species has been given a threatened status in the 2010 Red List of Finnish species (Syrjänen et al. 2010): the endangered (EN) liverwort *Harpanthus scutatus* (F. Weber and D. Mohr) Spruce occurred at one undrained site.

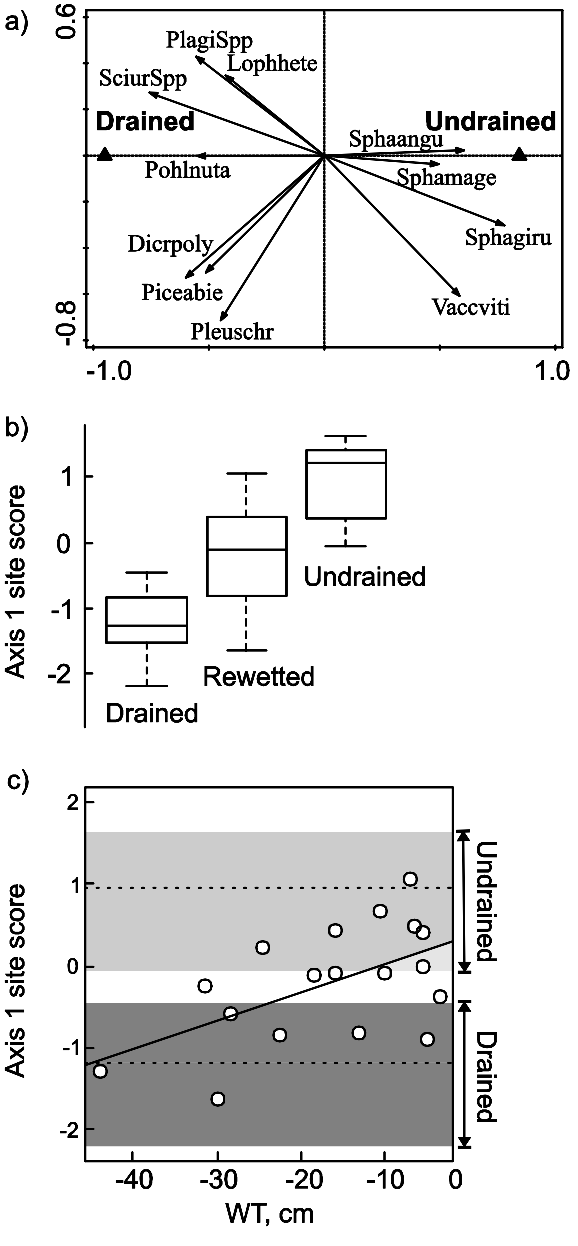


Figure 3. RDA results on plant community composition of the undrained, drained and rewetted sites. Undrained and drained state as explanatory variables, rewetted sites as supplementary cases, sampling region as covariate.

a) Plant species. Species with >18% fit with the constrained axis shown. Full species names in **I**, Appendix B, Sphagiru=*Sphagnum girgensohnii/russowii*. The constrained axis explains 30% of the data variation, *p*=0.002.

b) Axis 1 site scores, shown in quartiles, by management category.

c) Axis 1 site scores of the rewetted sites against mean water table position, *p*=0.017. Open circles depict the rewetted sites, light and dark grey areas the undrained and drained score ranges, respectively, dashed vertical lines the undrained and drained mean scores.

Moss community carbon assimilation potential (II)

When ditches were considered separate habitats in the analysis, the difference between the ditches and the main sites was the most important component of the variation in vegetation (Fig. 4b). High cover of *Sphagnum riparium* Ångström and *S. squarrosum* Crome was typical of the ditch habitats (Fig. 4ab). *Sphagnum girgensohnii* coupled with *S. russowii* was favoured by the undrained conditions where total moss cover was the highest, but it was common in all habitats (Fig. 4ab). *Pleurozium schreberi* and *Hylocomium splendens* were more common in drained and rewetted than in undrained sites, while *S. magellanicum* and *S. angustifolium* were typical species for undrained sites (Fig. 4ab).

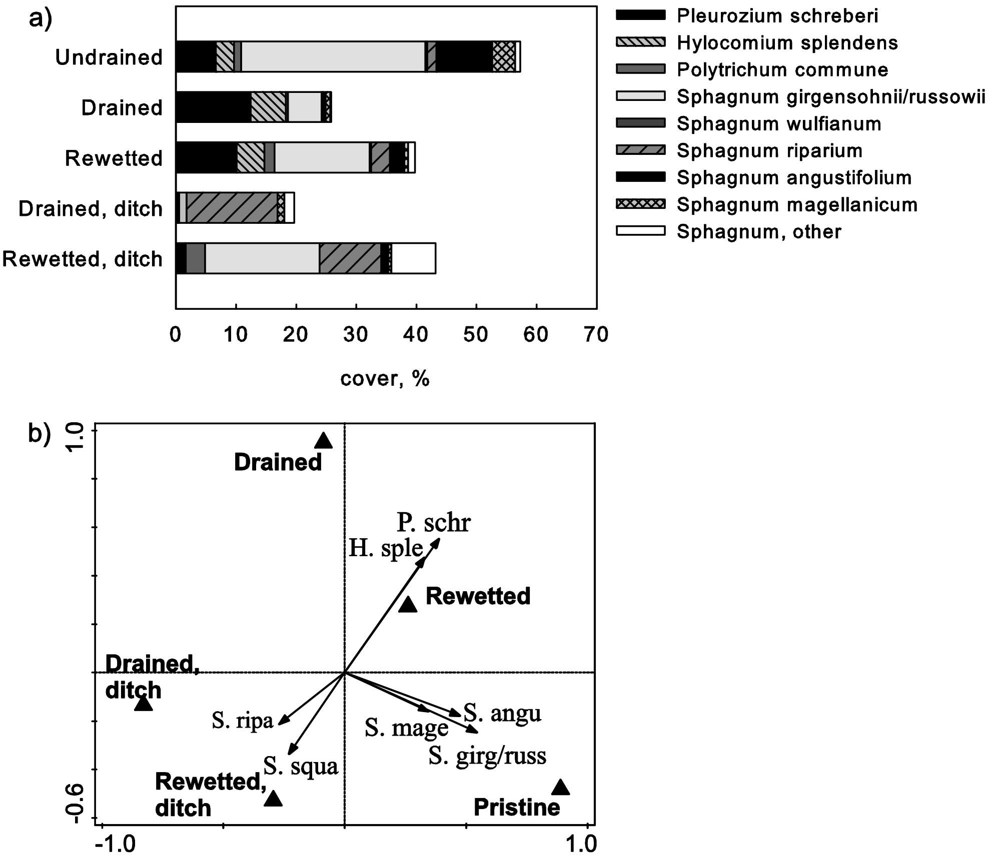


Figure 4. a) *Sphagnum* and feather moss species cover by habitat; b) redundancy analysis (RDA) on the effect of habitat on moss community composition. *Sphagnum* and feather moss species with >10% fit shown. First axis explains 15% of the data variation, p=0.004. Second axis explains 7% of the data variation, p=0.002.

Moss species affected variation in photosynthetic properties more than habitat directly: the direct habitat impact (undrained, drained, ditch of drained site, rewetted, ditch of rewetted site) explained 7%, while the species identity explained 31% of the variation. Maximum photosynthetic capacity and maximum net productivity (the difference between maximum photosynthetic capacity and respiration) were higher in ditches and in rewetted sites than in undrained and drained sites. Light compensation point for net photosynthesis was higher in drained and rewetted sites than in undrained sites, but lowest of all in ditches of drained sites. The direct effects of the habitat amplified the more important effects that worked via species turnover.

The species differed along a productivity gradient, defined by their maximum photosynthetic capacity, which placed the moss species in the following order from high to low productivity: *Sphagnum riparium*, *S. wulfianum*, *S. girgensohnii*, *S. angustifolium*, *S. russowii*, *Hylocomium splendens*, *Pleurozium schreberi*, *S. magellanicum*, and a light-adaptation gradient, which separated shade-adapted feather mosses from *Sphagnum* mosses and *Sphagnum girgensohnii* from other *Sphagna*. The indicator of the physiological state, F_v/F_m, showed low levels of stress everywhere. Thus, drainage and rewetting affected moss carbon assimilation mainly through species turnover.

The species could be classified in three categories after Grime (1977): ruderal, competitive and stress-tolerant, based on their $PPFD_c$ and *PMAX*. The stress-tolerant category was further divided into stress-tolerant, shade species, and stress-tolerant, light species (Table 1). The successional changes in the moss community after drainage and rewetting can be summarized using these four categories instead of species (Fig. 6b).

Table 1. Species classified by their light adaptation, productivity and strategy, based on the photosynthetic response parameters $PPFD_C$ (light adaptation) and *PMAX* (productivity).

Species	light adaptation (shade/light)	productivity (+/–)	strategy (after Grime 1977)
Pleurozium schreberi	shade	–	stress-tolerant (shade)
Hylocomium splendens	shade	–	stress-tolerant (shade)
Polytrichum commune	shade	+	competitive
S. girgensohnii	shade	+	competitive
S. wulfianum	shade	+	competitive
S. riparium	light	+	ruderal
S. magellanicum	light	–	stress-tolerant (light)
S. russowii	light	–	stress-tolerant (light)
S. angustifolium	light	–	stress-tolerant (light)

Sphagnum height and biomass increment (III)

Rewetting led to a recovery of *Sphagnum* growth at the moss patch level: a higher water table increased *Sphagnum* growth (Fig. 5a), and *Sphagnum riparium*, a species favoured by rewetting (Fig.4a), grew more rapidly than the other species (Fig. 5a). Height and biomass increment at the rewetted sites was similar to increment at the undrained sites, while remnant patches of *Sphagnum* at the drained sites showed lower growth rates (Fig. 5b). *Sphagnum* in the ditches at the drained sites showed similar growth rates as the moss at the undrained and rewetted sites, while ditches at the rewetted sites had the highest height and biomass increment (Fig. 5b).

At the ecosystem level, rewetting had increased *Sphagnum* production to levels close to the undrained sites (Fig. 5c). *Sphagnum* cover was the most important variable that determined *Sphagnum* production of the ecosystem (see Fig. 6 in **III**). Among the rewetted sites, also high variability in water table position and *Sphagnum riparium* abundance caused large differences in production between sites (Fig. 6 in **III**). The ditches of rewetted sites, despite the high biomass increment (Fig. 5b), did not have much importance for the ecosystem-level production due to their small relative area.

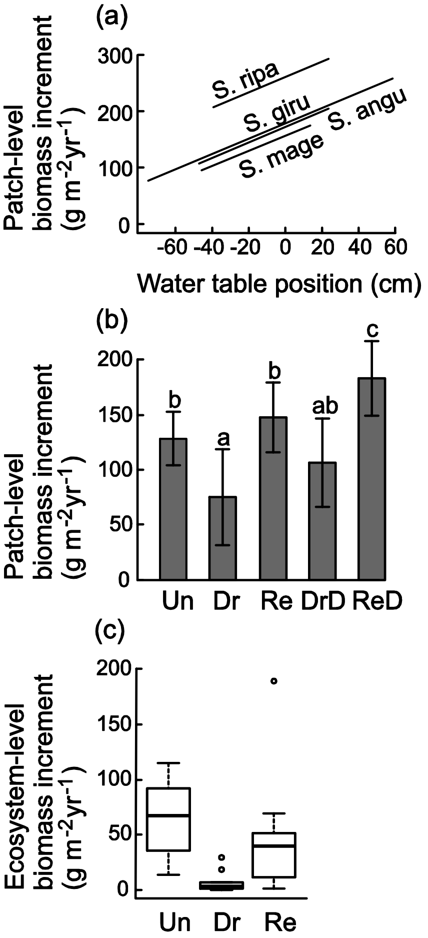


Figure 5. a) Modelled biomass increment for patches of different dominant *Sphagnum* species along their water table position ranges. S. giru =*Sphagnum girgensohnii*/*russowii*, these species were treated as one species unit.

b) Patch-level *Sphagnum* biomass increment in undrained (Un) drained (Dr) and rewetted (Re) spruce swamp forests, and in the ditch line of the drained (DrD) and rewetted (ReD) sites Different letters mark significant differences in the *post-hoc* test for multiple comparisons. Error bars ± SE.

c) Ecosystem-level *Sphagnum* production by management category, based on *Sphagnum* cover data (**I**). Boxes show quartiles of annual biomass increment for undrained, drained and rewetted sites, including the ditches. Bars represent the most extreme data points that do not extend more than 1.5 times the nearest interquartile range from the box.

Peat biogeochemistry (IV)

Surface peat of the drained sites was more decomposed, i.e. had higher bulk density and lower C/N than the surface peat of the undrained sites. Microbial biomass and decomposition activity, measured as aerobic CO_2 production and activities of decomposing enzymes, were lower in this decomposed peat than in pristine surface peat. Among peat properties, three types of responses to rewetting were observed: 1) peat C/N and microbial biomass showed no significant change from the drained state, 2) bulk density decreased and decomposition activity increased towards pristine levels, and 3) NH_4-N mobilization and CH_4 production increased to levels that were higher than in either the undrained or drained state.

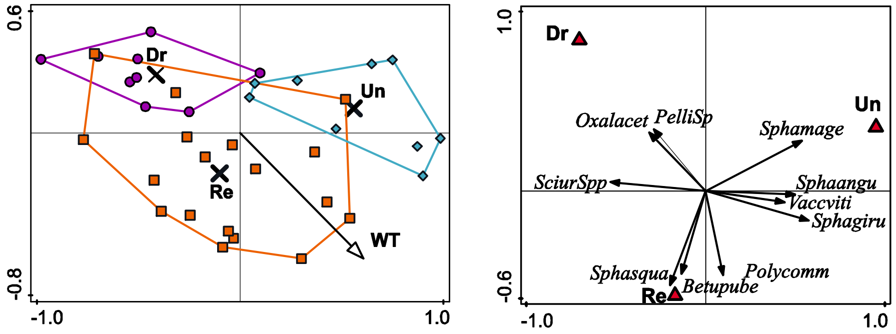
DISCUSSION

Recovery of ecosystem structure and function

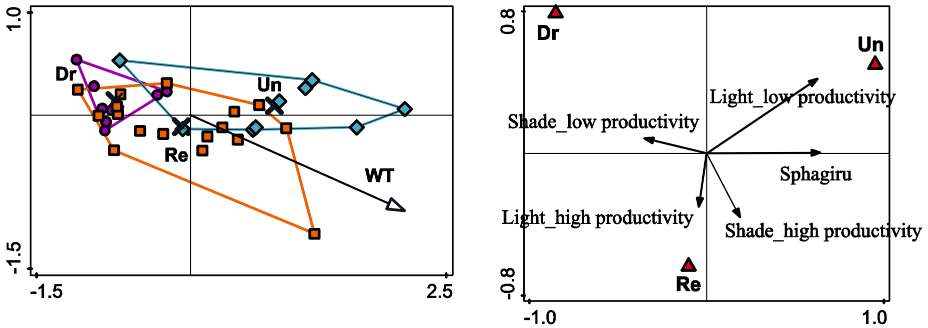
In this study, four key components of the ecosystem structure and function were examined to evaluate the recovery of the ecosystem services they produce, using undrained sites to represent the restoration target. But is it even feasible to restore an ecosystem to a pristine-like state? Ecological restoration practice is based on the principle that yes, by changing the main environmental drivers, it is (Dobson et al. 1997, SERI 2004). However, the view has been challenged by a notion that directional changes in abiotic conditions or persistent assemblages of alien species may render ecosystems incapable of recovering to the pre-disturbance conditions (Hobbs et al. 2009). Furthermore, the simple view of ecological restoration is based on a Clementsian idea of succession as development towards a single end point (Clements 1916), a view that has been challenged since his days (Hilderbrand et al. 2005). The current view of natural ecosystems is that they are dynamic, shaped by disturbance legacies at several spatial and temporal scales (Wu and Loucks 1995, Mori 2011), which makes it as impossible to go back to a certain ecosystem stage. In the development of spruce swamp forests after rewetting, two directions (represented by the ordination axes in Fig. 6) emerged throughout the different components of the ecosystem: development towards the undrained reference state and development towards a new direction, different from both the undrained and the drained state.

In those spruce swamp forests, where ditch blocking had raised the water table high enough (Fig. 3c), *Sphagnum* mosses increased their cover rapidly, bringing the plant community structure within the variation of the undrained sites (**I**). The result is consistent with other restoration studies, which show that *Sphagnum* species recover fairly predictably and rapidly once suitable conditions for colonization are created (Lanta et al. 2006, Hedberg et al. 2012, González and Rochefort 2014): successful rewetting pushes the ecosystem across a threshold to a new successional pathway (Suding and Hobbs 2008), in this case one of secondary mire succession. Mire ecosystems could be considered more Clementsian than perhaps any other because of *Sphagnum* moss, the powerful ecosystem engineer. *Sphagnum* mosses are specialized in creating a habitat for themselves (van Breemen 1995) and by that, directing the ecosystem to their track rapidly (Tahvanainen 2011, Loisel and Yu 2013, Tuittila et al. 2013). In the studied spruce swamp forests, the newly formed *Sphagnum* carpet increased *Sphagnum* biomass production and

a) Plant community composition



b) Moss trait composition



c) Peat biogeochemical properties

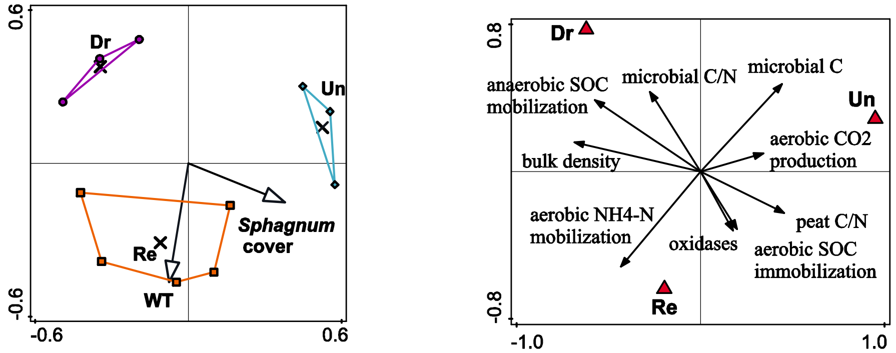


Figure 6. Summary of the changes in ecosystem structure and function following rewetting. RDA results on a) plant community composition (**I**), b) moss trait composition, using the classification in Table 1 (**II**), and c) peat biogeochemical properties (**IV**). Management categories (undrained, drained, rewetted) as explanatory variables, water table position (WT) and in (c) *Sphagnum* cover as supplementary variables. The first, horizontal axis shows the position of the rewetted sites between the drained and the undrained sites; it correlates with *Sphagnum* cover. The second, vertical axis shows the impact of rewetting as an intervention that shifts the ecosystem into a new state; it correlates with an increasing cover of opportunistic, productive understory plant species and high NH_4-N mobilization in the surface peat.

height growth rapidly (**III**). The height growth was particularly rapid (**III**), typical of minerotrophic, shaded places (Clymo 1973). The new growth started the build-up of the new acrotelm, which is considered essential for the recovery of the pristine-like hydrological, microbial and biogeochemical functioning (Lucchese et al. 2010). The formation of the new *Sphagnum* layer was evident in the rapid decrease observed in the surface peat bulk density (**IV**). The new organic surface layer exhibited high microbial activity per unit weight, similarly to the surface layer of the undrained sites (**IV**).

However, rewetting does not simply re-establish the conditions that prevailed prior to drainage: it is an intervention that shifts the ecosystem into a new state. The rewetted site differs from an undrained spruce swamp forests in fundamental ways, even after successful *Sphagnum* establishment: surface peat compaction and physicochemical alteration during the drained phase (**IV)** affect the hydrology and biogeochemistry of the site. Even though the mean water table of the rewetted group was similar to the undrained mean, the rewetted group showed larger between-site variation. At several sites, the water table rise had not been sufficient to initiate *Sphagnum* colonization (**I**), but at the successfully rewetted sites, water table position was higher than at the undrained sites (**I**). It should be noted, however, that the water table at the time of measurements is a product of the interaction between the initial water table rise, tree mortality after rewetting, and ground-layer vegetation, not a measure of the initial rewetting. The low hydraulic conductivity between the old peat and the new organic matter can cause unstable moisture conditions in the surface peat layer of a rewetted site (McCarter and Price 2014). The wet, unstable hydrological conditions increase the cover of opportunistic plant species, most importantly *Sphagnum riparium* (**II**), and are likely to be the reason behind the increased NH_4 mobilization and CH_4 production observed in the peat of the rewetted sites (**IV**) and in field measurements (Koskinen et al. 2011, Koskinen et al. 2012). Rewetting by ditch blocking also creates a new habitat, the blocked ditch, with a high cover of rapidly growing *Sphagnum riparium* (**II**, **III**) and high CH_4 production (Koskinen et al. 2012). However, because the ditches constitute only a small proportion of the area, the increased biomass production and CH_4 production do not have great importance for the ecosystem balances (**III**, Koskinen et al. 2012).

Impact of spuce swamp forest rewetting on benefits gained through ecosystem services

The results of this thesis contribute to our understanding of the benefits gained through spruce swamp forest rewetting. The structure of and the processes within the rewetted spruce swamp forest ecosystem produce, or counteract, the ecosystem functions that deliver the benefits (Fig. 7).

Aesthetic benefits

The rapid recovery of *Sphagnum* cover and height growth rapidly restores the characteristic ground layer appearance, an important constituent of the perceived naturalness of a spruce swamp forest and the resulting aesthetic benefits (Fig. 7). Meanwhile, the rewetted sites show features that result from the drainage and rewetting disturbances, such as the blocked ditches with opportunistic moss species, which contradict the perception of a natural spruce swamp forest.

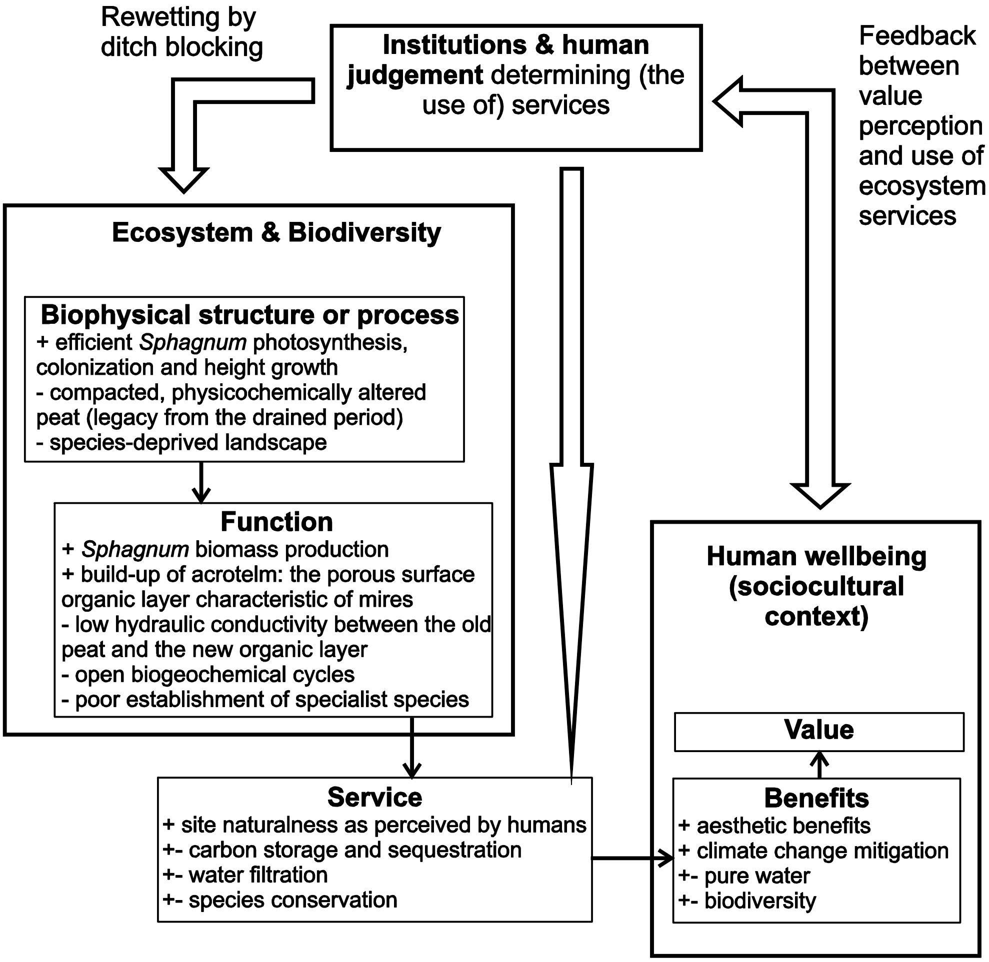


Figure 7. The pathway from spruce swamp forest ecosystem structure and processes to human well-being. Rewetting enhances (+) or counteracts (-) the ecosystem functions that deliver the benefits, +- marks conflicting or unknown effects. Adapted from de Groot et al. 2010, Haines-Young and Potschin 2010 and Maltby (ed.) 2010.

Biodiversity benefits

In undrained *Vaccinium myrtillus* spruce mires (Laine J. et al. 2012), *Sphagnum* mosses dominate the understory to the extent that there is not much space available for other species (**I**) – logs and tree base crevices that provide habitats for specialized species are rapidly overgrown by *Sphagnum*. In the drained sites, on the other hand, dry conditions reduce habitat quality, resulting in lower moss coverage (**I**). Rewetting creates a window of opportunity for subordinate species in the spruce swamp forest ecosystem, increasing site-level biodiversity, although perhaps only temporarily (**I**).

The specialized dead-wood dependent species in boreal spruce swamp forests are largely from organism groups such as epiphytic lichens, mosses and hepatics, polypores and coleopterans (Kuusinen 1996, Ohlson et al. 1997, Laaksonen et al. 2008, Syrjänen et al. 2010). Of these, mosses and hepatics were included in this study, although the sampling strategy was not designed to target the species of conservation value specifically. Threatened species or species of conservation value were not detected even at the undrained sites, with one exception: a threatened hepatic at an old-growth undrained site. This was probably due to a lack of source populations in the surroundings. In Finland, the southwestern part of the country has been under intensive human land use for a longer time than the northeastern part. Also, the east maintains contact to large, relatively pristine forest areas in Russia. Due to these differences in landscape history, the colonization of new habitat patches by saproxylic invertebrate (Kouki et al. 2012) and polypore species (Hottola and Siitonen 2008) shows a clear distinction between the species-impoverished southwest, where also these spruce swamp forests are located, and the species-rich eastern part. Thus, the landscape context limits the biodiversity benefits that can be attained by restoration (Kouki et al. 2012) (Fig. 7).

Functional benefits: climate change mitigation and water purification

Rewetting of boreal spruce swamp forests successfully initiates the accumulation of *Sphagnum* biomass (**III**), the first step in the peat accumulation process and carbon sequestration function (Fig. 7). *Sphagnum* biomass increment in the spruce swamp forests was similar to the increment in ombrotrophic bogs (Laine *et al*. 2011); a similar conclusion has been drawn previously by Pakarinen and Rinne (1979). However, because *Sphagnum* species of nutrient-rich habitats decompose more rapidly than *Sphagna* of nutrient-poor habitats (Johnson and Damman 1991, Beleya 1996, Limpens and Berendse 2003) carbon accumulation in *Sphagnum* biomass is likely to be less than in poorer systems. *Sphagnum* growth has larger carbon effect than its biomass though: the height growth (**III**) buries spruce logs, which contributes to the formation of wood peat that is characteristic of spruce swamp forests (Pakarinen 1984).

High water table maintains anaerobic conditions in peat, which may halt further CO_2 emissions from the decomposition of old peat, a significant carbon source at nutrient-rich drained peatlands (Ojanen et al. 2013). Initially though, the accumulation of fresh organic matter can accelerate decomposition through priming (Limpens et al. 2008): the increasing microbial decomposition activity in the surface peat of the rewetted sites (**IV**) could relate to this. Increased CH_4 emissions (**IV**), measured also in the field (Koskinen et al. 2012) may counteract the positive climate impacts at least at some sites. At the undrained spruce swamp forests sites, surface peat showed no significant CH_4 production (**IV**). At the rewetted sites, waterlogged conditions and a time lag in methanotroph colonization (Juottonen et al. 2012) are the probable causes of the high production (**IV**) and emissions (Koskinen et al. 2012). More research is needed on the decomposition of organic matter at forested nutrient-rich peatlands under undrained, drained and rewetted conditions to estimate the carbon benefits from rewetting of spruce swamp forests (Fig. 7).

The accumulation of *Sphagnum* biomass (**III**) forms a similar porous low bulk-density surface layer (**IV**) that is responsible for the water filtration capacity of undrained spruce swamp forests (Fig. 7). However, peat biogeochemistry does not reach pristine-like functioning rapidly, so pristine-like water filtration function is not to be expected during the first decade following rewetting. Rewetting is likely to cause release of nitrogen to pore water and slight leaching of nitrogen to the surface waters or groundwater (**IV**). As this nitrogen is in the form of ammonia, its mobility is lower than that of nitrates, and therefore it is likely to be partly or completely consumed by plants and microbes during the growing season. More detrimental leaching of phosphorus has been observed in field studies (Koskinen et al. 2011).

Implications for restoration practice

The results of this thesis show that the water table rise has to be sufficient to initiate any changes in the drained spruce swamp forest ecosystem – but if it is, the changes that occur will be rapid. This information is helpful for the practical restoration work: if rapid *Sphagnum* colonization does not occur during the first years, the ditches should be blocked better or trees felled to raise the water table more. When the sites rewetted only one year prior to the survey are left out, 31% of the sites had water table positions too low for successful restoration. A similar proportion, 38% of the sites, was already within the variation of the undrained sites regarding their plant community composition. The result shows that a one-off rewetting intervention, if it raises the water table successfully, is enough to restore the composition of the understory plant community regarding the common species. In many contemporary species-impoverished landscapes, southwestern Finland included, the more demanding species might be impossible to obtain without translocations in any case. The aesthetic and functional benefits anticipated from restoration build on the change in the abundances of common species: on the colonization of *Sphagnum* mosses.

REFERENCES

Aapala K., Tukia H. (2008). Restoration as a tool to improve the quality of drained spruce mires in conservation areas. In: Farrell, C., Feehan, J. (eds.) Proceedings of the 13th International Peat Congress, Volume 1: Oral Presentations. International Peat Society, Tullamore, Ireland. p. 17–20.

Andersen R., Francez A.-J., Rochefort L. (2006). The physicochemical and microbiological status of a restored bog in Québec: Identification of relevant criteria to monitor success. Soil Biology and Biochemistry 38: 1375–1387. http://dx.doi.org/10.1016/j.soilbio.2005.10.012

Bates D., Maechler M., Bolker B. (2012). lme4: Linear mixed-effects models using S4 classes, R package version 0.999999–0. http://CRAN.R-project.org/package=lme4

Belyea, L.R. (1996). Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77: 529–539. http://dx.doi.org/10.2307/3545942

Blain D., Murdiyarso D., Couwenberg J., Nagata O., Renou-Wilson F., Sirin A., Strack M., Tuittila E.-S., Wilson D. (2014). In: Hiraishi T., Krug T., Tanabe K., Srivastava N., Baasansuren M., Fukuda M., Troxler T. G. (eds.) Rewetted organic soils. 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands. Intergovernmental Panel on Climate Change, Switzerland.

Bullock J.M., Aronson J., Newton A.C., Pywell R.F., Rey Benayas J.M. (2011). Restoration of ecosystem services and biodiversity: Conflicts and opportunities. Trends in Ecology & Evolution 26: 541–549. http://dx.doi.org/10.1016/j.tree.2011.06.011

Clements F.E. (1916). Plant succession: An analysis of the development of vegetation Carnegie Institution of Washington, Publication no. 242, 512 pp.

Clymo R.S. (1973). Growth of *Sphagnum* – some effects of environment. Journal of Ecology 61: 849–869. http://dx.doi.org/10.2307/2258654

Convention on Biological Diversity. (2010). Strategic plan for biodiversity 2011–2020. COP 10 decision X/2. Nagoya, Japan.

Cooper M.D.A., Evans C.D., Zielinski P., Levy P.E., Gray A., Peacock M., Norris D., Fenner N., Freeman C. (2014). Infilled ditches are hotspots of landscape methane flux following peatland re-wetting. Ecosystems 17: 1227–1241. http://dx.doi.org/10.1007/s10021-014-9791-3

Dinsmore K.J., Billett M.F., Dyson K.E., Harvey F., Thomson A.M., Piirainen S., Kortelainen P. (2011). Stream water hydrochemistry as an indicator of carbon flow paths in Finnish peatland catchments during a spring snowmelt event. Science of the Total Environment 409: 4858–4867. http://dx.doi.org/10.1016/j.scitotenv.2011.07.063

Dobson A.P., Bradshaw A.D., Baker A.J.M. (1997). Hopes for the future: restoration ecology and conservation biology. Science 277: 515–522. http://dx.doi.org/10.1126/science.277.5325.515

de Groot R., Fisher B., Christie M., Aronson J., Braat L., Gowdy J., Haines-Young R., Maltby E., Neuville A., Polasky S., Portela R., Ring I. (2010). Integrating the ecological and economic dimensions in biodiversity and ecosystem service valuation. In: Kumar P.

(ed.) The Economics of Ecosystems and Biodiversity: The Ecological and Economic Foundations. Earthscan, London &Washington. p. 1–40.

Gobster P.H., Nassauer J.I., Daniel T.C., Fry G. (2007). The shared landscape: What does aesthetics have to do with ecology? Landscape Ecology 22: 959–972.
http://dx.doi.org/10.1007/s10980-007-9110-x

González E., Rochefort L. (2014). Drivers of success in 53 cutover bogs restored by a moss layer transfer technique. Ecological Engineering 68: 279–290.
http://dx.doi.org/10.1016/j.ecoleng.2014.03.051

Government of Finland. (2008). Government resolution on the forest biodiversity programme for Southern Finland 2008–2016 (METSO). 27 March 2008.

Grime J.P. (1977). Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169–1194.
http://dx.doi.org/10.1086/283244

Haines-Young R., Potschin M. (2010). The links between biodiversity, ecosystem services and human well-being. In: Raffaelli D., Frid C. (eds.) Ecosystem Ecology: A New Synthesis. p. 110-139. Cambridge University Press and BES, Cambridge.
http://dx.doi.org/10.1017/CBO9780511750458.007

Hannah L., Lohse D., Hutchinson C., Carr J., Lankerani A. (1994). A preliminary inventory of human disturbance of world ecosystems. Ambio 23: 246–250.

Hedberg P., Kotowski W., Saetre P., Mälson K., Rydin H., Sundberg S. (2012). Vegetation recovery after multiple-site experimental fen restorations. Biological Conservation 147: 60–67.
http://dx.doi.org/10.1016/j.biocon.2012.01.039

Hilderbrand R.H., Watts A.C., Randle A.M. (2005). The myths of restoration ecology. Ecology and Society 10: 19.

Hobbs R.J., Higgs E., Harris J.A. (2009). Novel ecosystems: Implications for conservation and restoration. Trends in Ecology & Evolution 24: 599–605.
http://dx.doi.org/10.1016/j.tree.2009.05.012

Hörnberg G., Zackrisson O., Segerström U., Svensson B.W., Ohlson M., Bradshaw R.H.W. (1998). Boreal swamp forests. Bioscience 48: 795–802.
http://dx.doi.org/10.2307/1313391

Hottola J., Siitonen J. (2008). Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. Biodiversity and Conservation 17: 2559–2577.
http://dx.doi.org/10.1007/s10531-008-9317-4

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

Johnson L.C., Damman A.W.H. (1991). Species-controlled *Sphagnum* decay on a South Swedish raised bog. Oikos 61: 234–242.
http://dx.doi.org/10.2307/3545341

Joosten H., Clarke D. (2002). Wise use of mires and peatlands – background and principles including a framework for decision-making, International Mire Conservation Group / International Peat Society. 304 p.

Joosten H., Tapio-Biström M.L., Tol S. (eds.) (2012). Peatlands – guidance for climate change mitigation through conservation, rehabilitation and sustainable use. FAO and Wetlands International, Rome. 112 p.

Juottonen H., Hynninen A., Nieminen M., Tuomivirta T.T., Tuittila, E.-S., Nousiainen H., Kell D.K., Yrjälä K., Tervahauta A., Fritze H. (2012). Methane-cycling microbial communities and methane emission in natural and restored peatlands. Applied and Environmental Microbiology 78: 6386–6389.
http://dx.doi.org/10.1128/AEM.00261-12

Kaakinen E., Kokko A., Aapala K., Kalpio S., Eurola S., Haapalehto T., Heikkilä R., Hotanen J.-P., Kondelin H., Nousiainen H., Ruuhijärvi R., Salminen P., Tuominen S., Vasander H., Virtanen K. (2008). In: Raunio A., Schulman A., Kontula T (eds.): Suot [Mires]. Suomen luontotyyppien uhanalaisuus [Assessment of Threatened Habitat Types in Finland]. Suomen ympäristö 8, Finnish Environment Institute, Helsinki. p. 75–109.

Kaakinen E., Kokko A., Aapala K. (2012). Assessment of threatened mire habitats in Finland. In: Lindholm T., Heikkilä R. (eds.): Mires from Pole to Pole. Finnish Environment 38/2012, Finnish Environment Institute, Helsinki. p. 181–195.

Koskinen M., Sallantaus T., Vasander H. (2011). Post-restoration development of organic carbon and nutrient leaching from two ecohydrologically different peatland sites. Ecological Engineering 37: 1008–1016.
http://dx.doi.org/10.1016/j.ecoleng.2010.06.036

Koskinen M., Maanavilja L., Minkkinen K., Tuittila E.-S. (2012). First results of CH4 measurements from pristine, drained and restored spruce swamp forests in southern Finland. In: Magnusson T. (ed.): Peatlands in Balance: Proceedings of the 14th International Peat Congress. International Peat Society, Stockholm. Article no. 329.

Kouki J., Hyvärinen E., Lappalainen H., Martikainen P., Similä M. (2012). Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. Diversity and Distributions 18 348–355.
http://dx.doi.org/10.1111/j.1472-4642.2011.00839.x

Kutenkov S. (2012). Vegetation of forested mires in the middle boreal subzone of Karelia. In: Lindholm T., Heikkilä R. (eds.): Mires from Pole to Pole. Finnish Environment 38/2012, Finnish Environment Institute, Helsinki. p. 121–132.

Kuusinen M. (1996). Importance of spruce swamp-forests for epiphyte diversity and flora on Picea abies in southern and middle boreal Finland. Ecography 19: 41–51.
http://dx.doi.org/10.1111/j.1600-0587.1996.tb00153.x

Laaksonen M., Peuhu E., Varkonyi G., Siitonen J. (2008). Effects of habitat quality and landscape structure on saproxylic species dwelling in boreal spruce-swamp forests. Oikos 117: 1098–1110.
http://dx.doi.org/10.1111/j.0030-1299.2008.16620.x

Laine A.M., Juurola E., Hájek T., Tuittila E.-S. (2011). *Sphagnum* growth and ecophysiology during mire succession. Oecologia, 167, 1115–1125.
http://dx.doi.org/10.1007/s00442-011-2039-4

Laine J., Vasander H., Laiho R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. Journal of Applied Ecology 32: 785–802.
http://dx.doi.org/10.2307/2404818

Laine J., Vasander H., Hotanen J.-P., Nousiainen H., Saarinen M., Penttilä T. (2012). Suotyypit ja turvekankaat – opas kasvupaikkojen tunnistamiseen, Metsäkustannus, Hämeenlinna. 160 p.

Lanta V., Mach J., Holcová V. (2006). The effect of dam construction on the restoration succession of spruce mires in the Giant Mountains (Czech Republic). Annales Botanici Fennici 43: 260–268.

Limpens J., Berendse F. (2003). How litter quality affects mass loss and N loss from decomposing *Sphagnum*. Oikos 103: 537–547. http://dx.doi.org/10.1034/j.1600-0706.2003.12707.x

Limpens J., Berendse F., Blodau C., Canadell J.G., Freeman C., Holden J., Roulet N., Rydin H., Schaepman-Strub G. (2008) Peatlands and the carbon cycle: From local processes to global implications – a synthesis. Biogeosciences 5: 1475–1491. http://dx.doi.org/10.5194/bg-5-1475-2008

Loisel J., Yu Z. (2013). Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. Journal of Geophysical Research-Biogeosciences 118: 41–53. http://dx.doi.org/10.1029/2012JG001978

Lucchese M., Waddington J.M., Poulin M., Pouliot R., Rochefort L., Strack M. (2010). Organic matter accumulation in a restored peatland: evaluating restoration success. Ecological Engineering 36: 482–488. http://dx.doi.org/10.1016/j.ecoleng.2009.11.017

Maltby E. (ed.) (2009). Functional assessment of wetlands: Towards evaluation of ecosystem services. Woodhead Publishing, Abington, Cambridge. 694 p. http://dx.doi.org/10.1201/9781439829141

Maxwell K., Johnson G. (2000). Chlorophyll fluorescence – a practical guide. Journal of Experimental Botany 51: 659–668. http://dx.doi.org/10.1093/jexbot/51.345.659

McCarter C.P.R., Price J.S. (2014). The hydrology of the Bois-des-Bel peatland restoration: hydrophysical properties limiting connectivity between regenerated *Sphagnum* and remnant vacuum harvested peat deposit. Ecohydrology 8: 173–187. http://dx.doi.org/10.1002/eco.1498

Millennium Ecosystem Assessment (2005). Ecosystems and human well-being: Synthesis. Island Press, Washington DC. 155 p.

Moreno-Mateos D., Power M.E., Comin F.A., Yockteng R. (2012). Structural and functional loss in restored wetland ecosystems. PLOS Biology: 10 e1001247. http://dx.doi.org/10.1371/journal.pbio.1001247

Mori A.S. (2011). Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48: 280–292. http://dx.doi.org/10.1111/j.1365-2664.2010.01956.x

Nieminen M., Ahti E., Nousiainen H., Joensuu S., Vuollekoski M. (2005a). Does the use of riparian buffer zones in forest drainage sites to reduce the transport of solids simultaneously increase the export of solutes? Boreal Environment Research 10: 191–201.

Nieminen M., Ahti E., Nousiainen H., Joensuu S., Vuollekoski M. (2005b). Capacity of riparian buffer zones to reduce sediment concentrations in discharge from peatlands drained for forestry. Silva Fennica 39: 331–339. http://dx.doi.org/10.14214/sf.371

Ohlson M., Söderström L., Hörnberg G., Zackrisson O., Hermansson J. (1997). Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biological Conservation 81: 221–231. http://dx.doi.org/10.1016/S0006-3207(97)00001-3

Ojanen P., Minkkinen K., Penttilä T. (2013). The current greenhouse gas impact of forestry-drained boreal peatlands. Forest Ecology and Management 289: 201–208. http://dx.doi.org/10.1016/j.foreco.2012.10.008

Økland R.H., Rydgren K., Økland T. (2008). Species richness in boreal swamp forests of SE Norway: the role of surface microtopography. Journal of Vegetation Science 19: 67–74.
http://dx.doi.org/10.3170/2007-8-18330

Pakarinen P., Rinne R. (1979). Growth-rates and heavy-metal concentrations of five moss species in paludified spruce forests. Lindbergia 5: 77–83.

Päivänen J., Hånell B. (2012). Peatland ecology and forestry – a sound approach. University of Helsinki, Department of Forest Sciences, Helsinki. 267 p.

Pakarinen P. (1984). Definitions of peats and organic sediments. Bulletin of the International Peat Society 15: 1–7.

Pinheiro J.C., Bates D.M., DebRoy S., Deepayan S., R development core team (2012). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-105.

R core team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.r-project.org/.

Sallantaus T. (1992). Leaching in the material balance of peatlands: preliminary results. Suo 43: 253–258.

Sanderson E.W., Jaiteh M., Levy M.A., Redford K.H., Wannebo A.V., Woolmer G. (2002). The human footprint and the last of the wild. Bioscience 52: 891–904. http://dx.doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

SERI (Society for Ecological Restoration International) Science & Policy Working Group (2004). SER international primer on ecological restoration, version 2. http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration [Cited 31 January 2015].

Suding K.N., Hobbs R.J. (2009). Threshold models in restoration and conservation: A developing framework. Trends in Ecology & Evolution 24: 271–279. http://dx.doi.org/10.1016/j.tree.2008.11.012

Syrjänen K., Anttila S., Ulvinen T., Laaka-Lindberg S., Huttunen S., Laitinen T., Ahonen I., Fagerstén R., He X., Juslén A., Korvenpää T., Korvenpää T., Parnela A., Sallantaus T., Vainio O., Virtanen R., Piippo S., Rikkinen J. (2010). In: Rassi P., Hyvärinen E., Juslén A., Mannerkoski I. (eds.): Bryophytes. The 2010 Red List of Finnish Species. Ministry of Environment and Finnish Environment Institute, Helsinki. p. 336–343.

Tahvanainen T. (2011). Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. Journal of Ecology 99: 404–415. http://dx.doi.org/10.1111/j.1365-2745.2010.01778.x

ter Braak C.J.F., Šmilauer P. (2012). Canoco reference manual and user's guide: Software for ordination. Version 5. Microcomputer Power, Ithaca, NY. 496 p. (www.canoco.com)

Tuittila E.-S. (2000). Restoring vegetation and carbon dynamics in a cut-away peatland. Publications in Botany from the University of Helsinki 30: 1–38.

Tuittila E.-S., Juutinen S., Frolking S., Väliranta M., Laine A.M., Miettinen A., Seväkivi M., Quillet A., Merilä P. (2013). Wetland chronosequence as a model of peatland development: Vegetation succession, peat and carbon accumulation. Holocene 23: 25–35.
http://dx.doi.org/10.1177/0959683612450197

Tuomisto H. (2012). An updated consumer's guide to evenness and related indices. Oikos 121: 1203–1218. http://dx.doi.org/10.1111/j.1600-0706.2011.19897.x

Tuomisto H. (2010). A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164: 853–860. http://dx.doi.org/10.1007/s00442-010-1812-0

Väänänen R., Nieminen M., Vuollekoski M., Nousiainen H., Sallantaus T., Tuittila E.-S., Ilvesniemi H. (2008). Retention of phosphorus in peatland buffer zones at six forested catchments in southern Finland. Silva Fennica 42: 211–231. http://dx.doi.org/10.14214/sf.253

van Breemen N. (1995). How *Sphagnum* bogs down other plants. Trends in Ecology & Evolution 10: 270–275. http://dx.doi.org/10.1016/0169-5347(95)90007-1

Vesterinen P., Similä M., Rehell S., Haapalehto S., Perkiö R. (2014). In: Similä M., Aapala K., Penttinen J. (eds.) Restoration work. Ecological restoration in drained peatlands – best practices from Finland. Metsähallitus, Natural Heritage Services, Vantaa. p. 38–47.

Vikman A., Sarkkola S., Koivusalo H., Sallantaus T., Laine J., Silvan N., Nousiainen H., Nieminen M. (2010). Nitrogen retention by peatland buffer areas at six forested catchments in southern and central Finland. Hydrobiologia 641: 171–183. http://dx.doi.org/10.1007/s10750-009-0079-0

Weiss R., Alm J., Laiho R., Laine J. (1998). Modeling moisture retention in peat soils. Soil Science Society of America Journal 62: 305–313. http://dx.doi.org/10.2136/sssaj1998.03615995006200020002x

Wu, J. & Loucks, O. (1995). From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. *Quarterly Review of Biology*, **70**, 439–466. http://dx.doi.org/10.1086/419172