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Tuomas Haapalehto

Restoring Ecosystem Structure and Functions: Results from *Sphagnum* Peatlands Degraded by Forestry Drainage

JYVÄSKYLÄN YLIOPISTO

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Editors
Jari Haimi
Department of Biological and Environmental Science, University of Jyväskylä
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Cover photo: An aerial view over Mustakeidas bog in Kauhaneva-Pohjankangas national park,western Finland. The drained part of the bog was restored two years before the photograph was taken.
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ABSTRACT

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Restoring ecosystem structure and functions: results from *Sphagnum* peatlands
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The wide and rapidly increasing human land use has caused extensive degradation of natural landscapes, extinctions of species and loss of ecosystem functions and services. Subsequently, ecological restoration has been raised to a major global strategy for safeguarding ecosystem values. However, concerns have been raised on the real potential of restoration to re-establish ecosystem structures and functions. Here, I studied the effects of ecological restoration on the structure and functions of forestry drained boreal peatland ecosystems in southern Finland. To better understand structural and functional changes, the effects of drainage and restoration on water table level, pore water chemistry and peat chemistry were explored as well. Drainage lowered the water table and induced changes in pore water chemistry and plant community composition. Drainage retarded the accumulation of surface peat and resulted in significant reduction in the sequestration of carbon therein. Re-establishment of water table level and significant recovery of pore water and surface peat chemistry were observed after restoration. Restoration induced the recovery of ecosystem structure i.e. plant community composition towards the target. The recovery was dependent on the within-site degree of ecosystem degradation. The original ecosystem structure was not needed for the re-establishment of important peatland ecosystem functionality in terms of surface peat accumulation. However, a more profound recovery of structure and conditions may be needed for some other functions like surface peat carbon sequestration to recover. Overall, my results are promising from the perspective of restoration. However, they highlight the need for patience in drawing conclusions on the effectiveness of restoration. Practitioners should also be prepared for temporarily increased leaching of nutrients into downstream water courses.

Keywords: C accumulation; degree of degradation; disturbance; ecosystem resilience; ecosystem service; land-use change; mire; recovery; spatial variation.

Tuomas Haapalehto, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author’s address Tuomas O. Haapalehto
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
tuomas.o.haapalehto@student.jyu.fi,
tuomas.haapalehto@metsa.fi

Supervisors Professor Janne S. Kotiaho
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Docent Teemu Tahvanainen
Department of Biology
University of Eastern Finland
P.O. Box 111
FI-80101 Joensuu
Finland

Professor Markku Kuitunen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Reviewers Professor Hans Joosten
Institute of Botany and Landscape Ecology
University Greifswald
Soldmannstraße 15
17487 Greifswald
Germany

Docent Heikki Simola
Department of Biology
University of Eastern Finland
P.O. Box 111
FI-80101 Joensuu
Finland

Opponent Professor Raija Laiho
Metsäntutkimuslaitos, Finnish Forest Research Institute
Kaironiementie 15
FI-39700 Parkano
Finland

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV.

I Haapalehto, T.O. Kotiaho, J.S., Matilainen, R., Tahvanainen, T. 2014. The effects of long-term drainage and subsequent restoration on water table level and pore water chemistry in boreal peatlands. Submitted manuscript.

II Haapalehto, T.O., Vasander, H., Jauhiainen, S., Tahvanainen, T., Kotiaho, J.S. 2011. The effects of peatland restoration on water-table depth, elemental concentrations, and vegetation: 10 years of changes. Restoration Ecology 19: 587-598.

III Haapalehto, T., Kareksela, S., Juutinen, R., Kuitunen, M., Tahvanainen, T., Vuori, H., Kotiaho, J.S. 2014. Degree of degradation and effectiveness of restoration: trajectories of plant community recovery in drained peatlands. Submitted manuscript.

IV Kareksela, S.*, Haapalehto, T.O.*, Juutinen, R., Matilainen, R., Tahvanainen, T., Kotiaho, J.S. 2014. Fighting carbon loss of degraded peatlands by jump-starting ecosystem functioning with ecological restoration. Submitted manuscript.
*Shared first authorship.

The table shows the contributions to the original papers by the authors. Smaller contributions are stated in the acknowledgements of the papers.

	I	II	III	IV
Original idea	TOH, TT, JSK	SJ, HVA, TOH	TOH, JSK	TT, TOH, JSK
Data	TOH, RM	TOH, SJ, HVA	SK, RJ, TOH	SK, RJ, TOH, RM, TT
Analyses	TOH, TT, JSK, RM	TOH, JSK	TOH, JSK, HVU	TT, TOH, JSK, SK
Writing	TOH, TT, JSK, RM	TOH, JSK, TT, HVA, SJ	TOH, JSK, TT, SK, MK, HVU, RJ	TOH, SK, JSK, TT, RJ, RM

TOH = Tuomas Haapalehto, TT = Teemu Tahvanainen, JSK = Janne S. Kotiaho, RM = Rose Matilainen, SJ = Sinikka Jauhiainen, HVA = Harri Vasander, SK = Santtu Kareksela, RJ = Riikka Juutinen, HVU = Hilja Vuori, MK = Markku Kuitunen

1 INTRODUCTION

1.1 Ecological restoration

The growth of human population has resulted in a rapidly increasing pressure to convert land e.g. to agricultural and industrial use (Foley *et al.* 2005). Consequently, the human foot-print can be seen in marine and terrestrial ecosystems throughout the globe (Foley *et al.* 2005, Halpern *et al.* 2008). Conservation biologists are concerned about anthropogenic changes like increased land-use, because they are an important driver of the rapidly increasing rate of biodiversity decline (Pimm *et al.* 1995, Sala *et al.* 2000, Butchart *et al.* 2010). We humans are also dependent on the various life-supporting functions of ecosystems. Indeed, the capability of degraded ecosystems to sustain ecosystem services like food production, maintenance of freshwater and forest resources, regulation of climate and air quality, and amelioration of infectious diseases has been questioned (Costanza *et al.* 1997, Millennium Ecosystem Assessment 2005, Foley *et al.* 2005).

Ecological restoration was added to the toolbox of conservation a couple of decades ago in order to respond to the threats of environmental degradation (Dobson *et al.* 1997). In general, ecological restoration aims at complete restoration or partial rehabilitation of ecosystem structures and functions, such as species communities and carbon (C) sequestration, respectively (Fig. 1; Bradshaw 1984, 1996, Society for Ecological Restoration International 2004, Hobbs and Cramer 2008). Despite its young history as a conservation discipline, the societal expectations for ecological restoration are monumental: it has been entered into international political convention according to which 15 % of the degraded ecosystems should be restored by 2020 to secure biodiversity and provision of ecosystem services (Convention on Biological Diversity 2010). Ecological restoration is also increasingly being called upon to compensate for the biodiversity values lost in development projects by restoring degraded sites elsewhere (Maron *et al.* 2012).

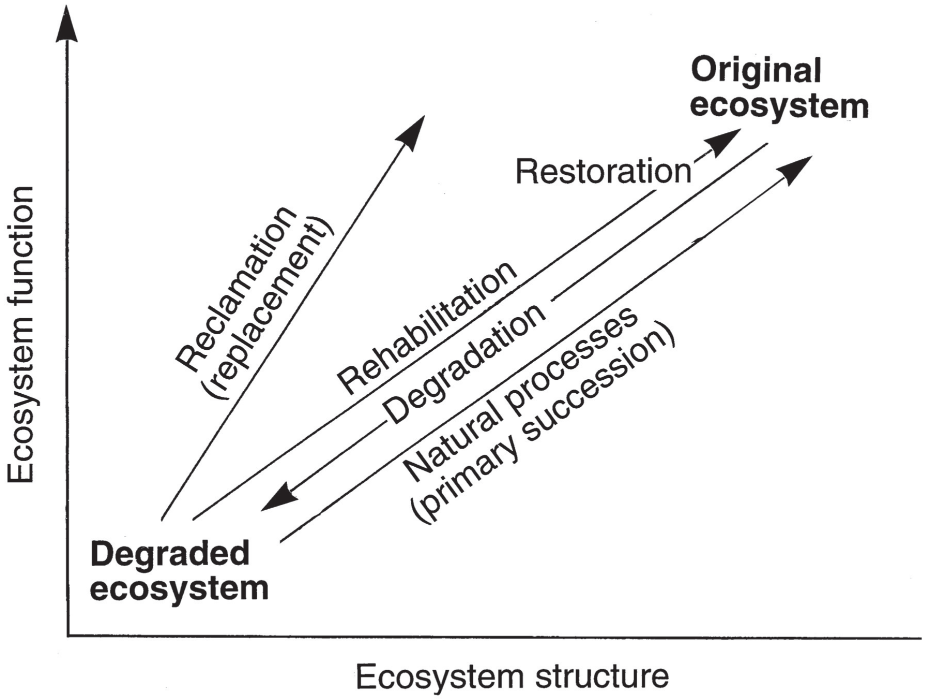

FIGURE 1 Relation between ecosystem structure (which would include species diversity and complexity) and ecosystem function (for example, biomass, nutrient content, and cycling), illustrating changes that occur as a degraded ecosystem recovers toward its original state. Reproduced from Dobson et al. 1997.

Encouraging empirical evidence exists that ecological restoration succeeds in recovering some of the degraded biodiversity and ecosystem services. However, values of both often remain lower in restored than in the targeted reference ecosystems (Benayas *et al.* 2009, Wortley *et al.* 2013). Moreover, in many cases there is still much uncertainty as to how effective ecological restoration really is (Suding 2011), and the number of empirical evaluations about the true effectiveness of ecological restoration has only recently started to increase (Wortley *et al.* 2013). Indeed, serious doubts have been cast for example on the ability of ecological restoration to really be able to recover the ecosystem services (Palmer and Filoso 2009) and to deliver biodiversity offsets such that losses at the impact site would be genuinely compensated by restoring a degraded site elsewhere (Maron *et al.* 2012). Due to the young age of the discipline, most of the evaluations are based on short-term investigations. Therefore, even when restoration has been successful in initiating a true process of recovery, the possibility that the recovery towards the target is following an unanticipated trajectory, may lead to unjustified concerns. To be able to judge whether the goals of restoration are likely to be achieved, we need to understand the trajectories, i.e. the development of structures and functions over time towards the target (Matthews *et al.* 2009, Montoya *et al.* 2012).

There is apparent need for more long-term studies exploring the affectivity of restoration (Montoya *et al.* 2012). Additionally, we need better understanding on the mechanisms behind the changes. Manipulations of the physical and chemical environment like modification of hydrological and disturbance regimes are often needed to enable recovery of the ecosystem structures and functions (Hobbs and Cramer 2008). Hence, we need to understand how such environmental factors change due to degradation, and how effectively they can be re-established by restoration (e.g. Moreno-Mateos *et al.* 2012). On the other hand, dynamics of the species community composition are, basically, characterized by changes in species identities and their abundances. Thus, with ecological restoration aiming at the original community composition we need, firstly, to recover the original species that may have been lost. Secondly, we may need to eradicate species that are not members of the pristine reference or other targeted species community. This implies that we need also to understand ecosystems' resistance and resilience, i.e. the ability of the structures and functions of the ecosystem to resist changes imposed by external disturbances, and the ability of the structures and functions of the ecosystem to recover from the external disturbance, respectively (Holling 1973, Pimm 1991, Tilman and Downing 1994, Society for Ecological Restoration International 2004).

The degree of degradation is one of the factors potentially influencing the effectiveness of ecological restoration. It may affect the probability of restoration measures to reach the targets and should therefore be considered e.g. when allocating resources for restoration (Hobbs and Kristjanson 2003, Alday and Marrs 2013). One aspect of the degree of degradation that has seldom been considered is within-site variability in the degree of degradation. Indeed, disturbances typically increase environmental heterogeneity e.g. the variation in the biogeophysical environmental factors within the impacted site (Sousa 1984). Moreover, restoration measures themselves are likely to cause temporary disturbance and possibly even further degradation of varying degree (Ilmonen *et al.* 2013). It is conceivable that the within-site variability in the degree of degradation may influence the recovery of the communities. Therefore, in addition to considering the among sites variability in the degree of degradation e.g. when prioritizing the sites for restoration, also the within-site variability should be considered.

The recovery of ecosystem functions is generally thought to depend on the recovery of original structures (Fig. 1; Bradshaw 1996, Dobson *et al.* 1997). However, the relationship of ecosystems' functions and structure is still far from well understood (Cortina *et al.* 2006, Cardinale *et al.* 2012, Hooper *et al.* 2012, Naeem *et al.* 2012, Reich *et al.* 2012). From the practical restoration perspective the magnitude of plasticity in this relationship is important to understand because it relates to the net costs of restoration actions. It is likely that the stronger and more causative the relationship of ecosystem functions and certain community composition or biodiversity per se, the more complicated and costly are the actions needed to reach the restoration targets. On the other hand, the economic feasibility of restoration can be increased with possible economic gains produced by the outcomes of restoration. Increased ecosystem service like climate regulation due to C sequestration (Nelson *et al.* 2009, Alexander and McInnes 2012, Kettunen *et al.* 2012), is one example of possible economic gains. Bearing in mind the possible caveats related to restoration of ecosystem services for environmental markets (Palmer and Filoso 2009, Bullock *et al.* 2011), there is an apparent need to search for solutions to finance the huge globally accepted restoration targets.

1.2 Degradation and restoration of peatland ecosystems

Boreal and subarctic peatlands store one third of global soil C, but cover only 3 % of the global land-area (Yu 2011). This is possible because the conditions within them impede the decay of the plant material produced by their surface vegetation (Clymo 1984). Hence the organic material is accumulated as peat during hundreds and thousands of years of peatland ecosystem development. In addition to sequestering atmospheric carbon dioxide (CO_2), peatlands affect the circulation of C by releasing dissolved organic carbon (DOC; Tranvik and Jansson 2002). Furthermore, peatlands affect the global climate by emitting methane (CH_4) and nitrous oxide (N_2O) (Juszczak and Augustin 2013, Gong *et al.* 2013). Hydrologic factors like water level fluctuations and water chemistry largely regulate the development of peatland plant communities (Glaser *et al.* 1990). They also control the accumulation and decomposition of peat and consequently the fluxes of C as CO_2, CH_4 and DOC in peatlands (Moore and Knowles 1989, Tranvik and Jansson 2002, Belyea and Malmer 2004, Holden 2005, Jungkunst and Fiedler 2007). On the other hand, changes in these important peatland ecosystem functions are closely related to the characteristics of peatland plant communities (Ward *et al.* 2013). Most pristine boreal and subarctic *Sphagnum* peatlands are expected to consist of two layers: an upper 10-50 cm deep aerobic layer (the acrotelm) in which the hydraulic conductivity and the rate of decomposition are relatively high; and the usually anaerobic lower layer (the catotelm), where the hydraulic conductivity and decomposition rate are much lower (Clymo 1984). Hence, from the functional perspective, the long-term C sequestration in pristine peatlands results from the deposition of plant biomass to form raw humus in the acrotelm and its subsequent transition to long-term storage in the catotelm (e.g. Clymo 1984). Changes in the uppermost peat layer are especially important for the C accumulation processes, because more than 90 % of the C fixed by plants may be lost by decomposition before transition to catotelm (Francez and Vasander 1995).

Like many other ecosystems, peatlands have been severely degraded. Approximately 50 million hectares (13 % of peatlands) have been directly altered by human land-use (Lappalainen 1996, Strack 2008; Tanneberger and Wichtmann 2011). One major cause of degradation is drainage for timber production affecting approximately 15 million hectares of peatlands (Strack 2008). Drainage of certain peatland areas may also induce significant changes to hydrology of undrained peatland areas beyond considerable distances (Tahvanainen 2011).

The total peatland area impacted by drainage and other land-use may, therefore, be much larger than often reported based on the actual drained areas. As discussed above, hydrology is perhaps the most important environmental factor shaping the structures and functions in peatlands ecosystems. Drainage alters peatland hydrology by lowering the water-table level (Laine and Vanha-Majamaa 1992). Drainage also results in unnatural within-site spatial gradients in water table level connected to distance from the ditches (Price *et al.* 2003). The drawdown of water table together with uneven destruction of peatland surface during the excavation of ditches creates a complex gradient in the degree of degradation within drained sites. In the severe degradation end of the gradient are the ditches where the original vegetation has been almost completely destroyed, bare peat exposed to erosion, and fluctuation of water level intensified. In the other end of the gradient are the areas furthest away from the ditches where, in general, the only degrading factor is the much less decreased water table level. It appears, therefore, that drained peatland ecosystems provide a unique but previously unexplored set up for studying how such a gradient in the within-site degree of degradation affects ecosystem structures and functions.

Lowering of the water table distracts the acrotelm-catotelm stratification and promotes aerobic decomposition especially in the uppermost peat layer (Niedermeier and Robinson 2007). Significant changes like elevated total concentrations of nitrogen (N) and phosphorus (P) and decreased concentrations of major exchangeable cations such as potassium (K), calcium (Ca), and magnesium (Mg) are observed in the surface peat after drainage (Laiho *et al.* 1999, Sundström *et al.* 2000). pH and concentrations of several chemical elements increase in the pore and outflow water shortly after drainage (Prévost *et al.* 1999, Åström *et al.* 2001, Moore *et al.* 2013). In contrast, long-term changes of pore water chemistry after drainage are not well understood (Holden *et al.* 2004). Drainage has also marked effects on peatland ecosystem structures like plant community composition (Laine *et al.* 1995, Mälson *et al.* 2008). It appears that previous studies are partly contradictory in their conclusions about how drainage affects peat C storage, which is globally one of the most important peatland ecosystem functions. Indeed, both negative and positive C balances are reported in drained boreal peatlands (Laine and Minkkinen 1998, Ojanen *et al.* 2010, 2012, 2013; Lohila *et al.* 2011, Simola *et al.* 2012, Pitkänen *et al.* 2013).

Ecological restoration of forestry drained peatlands rests upon recovering the original hydrology (water table level, water flow paths) by blocking the water flow along the ditches (Vasander *et al.* 2003, Aapala *et al.* 2009). This is expected to result in the recovery of ecosystem structure and functions. Early results on the hydrological recovery of peatlands are now starting to accumulate. However, they seem to be controversial to some extent. For example, both successes and failures of regaining original water table level (Worrall *et al.* 2007, Klimkowska *et al.* 2010, Laine *et al.* 2011, Hedberg *et al.* 2012, Schimelpfenig *et al.* 2013) as well as both intended and unintended effects on water chemistry (Höll *et al.* 2009, Koskinen *et al.* 2011, Wilson *et al.* 2011a, b) have been reported. Despite the results from some early case studies (Jauhiainen *et al.* 2002, Tarvainen *et al.* 2013), the effects of boreal peatland restoration on surface peat chemistry - another important environmental factor - are not well understood. Some promising results on the recovery of peatland structure after peatland restoration exist (Mälson *et al.* 2010, Laine *et al.* 2011). However, there are also concerns on the effectiveness of restoration in recovering the targeted plant community composition (Moreno-Mateos *et al.* 2012). For example, uneven hydrological recovery within restored sites is suggested to hamper the recovery of peatland communities (Hedberg *et al.* 2012). Indeed, insufficient blocking of ditches can, for example, redirect water flow along the artificial flow paths formed by the lines of blocked ditches. This may act to sustain hydrological differences related to water table level and water chemistry between the blocked ditches and the intervening peat strips. The recovery of peatland ecosystems is likely to be affected by the complex within-site gradient in the degree of degradation as discussed above. The recovery of peatland hydrology and plant communities in relation to the variability within restored sites is, however, poorly understood.

The efficiency of current restoration methods in re-establishing the peatland C sequestration capacity has not been studied much. Furthermore, the research seems to be concentrated mainly on peat mining areas (e.g. Komulainen *et al.* 1999, Cagampan and Waddington 2008, Soini *et al.* 2010, Waddington *et al.* 2010, Moreno-Mateos *et al.* 2012, Strack and Zuback 2013). The functional processes like peat accumulation in the surface peat layer are highly important for the long-term C accumulation in peatlands (Ohlson and Dahlberg 1991). Therefore, we need a deep understanding on such processes in restored peatlands also. In general, the recovery of biological structure is suggested to precede the recovery of ecosystem functions in restored wetland ecosystems (Moreno-Mateos *et al.* 2012). Still, the relationship between the recovery of plant communities and functionality related to C accumulation in boreal peatland ecosystems remains unexplored.

1.3 Aims of the thesis

I explore the effects of long-term degradation and subsequent restoration on the structure and function in boreal peatland ecosystems. The broad aim is to seek answer for the question "Is restoration an effective tool for recovery of ecosystem structures and functions?". Ecosystem structure is studied by changes in plant community composition. Ecosystem functionality related to long-term C accumulation in pristine, drained and restored peatlands is explored by studying the surface peat growth rate and C sequestration capacity. To better understand the structural and functional changes, the effects of drainage and restoration on the environmental factors (hydrology and surface peat elemental concentrations) underlying those changes in peatland ecosystems are studied as well. Special attention is paid to the variation within sites - especially related to the degree of degradation in the case of plant communities - when studying the changes in hydrology and plant communities. More specifically, I focus on following questions:

1. What is the long-term effect of drainage on peatland hydrology i.e. water table level and pore water chemistry? (I)
2. To what extent restoration will lead to recovery of the hydrology and surface peat chemistry degraded by drainage? (I, II)
3. To what extent the pristine ecosystem structure (plant community composition) is changed after drainage, and does the change depend on the within-site gradient in the degree of degradation (i.e. distance from the ditch)? (III)
4. To what extent ecological restoration is effective in recovering the structure of targeted pristine ecosystems, and is the recovery dependent on the within-site degree of degradation? (II, III, IV)
5. What is the effect of drainage on the peatland ecosystem function of surface peat growth rate, and is restoration able to re-establish the function? (IV)
6. How does long-term drainage affect C sequestration in the surface peat, and what is the rate of C sequestration in the surface peat of restored sites when compared to the accumulation at pristine sites? (IV)
7. Is an original peatland structure (plant community composition) needed to regain an original function (surface peat growth)? (IV)

2 MATERIALS AND METHODS

2.1 Study sites and set-ups

2.1.1 Set-up 1: Comparison of pristine, drained and restored peatland sites

I established the set-up 1 consisting of 38 study sites to explore changes in hydrology (I), ecosystem structure (plant community composition; III, IV), ecosystem functionality (surface peat accumulation and C sequestration therein; IV) and the relationship between ecosystem structure and function (IV). The sites were located within a 75 km radius (range of 200 m - 150 km between the sites) in the area between 61° 53´ and 62° 51´ N and 22° 53´ and 25° 26´ E in southern Finland. The area belongs to the South-Boreal climatic-phytogeographical zone in the area where mean annual temperature is *ca.* +4°C and the annual average precipitation *ca.* 650 mm. The sites were divided into four categories according to their management status: i) pristine (n = 10), ii) drained (n = 9), iii) previously drained and restored 3-7 years before the study (restored 5 years ago, n = 9), iv) previously drained and restored 9-12 years before the study (restored 10 years ago, n = 10). I based the selection of sites on close examination of old and new aerial photographs accompanied with field observations. The vegetation type (weakly minerotrophic pine fen) and tree stands of the drained and restored sites were originally roughly similar to those of the pristine sites. The sites were considered independent from each other in their surface water flow based on topographic data and field observations.

All of the drained and restored sites were drained for forestry by the state with ditch interval of 30-50 meters most likely during 1960s and 1970s. Although no recordings were made, the sites were likely fertilized soon after drainage with PK fertilizer. At some of the drained sites ditches had been cleared again in 1990s. Growth of Scotch pine (*Pinus sylvestris*) and downy birch (*Betula pubescens*) at originally sparsely pine covered sites had variably increased after the drainage. Some of the sites were designated to conservation in 1980s with a subsequent decision to restore them. The restoration measures included filling in the ditches with peat excavated near the ditches, construction of dams and removal of the tree stands in cases where drainage had significantly increased tree growth. The amount of trees removed was adjusted so that all the sites had more or less the same tree cover in the end, mimicking the pre-disturbance tree cover determined from aerial photographs. Restoration was conducted by Natural Heritage Services of Metsähallitus (governmental institution responsible for management of conservation areas). Due to the compression and decomposition the peat near to the ditches has often been observed to be subsided more than the peat elsewhere in the drainage area (van der Schaaf 2012). Therefore, the filling was supplemented by peat dams elevating *ca.* 50 cm over the peat surface and extending perpendicularly a few meters at both sides of the ditch to prevent water flow along the subsided areas.

A set-up with 20 1-m^2 plots for studying differences in plant community composition and 40 permanent 20-mm pipe wells for studying changes in water table level was established at each study site (Fig. 2). At the drained and restored sites, the vegetation plots with a pair of 20-mm wells were placed in five transects running perpendicular to the ditch with each transect having a plot at four distances from the ditch (0, 5, 10 and 15 m). As the distance between transects was four meters, the wells formed a rectangular grid with an area of 15 × 20 m. A similar grid of wells was laid at pristine sites. At all sites, the location of the first transect (laid in the ditch at drained and restored sites) was randomized. At the drained and restored sites, three 32-mm pipe wells with 10-m intervals to each other were laid to the distance of 15 m from the ditch (sampling location "Peat strip") to collect water samples for chemical analyses (Fig. 2). Additionally, one and three more wells were laid into the ditch at the drained and restored sites (sampling location "Ditch"), respectively. Altogether three wells were laid at the pristine sites for water sampling (Fig. 2).

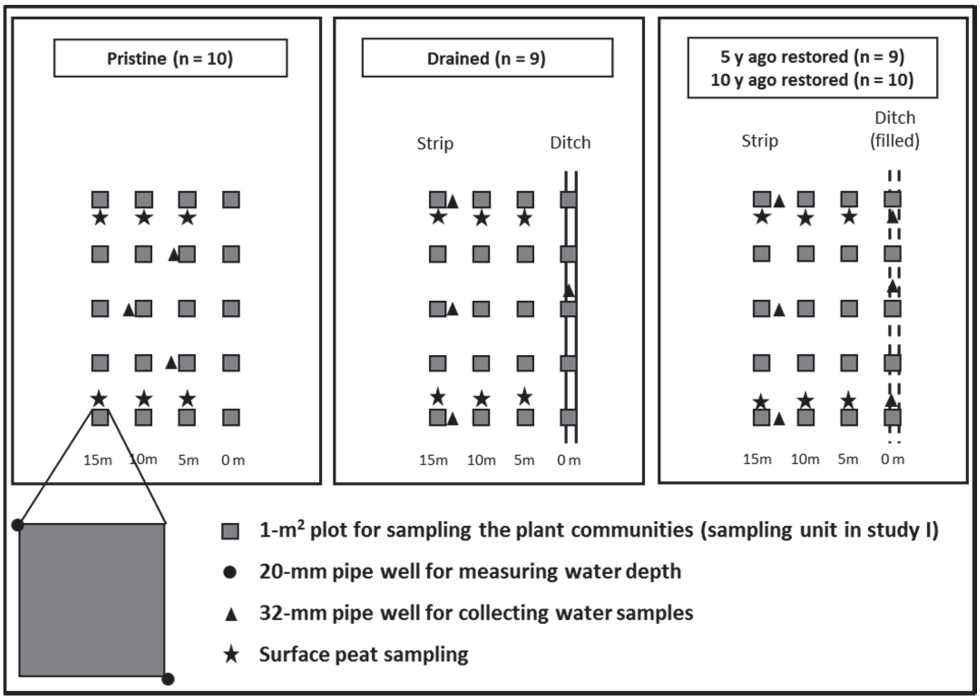

FIGURE 2 Set-up 1 used for studying hydrology, plant community composition, peat accumulation and carbon sequestration in original publications I, III and IV. Distances (m) refer to the distance of 1-m^2 plots (sampling units) from the ditches at restored and drained sites. A similar grid of plots was laid at pristine sites. Only the plots at 5-15 m distance from the ditch were used to study plant community composition in publication IV.

2.1.2 Set-up 2: 10-year monitoring of two partly restored peatlands

A set-up consisting of two *Sphagnum* peatlands, an ombrotrophic bog (61° 51′ N, 24° 14′ E) and a minerotrophic fen (61° 48′ N, 24° 17′ E), was established originally by Jauhiainen *et al.* (2002) to study the changes in hydrology, vegetation and peat chemistry shortly after restoration. The mean annual precipitation in the area is 675 mm and the long-term annual mean temperature is +3.4°C. Longer-term time series on the effects of restoration are rare and, therefore, highly valuable. Consequently, I made a decision to repeat the sampling in co-operation with previous authors 10 years after the restoration in 2006 (I).

The total area (200 hectares) of the studied bog was drained for forestry in 1955 using 30 m ditch spacing. In the central part of the bog, an area of 10.5 ha was re-wetted in 1995. The re-wetting was done mainly by filling in the ditches with peat excavated from the ditch banks and the bog surface. However, in places where volumes of peat in the ditch banks were insufficient for filling the ditches completely, more localized peat dams were constructed. Inside the re-wetted part of the bog, an area of 0.5 ha was chosen for monitoring. To regain the openness typical of natural bogs, the monitoring area was clear-cut and the logging slash was removed. Approximately 100 meters away from the restored bog site, a similar but unwetted and uncut drained area was selected as an experimental control location. The vegetation type of the bog prior to the drainage had been ombrotrophic short-sedge bog (sensu Laine and Vasander 1996).

The minerotrophic fen (150 hectares) was drained for forestry in 1955 with a ditch spacing of 50 meters. In 1995, an area of 1.1 ha was re-wetted by filling in one ditch with peat and damming an adjacent ditch with water-tight peat dams. The peat was excavated from the fen surface close to the ditches. A short feeder ditch was excavated upstream to enhance water flow from a nearby pond and mineral soils. Inside the re-wetted area, an area of 0.6 ha was selected for monitoring. This monitoring area was clear-cut and the logging slash and trees were removed. Approximately 50 m away from the restored fen site, a similar but unwetted and uncut area was selected as an experimental control location. Prior to drainage, the fen was of the tall-sedge pine fen type (sensu Laine and Vasander 1996).

Systematically laid vegetation sample plots (100 × 50 cm) were permanently marked on the restored and drained sites of the bog and the fen before the restoration in 1994 (Table 1). The plots, which had a minimum distance of 5 m from each other, were located in transects between the ditches and running coaxial to the ditches. Pipe wells (PVC) were established to measure the water-table depth.

2.2 Data collection

2.2.1 Measurements of water table and sampling of water for chemical analysis

The depth of the water table (the distance of water to peat surface) in each well was measured five times (May, June, July, August, and September) in 2008 (I) and several times during a snow free period in 1994-2005 (II, Table 1). Each time, the measurements were taken under stable climatic conditions.

I was also interested in the effects of drainage and restoration on water table level (question 2). Therefore, the peat surface was leveled at the location of each well (set up 1), and the measurements of water table depth in each well were converted to the absolute level of water table throughout the site. Most peatlands have a naturally sloping surface and, consequently, a sloping water table level. I was also interested in the effects of drainage and restoration on within-site variation in the water table level (I). Therefore, the variation in water table level caused by the ditch needed to be separated from the variation caused by the natural slope in the water table. Therefore, the lowest peat surface within and near to the study sites was leveled, and the leveling values were used to correct the water table level measurements for the natural slope of water table.

TABLE 1 The number of sample plots and pipe wells established and sampled in set-up 2.

	Restored Bog	Drained Bog	Restored Fen	Drained Fen
Vegetation plots established and sampled	12	9	12	9
Pipe wells established 1994	19	11	20	14
Pipe wells sampled 1994-1997	12[a-e]	9[a-e]	12[a-e]	9[a-e]
Pipe wells sampled 2005	7[a], 18[b], 12[c], 12[d], 19[e]	4[a], 13[b], 9[c], 9[d], 13[e]	8[a-e]	5[a], 8[b], 8[c], 9[d], 14[e]

[a]June, [b]July, [c]Beginning of August, [d]End of August, [e]Beginning of September and end of November

Water samples to study water chemistry (I) were collected in August 2007 with a plastic vacuum pump into 250-ml plastic bottles and kept cool with ice coolers during the transport before analyses.

2.2.2 Sampling of plant community composition

Plant communities were sampled at the end of July in 1994, 1995, 1996, 1997 and 2005 (II) and between June and August 2007 (III, IV). A visual estimation of the percentage of the plot covered by each vascular plant and bryophyte species (Bryophyta, Marchantiophyta) and some lichens was used as a measure of their relative abundance (II, III, IV).

2.2.3 Collection of surface peat samples and pine seedlings

Cores of surface peat (8.3 × 8.4 cm in width, 20 cm in depth) near to the plots used for sampling the plant communities were collected with a side-cutting box sampler in August 1994, 1997 and 2006 to study the peat elemental concentrations (II). Additionally, six similar cores were collected at each site of set-up 1 in autumn 2006 to study the C loss due to drainage and the C sequestration after restoration (IV). At the drained and restored sites, samples were collected close to the 1-m^2 plots at 5 to 15 m from the ditch (Fig. 2). The samples were divided into two segments (0-10 cm and 10-20 cm) in the field and stored in plastic bags after collection. The samples were carefully examined in the laboratory and, where necessary, stretched to their original length for peat growth measurements (IV) to compensate for the physical compaction during the sampling and transportation. To study the amount of C accumulated after restoration (IV), the boundary between the layers accumulated before and after restoration was visually detected from the samples of restored sites. The post-restoration layer was separated with a knife for further analyses in the laboratory.

The pine method (Borggreve 1889, Ohlson and Dahlberg 1991) was used to construct empirical age-depth models of surface peat and to determine the annual surface peat growth rate for each site to study surface peat accumulation

(IV). For this, 25-35 small (< 1.5 m) Scots pines were collected at each study site in autumn 2007. In each site half of the pines were collected from hummocks and the other half from lower-lying peat surfaces. For one five years ago restored site no pines were found and the site was excluded from this analysis. The vertical distance from the root collar (root to shoot transition) of the trees to the peat surface was determined to estimate rooting depth of each pine. The ages of pines were determined by counting the annual rings under a stereomicroscope.

2.2.4 Chemical analyses

Electrical conductivity (EC), pH, redox potential (E_{h7}) and concentrations of Ca, iron (Fe), sodium (Na), N, P, and DOC were analysed from the water samples (I). Measurements of pH, EC and E_{h7} were conducted after 2 to 5 hours of collection using a Consort SP50X meter and electrodes SP10B, SK10T, SP50X. The samples were then stored in cold and dark before further analyses. The concentrations of cations (Ca, Fe, Na) and DOC were analysed after filtration with 0.45 µm membrane filters with PerkinElmer Optima 4300 DV inductively coupled plasma optical emission spectrometer and Shimadzu TOC-5000 analyser, respectively. The analyses of cations were performed in the laboratory of Inorganic and Analytic Chemistry of the University of Jyväskylä and the analyses of N, P and DOC in the Ecology Research Institute laboratory of the University of Eastern Finland, Joensuu. The concentrations of N and P were analysed from two samples per site (one sample per sampling location) except for three drained sites for which only samples from the peat strips were analysed, and pristine sites for which only one sample per site was analysed.

Peat samples were dried at 105 °C to a constant mass and milled before the analyses of their chemical properties. In study II, the samples were digested with HNO_3-H_2SO_4-$HClO_4$, and the total concentrations of aluminum (Al), Ca, Fe, K, Mg, manganese (Mn) and P were analysed in the laboratory of the Finnish Forest Research Institute (Vantaa research unit), using an ARL 3580 vacuum ICP plasma emission spectrometer and a TJA IRIS Advantage ICP spectrometer. Digestion with HNO_3 and H_2O_2 and a PerkinElmer model Optima 4300 DV inductively coupled plasma optical emission spectrometer was used for the concentration measurements of Al, Ca, Fe, K, Mg, Mn and P in peat samples in the laboratory of Inorganic and Analytic Chemistry of the University of Jyväskylä (IV). Moisture content (%), ash content (%) and organic matter content (%) of the peat samples were also calculated, and C, hydrogen (H) and N content were measured with a CHN analyzer (VARIO EL III Elementar Analysensystem) in the laboratory of Inorganic and Analytic Chemistry of the University of Jyväskylä (IV). For the calculations of C sequestered into the post-restoration peat layer (IV) the samples were dried to constant weight at 70 °C for the determination of dry weight in the laboratory of the University of Eastern Finland. The mass of C in the samples was calculated by multiplying the dry mass with C concentration.

2.2.5 Data analysis

The changes in water table level were tested with linear mixed model analysis and Fisher's Least significant Difference (LSD) pairwise comparisons in study I. Furthermore, principal component analysis (PCA), Multi-Response Permutation Procedures (MRPP), LSD tests, t-tests and repeated measures ANOVA were applied to study pore water chemistry.

In study II, repeated measures ANOVA was used to analyse the effect of time and the restoration treatment on the water table depth, elemental concentrations in the peat, and the abundance of individual plant species. Furthermore, Pearson correlation was used to study the relationship between rainfall, temperature and water table depth. Changes in the plant community composition were analysed employing detrended correspondence analysis (DCA), and nonparametric Mann–Whitney test was used to test the differences in the Euclidean distances between site scores of different treatments and selected indicator species scores within DCA ordinations.

Bray-Curtis dissimilarity measure calculated separately for species presence/absence data and species abundance data was used to study changes in plant communities in study III. The effect of management status and distance from the ditch as well as their interaction on plant community composition in relation to communities of pristine reference sites (dissimilarity-from-pristine) were analysed with linear mixed models. LSD tests were used for pairwise comparisons. Non-metric multidimensional scaling (NMS) ordination was used to further illustrate the results.

To study the effect of drainage on surface peat C storage, we, firstly, calculated the expected mass of C for the drained samples (IV). This was done by multiplying the observed ash content in the drained samples with the average C to ash and C to Al ratios obtained from the samples collected from pristine peatlands. The loss of C (ΔC_{ASH}, ΔC_{AL}) for each sample was then estimated as the difference between the expected and the observed mass of C of the samples from the drained sites. The estimated C loss per m^2 for each drained site was then calculated by multiplying the average C loss of each sample with 1/sampler area (m^2).

The apparent annual vertical growth of the surface peat layer was calculated as a linear regression coefficient between the rooting depth and age of the pines for each site to study changes in surface peat growth rate (IV). ANOVA and LSD test were used to compare the coefficients between the management statuses.

The recent apparent rate of C accumulation (RERCA, g m^{-2} yr^{-1}) in surface peat after restoration and for comparable period for the pristine sites were determined to study the C sequestration rate in surface peat (IV). The slope of a linear regression modelling the cumulative C mass with time was interpreted as RERCA. The linear regression was forced through origo (i.e. zero peat depth corresponded to zero age) and the slope was tested against the expected slope (Extra sum-of-squares F test), i.e. the average 10-year RERCA of pristine sites, which was calculated according to the depth of 10-year old strata based on the pine method (see above).

The similarity of the composition of the plant communities between drained, 5 and 10 years ago restored and pristine sites (IV) was studied by comparing the Bray-Curtis community similarity of the study sites with non-parametric MANOVA. NMS ordination was applied for visual inspection of community changes.

ANOVAs, linear mixed models, LSD tests, t-tests, Pearson correlations, Mann-Whitney tests and linear regression coefficient calculations were performed with SPSS 15.0 (II) and IBM SPSS Statistics 20 (I, III, IV). DCA, PCA, MRPP and NMS were performed with PC-Ord 5.3. PAST 2.17b was used for non-parametric MANOVA and GraphPad Prism 5 for Windows for the F test.

3 RESULTS

3.1 Degradation and recovery of hydrology and recovery of surface peat chemistry

The long-term effect of drainage on peatland hydrology was studied in set-up 1 to answer question 1 (I). The results showed that significant lowering of the average water table level by peatland drainage is sustained for decades and that the draw down remains largest near the ditches. There were also significant differences in water chemistry between drained and pristine sites. An overall rise of pH and EC as well as increased average concentrations of Ca and DOC were observed at the drained sites when compared to the pristine sites. However, there were large differences between the samples collected from ditches and adjacent peat strips. For example, increased pH and EC after drainage were driven by significantly higher values in the ditches when compared to the peat strips. Furthermore, despite higher N and P concentrations at the peat strips, the overall effect of drainage, when compared to the concentrations at the pristine sites, was not significant due to low concentrations in ditch water.

To answer the question 2, the recovery of hydrology after restoration was studied, firstly, by 10-year monitoring of the water table at two drained and partly restored peatlands (II). Permanent plots established on a bog and a fen were sampled one year before, and one, two, three and 10 years after the restoration. The rewetting resulted in a raised water table in the restored systems. The rise took place immediately after ditch blocking and the elevated water table remained higher than at the drained sites 10 years after the restoration. However, signs of decreasing water tables 10 years after the restoration were found. In the comparative study of 38 peatland sites (I), the natural pattern of high and even water table level was observed five years after restoration. The water table level was, on average, at the pristine level also at the 10 years ago restored sites. However, increased within-site unevenness of the water table level was observed again 10 years after restoration: water table level in the filled ditches was on average slightly lowered when compared to the water table level in the surrounding areas and at the pristine sites.

Analysis of pore water chemical variables (I) suggests that restoration induced a recovery of pore water chemistry towards the targeted pristine chemistry. Especially the water chemical factors related to minerogenic influence of pore water were, on average, closer to the pristine values than the values at the drained sites. For Ca, pH, DOC, E_{h7} overall values close to pristine levels were measured after the first few years after restoration. Most of the water chemical differences (especially related to pH and DOC) between the ditches and peat strips were smaller at the restored sites when compared to the differences at the drained sites. The concentrations of N (especially in the ditches) and P were higher at the five years ago restored than drained sites. However, the concentrations of both appeared to decrease 10 years after restoration. Fe showed an increasing pattern after restoration especially in the filled ditches.

Changes in the elemental concentrations in the 0-20 cm layer of the peat were studied in set-up 2 (II). Restoration resulted in significant changes to the concentrations of Ca, K, Mg, Mn and P in the bog and to Ca, K, Mg and Mn in the fen. Increase in the concentrations of Ca, K, Mg and Mn was observed at both of the restored sites after the blockage of the ditches. In comparison with the results of studies of comparable natural peatlands (Damman 1978, Pakarinen 1978, Laiho *et al.* 1999, Minkkinen *et al.* 1999), the average concentrations of Ca, K, Mg and Mn reached natural levels in the restored bog within the 10-year period after restoration. In the fen, restoration increased the concentrations of Ca close to the values recorded from pristine fens in the region (Laiho *et al.* 1999, Minkkinen *et al.* 1999). The concentration of P initially decreased in the surface peat in the restored bog and subsequently increased to the pre-restoration concentrations within 10 years post restoration.

3.2 Degradation and recovery of peatland ecosystem structure

The effect of drainage-induced degradation on peatland structure in relation to the within-site degree of degradation (question 3) was studied in set-up 1 (III). In general, drainage had a strong effect on peatland ecosystem structure measured as plant community composition. The effect was dependent on the degree of degradation (distance from the ditch) such that the difference between drained and pristine communities (dissimilarity-from-pristine) decreased with increasing distance from the ditch. However, even the smallest degree of degradation (mainly due to average decrease of water table level by 10 cm) seemed to have an effect on plant community composition. At 0-m distance from the ditches, where the disturbance was strongest, the communities were separated from pristine communities by the presence of species tolerant to harsh environmental conditions of bare peat and flowing water (e.g. *Polytrichastrum longisetum*, *Carex canescens*). On the other hand, the communities outside the ditches (smaller degree of degradation) were characterized by increased relative abundance of species mainly found from closed forested habitats (e.g. *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Pleurozium schreberi*, *Dicranum polysetum*) and decreased relative abundance of species typical to bogs and fens (e.g. *Vaccinium microcarpum/oxycoccos*, *Drosera rotundifolia*, *Andromeda polifolia* and *Carex rostrata*, *Carex pauciflora*, *Dactylorhiza maculata*, *Sphagnum fallax*, respectively) when compared to the pristine sites. Some species typical to targeted pristine sites (such as *Sphagnum magellanicum*, *Sphagnum angustifolium*) were present in low abundances at most drained sites at most of the 5-15 m distances from the ditch. In contrast, some typical peatland species (e.g. *Carex rostrata*, *Sphagnum fallax*) were almost exclusively found in the ditches at the drained sites, albeit in very low abundances. A few species occasionally found from the wettest surfaces of pristine sites (e.g. *Carex limosa*, *Scheuchzeria palustris*) were not observed at the drained sites. The development of plant communities at the drained parts of studied peatlands in set-up 2 appeared to be towards dryer conditions during the 10-year monitoring period (II).

The recovery of peatland structure (plant community composition, question 4) after restoration was studied in both set-ups. In general, restoration seemed to induce a development towards the target community composition during the first 10 years after the restoration (II, III, IV). However, the development on plant communities after restoration appeared to be dependent on the distance from the ditch (i.e. the within-site degree of degradation caused by drainage, III). Communities in the plots with less degradation at 10 and 15 meters from the ditch were very similar to pristine communities at the 10 years ago restored sites, while the plots with a greater degree of degradation at 0 and 5 meters from the ditch showed no, or only some recovery towards targeted communities during the same time period, respectively. NMS ordination suggested that while the post-restoration community development trajectories at all distances from the ditch were fairly similar and indicated the initiation of recovery, the restoration itself may cause further albeit transient disturbance in communities (III). Moreover, the trajectory of the communities subject to most severe disturbances during both drainage and restoration measures (nearly complete destruction of plant communities and opening of bare peat surfaces) appeared not to point towards pristine target communities in the NMS ordination plot 10 years post restoration (III).

The recovery of plant communities seems to be driven by changes in species abundances rather than in their identities (III). It appears that the abundance of some species benefiting from drainage decreased outside the ditches (especially *Pleurozium schreberi*, *Vaccinium myrtillus*) after restoration, while the abundance of some typical peatland species with wide ecological niches increased after restoration (e.g. *Sphagnum angustifolium*, *Sphagnum magellanicum*; II, III). At the most severely degraded areas (0 m from the ditch) the communities were characterised by increased relative abundance of species capable of utilizing the free peat surfaces and released nutrients (e.g. *Carex magellanica*, *Eriophorum vaginatum*) five years after restoration (III). However, the abundance of species typical to bare peat (*Carex magellanica*, *Dicranella cerviculata*, *Polytrichastrum longisetum*, *Eriophorum vaginatum*) seemed to decrease again 10 years after restoration. Whereas some typical fen species (such as *Carex rostrata*, *Sphagnum fallax*, *Straminergon stramineum*) were completely missing (II) or very rarely present (III) outside the filled ditches, they were abundant within the infilled ditches (III). At the ombrotrophic bog site, the recovery was driven especially by the increased abundance of *Sphagnum balticum* in the hollows (II). Some species typical of wet pristine habitats but not observed from drained sites (*Scheuchzeria palustris*, *Carex limosa*), were neither observed at the 10 years ago restored sites (II, III).

3.3 Degradation and recovery of peatland ecosystem function

The effect of drainage and restoration on peatland ecosystem function of surface peat growth rate (question 5) was studied in set up 1 (IV). The growth rate of surface peat at the drained sites was significantly retarded when compared to the pristine, five years ago and 10 years ago restored sites. In contrast, there were no differences between the pristine and the five years or 10 years ago restored sites.

The long-term effect of drainage on C sequestration in the surface peat and the rate of C accumulation in surface peat after restoration (question 6) were studied in set up 1 (IV). The comparison of expected and observed C masses in surface peat of drained sites suggested substantial loss of C due to drainage. The estimates for average C loss from the 0-20 cm surface peat samples were ΔC_{ASH} 5172 g m^{-2} (SE 2339 g m^{-2}) and ΔC_{AL} 6714 g m^{-2} (SE 2908 g m^{-2}). As the focal peatlands were drained *ca.* 40 years prior to the study, the average per annum C loss were 129.3 g m^{-2} (SE 58.5) and 167.8 g m^{-2} (SE 72.7) for ΔC_{ASH} and $\Delta C_{AL,}$ respectively. According to the slope of the regression model the regenerated surface peat layer of restored sites accumulated C with an average rate of 116.3 g m^{-2} yr^{-1} for the 3-12 years period (SE 12.7). In comparison, the RERCA for 10-year period for pristine sites was 178.2 g m^{-2} yr^{-1} (SE 13.3). The difference of the slope was statistically significant ($F = 23.73$, $P < 0.001$), but the variation of the accumulation rate at the restored sites was large, and some of the restored sites had even higher post-restoration surface peat C accumulation than predicted by the pristine reference estimate

4 DISCUSSION

4.1 Hydrology and surface peat chemistry

Taken together, my results suggest that drainage for forestry lowers the water table level for decades. In addition to short-term changes due to drainage (Prévost *et al.* 1999, Åström *et al.* 2001, Holden *et al.* 2004), chemical differences in pore water between pristine and drained sites can be observed still decades after drainage. There was also much larger variation in the water table level and water chemistry within the drained than the pristine sites. The higher mineral element concentrations and pH in ditches than in peat strips suggests that the flow of mineral-rich water from catchment was directed along the artificial flow paths formed by ditches. Whereas the concentration of DOC was expectedly low in the ditches, significantly increased concentration of pore water DOC of the drained sites was found at the peat strips between ditches. This is noticeable because pore water DOC may be flushed to downstream aquatic ecosystems especially during peak flow periods (Worrall *et al.* 2002). The increased DOC loading can alter physical and chemical conditions such as acidity, light penetration and bioavailability of metals and nutrients or contribute to food webs as C source to microbes (Evans *et al.* 2005). My results, therefore, suggest that despite contradictory results on the effect of forestry drainage on DOC export to downstream water courses (Lepistö *et al.* 2008, 2014, Sarkkola *et al.* 2009, Rantakari *et al.* 2010, Räike *et al.* 2012), forestry drainage lasting for decades has potential to increase leaching of DOC depending on hydrological conditions.

My results on the hydrological and surface peat chemical differences between pristine, drained and restored sites appear promising from the perspective of restoration. They are also in line with a recent review, where hydrologic factors seemed to be comparably quickly restored for wetlands in general (Moreno-Mateos *et al.* 2012). In my study, the targeted average water table level, perhaps the most important condition controlling the recovery of peatland ecosystem structures and functions, could be rapidly re-established. In addition to regaining targeted water table level, restoration is expected to re-establish natural water-flow paths into and within restored sites. This is highly important especially in the minerotrophic peatlands, because the disruption of hydrological connections may severely affect peatland ecosystems (Tahvanainen 2011). My results suggest that restoration increased surface peat cation concentrations at the minerogenic fen site after restoration (II). This may, indeed, indicate that the flow of minerogenic water from the watershed into the restored sites could be re-established by restoration. Furthermore, the lessened water chemical differences between the ditches and the peat strips suggest that the artificial flow paths of water along the ditches were cut off by restoration. However, hints of decreasing water table level were observed 10 years after restoration especially in the filled ditches (I, II). This may be an early warning sign for future problems and should be taken seriously by the practitioners. For example, I encourage using peat dams for directing water flow away from the in-filled ditches especially when restoring minerotrophic peatlands. Furthermore, the dams should be constructed high and wide enough (extending several meters away from the ditch perpendicular to the ditch and several decimeters above the peat surface) to ensure that they preserve their functionality after decades of erosion by water and peat decomposition.

The changes in pore water and surface peat nutrient concentrations suggest that restoration may also have negative environmental effects: increased leaching of N and P to downstream water courses may be expected for some years after restoration. High P mobilization over decades is expected to take place when rewetting calcareous fens with agricultural history (Zak *et al.* 2008). My results suggest, however, that the risk of eutrophication of downstream waters diminishes after five to 10 years after restoration of nutrient-poor peatlands drained for forestry. While the results indicate that drainage has a large potential to increase leaching of DOC, it appears that restoration has a potential to reduce leaching of nutrients and DOC to downstream waters in the long term. This might be especially important in heavily drained areas such as Finland where meeting the global target of restoring 15 % of degraded ecosystems suggests restoring 0.75 million ha peatlands (Convention on Biological Diversity 2010).

My results show a very similar temporal P release pattern in pore water after restoration than the previous results derived from outflow monitoring of similar nutrient poor sites (Koskinen *et al.* 2011). This suggests that pore water measurements, which are often much easier and cheaper than outflow monitoring, could provide a proxy for the estimation of nutrient outflux patterns after restoration. However, quantification of fluvial fluxes would require discharge monitoring.

4.2 Peatland ecosystem structure

Drainage creates a gradient of water table draw down (I) resulting in a gradient in the degree of degradation within these ecosystems. Such degradation by drainage induced changes that were visible in peatland ecosystem structure i.e.

plant communities after several decades (III). Even a water table drawdown of 10 cm seems to be sufficient in disturbing peatland plant communities (III). In some cases, spontaneous recovery may be sufficient in re-establishing target communities (Hobbs and Cramer 2008, Jones and Schmitz 2009). When monitoring the plant communities at the drained peatland sites for a decade, an adverse development - rather than any recovery - was observed despite hints of slightly increased water table (II). My results, therefore, suggests that a recovery of the targeted plant communities in the studied ecosystems due to overgrowth and thus slow natural blockage of the ditches is unlikely within a time scale relevant for halting the loss of biodiversity (II).

The differences in plant communities between pristine, drained and restored sites are, generally, encouraging from the perspective of restoration. However, my studies highlight the need for patience and long-term monitoring before drawing conclusions on the efficiency of restoration in recovering ecosystem structures when reaching for the global restoration targets (Convention on Biological Diversity 2010, Maron *et al.* 2012). This seems to be the case especially with plant communities, which are expected to recover more slowly than vertebrate and invertebrate communities (Moreno-Mateos *et al.* 2012). The differences observed between communities at the sites restored 10 years ago and the target communities may, indeed, be due to the insufficient time for the re-establishment of original communities. This, in turn, may be caused e.g. by the poor dispersal potential of the absent peatland specialists (Seabloom and Valk 2003) or the competitive advantage of the indifferent peatland species survived through the drainage phase (e.g. Mälson *et al.* 2008). It may also be that the habitats remain unsuitable for more specialised species despite the restoration (Mälson *et al.* 2008, Aggenbach *et al.* 2013). The studied hydrological and peat chemical variables did not, however, indicate such unsuitability of conditions during the study period in my case (I, II). The results here, furthermore, suggest that the disturbance caused by the restoration measures themselves may delay the recovery (III). Such disturbance is probably of minor importance in studied nutrient poor habitats with relatively low species turn-over due to drainage and only few vulnerable species being present originally and after drainage. However, possibility for such unwanted impacts should be taken into account e.g. when restoring sites with vulnerable species and sites where the most valuable species inhabit the areas undergoing severe disturbance due to restoration measures. My results also suggest that understanding the time-scale of the recovery of ecosystem structures requires addressing the within-site variation in the degree of degradation. As regards to sites of the present studies, the least degraded communities appeared to recover nearly completely in 10 years. In contrast, the communities with greater degree of degradation showed only weak development towards the target composition during the same period.

In accordance with earlier studies, the recovery of wetland communities appeared to be driven by changes in species abundances rather than changes in their identities (Moreno-Mateos *et al.* 2012). It appears that some typical peatland species find refugia during the drainage outside the ditches irrespective of the degree of degradation. They can, hence, re-establish rather rapidly after re-establishment of suitable conditions. Other species expected to recover after restoration may, in fact, find novel refugia within the ditches at the drained areas. Their presence in the ditches, even though in very low abundances, may be important for the recovery of plant communities after restoration. This is because it is probable that these novel habitat refugia contributed to the high abundance of these species in the infilled ditches after restoration when compared to their presence at the ditches of drained sites (III). It should also be noted that there were some specialized species, growing typically in the wettest areas of studied pristine peatland types, which could not be found from either drained or restored sites (II, III). This is in line with earlier studies suggesting that the species once disappeared due to drainage re-establish poorly (Hedberg *et al.* 2012). Active transplantations of target species are suggested as a measure to completely restore target vegetation (Hedberg *et al.* 2012). However, it should also be carefully considered what else could be done with the resources that re-establishing the complete original communities by transplantations would take (see e.g. Bottrill *et al.* 2008, Gilbert 2011, Game *et al.* 2013). For example, if the intention is not to bring back a strictly defined set of target species, partial recovery of plant community composition may still be sufficient to recover some important peatland ecosystem functions in these nutrient and species poor habitats (III).

4.3 Peatland ecosystem functioning

There are several earlier estimates on the C balance of drained ecosystems similar to the ones focal here, but there appears to be no consensus on whether these drained boreal peatlands function as sinks or sources of C (e.g. Silvola *et al.* 1996, Laine and Minkkinen 1998, Ojanen *et al.* 2010, 2013; Lohila *et al.* 2011, Simola *et al.* 2012, Pitkänen *et al.* 2013). My results indicate significant degradation of functionality (in terms of peat growth and C sequestration of the surface peat) due to drainage. Furthermore, the observed loss of C is of magnitude comparable to recent studies that have found significant net loss of C from the peat after drainage (Pitkänen *et al.* 2013). It appears also that some of the controversy may be due to methodological differences, which should be understood when interpreting the results: the results derived from C exchange measurements describe the current real-time situation while the peat core analysis reveals the cumulative effect of drainage during the complete drainage period. Likewise, my estimates derived from the uppermost peat layer are not directly comparable to studies covering the entire peat deposit. It should also be noted that loss of C as DOC in surface run-off or into groundwater may approach 2/3 of the annual C sink of boreal peatlands (Roulet *et al.* 2007, Gažovič *et al.* 2013). This cannot be revealed by studying the soil-atmosphere C exchange. The significantly increased pore water DOC after drainage (I) may, therefore, partly explain studies that have found large net losses of C from the peat after drainage (Simola *et al.* 2012, Pitkänen *et al.* 2013).

The recovery of ecosystem functions appears to be slow and uncertain for wetlands in general (Moreno-Mateos *et al.* 2012). I studied the recovery related to the perhaps globally most important peatland function, long-term C storage in peat. Perhaps surprisingly, I found rapid recovery of functionality in the peat surface layer, which is a highly important layer for the long-term C accumulation in peatlands. Despite apparent retardation due to drainage, I observed surface peat growth rates that were at the level similar to pristine sites already five years after restoration, and the same rate was maintained 10 years after restoration (IV). On the other hand, a small difference was still observed between the C accumulation rates of restored and pristine sites (see also Tolonen and Turunen (1996) for pristine RERCA over 35 years) (IV). The difference in the annual C sequestration rate between pristine and restored sites is probably partly due to a time-lag in the response of the plant community to new selection pressures set by the restoration actions. Because restoration was found to have potential to reduce leaching of DOC to downstream water courses in long-term (I), restoration appears to be effective in recovering some important components of peatland C cycle.

K and Mn are easily exchangeable cations and effectively taken up by the growing vegetation. This results in a typical vertical pattern in which their concentration is clearly surface enriched in the peat matrix (Damman 1978, Pakarinen 1978). After drainage the concentration of these cations typically decreases, especially due to increased uptake by the tree stand and increased leaching (Finér 1989, Sallantaus 1992, Laiho *et al.* 1999). The re-enforcement of the typical vertical pattern and the general increase of concentrations towards typical pristine values were observed at the two monitored restored peatlands (II). Such results suggest the recovery of peatland functionality in terms of K and Mn cycling between the peatland vegetation and the peat. Overall, it appears that ecological restoration by raising the water table can, indeed, re-establish important ecosystem functionality in the surface peat of degraded peatland ecosystems already within a few years post-restoration. However, the re-establishment of some other functions like C sequestration or hydrological functioning (McCarter and Price 2013) may, indeed, take a longer time period.

4.4 Is original structure needed to regain original functions?

According to the simplistic model describing ecosystem recovery after restoration, the relationship between ecosystem structure and function is expected to be linear and positive (Bradshaw 1984, Dobson *et al.* 1997). In practice, instead of the linear positive relationship, non-linear and also negative relationships are possible (Cortina *et al.* 2006). In wetlands, the recovery of ecosystem structure has been suggested to be a prerequisite to the recovery of ecosystem functions (Moreno-Mateos *et al.* 2012). It was, therefore, somewhat surprising that while the restoration had not yet been successful in returning the original ecosystem structure (plant community composition), it seemed to be successful in recovering the important surface peat growth functionality (III). The results here, therefore, suggest considerable plasticity in the studied structure-function relationship of peatland ecosystems: it appears that the original structure (plant community composition) was not needed to regain an important ecosystem function (surface peat accumulation rate). It appears also that while this kind of a plastic ecosystem function could, indeed, be re-established with minor recovery of ecosystem structure, this did not result in similar recovery of C accumulation in surface peat layer. Not surprisingly, this suggests that evolution of the relationship between one ecosystem structural component (plant community composition) and two ecosystem functions may differ even between closely linked functions (peat growth rate and C accumulation rate in surface peat). The few studies exploring the relationship between the recovery of ecosystem structure and function have suggested that the relationship between structure and function may change over time. For example, salt marsh ecosystem functionality (e.g. in terms of shoot biomass accumulation) may be increased for a few years by increasing biodiversity (species richness), but the positive relationship between diversity and functioning is broken up soon after the active management is ceased and a few productive species become dominant (Doherty *et al.* 2011). Considering temporal changes, my results suggest that, in addition to increasing the functionality soon after rewetting, peatland restoration could maintain the functioning (in terms of surface peat accumulation rate) on the targeted level despite comparably slow and incomplete recovery of ecosystem structure.

Discussion about the relationship between restored ecosystem's structure and function is challenging in part because (1) the definitions of structure and function are not always made explicit, and (2) the definitions may differ depending on one's field of science (Sutton-Grier *et al.* 2010). On the other hand, huge expectations are set for restoration in safeguarding ecosystem services provided by functioning ecosystems (Convention on Biological Diversity 2010). Intuitively, the more causative the relationship of ecosystem functions and community composition or biodiversity per se, the more complicated and costly are the actions needed to reach the restoration targets. Hence, it is certainly important to understand better how much of the original structure needs to be recovered to regain original ecosystem functions. My studies support the view by Montoya *et al.* (2012) suggesting that in addition to focusing on the relationships between single attributes of ecosystem structures and functions, future studies should better address the multifunctionality of ecosystems.

5 CONCLUSIONS

The broad aim of this thesis was to answer the question "Is restoration an effective tool for recovery of ecosystem structures and functions?". Being aware of the millennial time-scale of peatland ecosystem development, it seems unrealistic to answer such a question in a study covering only the first decade after restoration. Furthermore, the answer may depend on studied attributes i.e. which ecosystem structures and functions were focal to the study (see Moreno-Mateos *et al.* 2012). However, I can conclude that peatland restoration clearly has potential to fulfil the societal expectations laid on it. Restoration can result in significant recovery of hydrologic and surface peat chemical features needed for the recovery of peatland ecosystem structures and functions. This leads to the initiated recovery of one main ecosystem structural component i.e. plant community composition already during the first 10 years post-restoration. My study also suggests that some ecosystem functionality related to the perhaps globally most important peatland ecosystem function i.e. long-term C sequestration can, indeed, be recovered to the targeted level within a decade. Huge global expectations are laid on restoration to recover ecosystem services (Convention on Biological Diversity 2010, Maron *et al.* 2012). Hence, it feels promising that some important functionality could, indeed, be recovered already with partial recovery of ecosystem structure within this relatively short time-scale. Ecological restoration of ecosystems is now increasing rapidly around the globe. However, there is still room for methodological fine-tuning to improve the success of restoration while patiently monitoring the ecological effects of the measures (Suding 2011). When combined with efficient share of knowledge on the best practices and possible caveats related to restoration (Keenleyside *et al.* 2012, Menz *et al.* 2013), ecological restoration may best serve as a tool to improve the structure and functions of ecosystems.

The concepts of ecosystem resistance and resilience are essentially linked to successful restoration (Society for Ecological Restoration International 2004, Suding 2011). Therefore, it is fruitful to view my results from their perspective. To be effective restoration needs i) to overcome the resistance and resilience of the degraded ecosystem state (Suding *et al.* 2004, Alday and Marrs 2013), and ii) to strengthen the resilience (and resistance) of the restored system in order to facilitate its long term persistency (Suding 2011). I found a development of plant communities towards the target (II, III, IV). This suggests that restoration was, indeed, efficient in overcoming the resistance of the ecosystem in its degraded state, and that the original ecosystem still shows some resilience despite significant changes after drainage (see Lake 2013). Additionally, no reversal of the trajectories of community development towards the degraded state was observed (II, III, IV). Hence the degraded peatland ecosystems appeared not be resilient to restoration within the studied time-scale. I hypothesize, that the successful overcoming of resistance and resilience in the degraded ecosystem was possible in this case especially because of the successful recovery of hydrology (I). Furthermore, most of the original species were apparently present also at the sites in their degraded state (III).

The results here suggest that variability in the degree of degradation (as a function of the distance from the ditch) increases the within-site variability in the community compositions: at least degraded drained plots (15 meters from the ditch) the communities were only slightly more dissimilar-from-pristine than the pristine communities but the dissimilarity-from-pristine increased with increasing degree of degradation at 10, 5 and 0 meters from the ditch (III). Thus drainage appears to increase within-site heterogeneity in the community composition when compared to the pristine communities. In contrast, restoration appears to decrease heterogeneity among the plots of 5, 10 and 15 meters from the ditch 10 years post restoration. The dissimilarity-from-pristine at 0 meters from the ditch was, however, still much larger than at the other distances. Consequently, significant heterogeneity still remained in the restored ecosystems when compared to pristine ecosystems. Such a heterogeneity can be considered an unfavorable deviation from the target ecosystem state. However, more heterogeneous communities are more likely to be able to adapt to the changing environments of the future (see e.g. Vellend 2005, 2010). Therefore, some increased heterogeneity in communities may in fact be desirable from the perspective of adaption of communities in changing environmental conditions (Harris *et al.* 2006, Jackson and Hobbs 2009). This speculation highlights the importance of consideration of the targets of restorations. It appears that the restoration practitioners are facing a challenging task. On one hand, they are expected to strengthen the resistance and resilience of the recovering system in order to facilitate its long term persistency. On the other hand, they should create ecosystems that are not resistant or resilient to the changing environment.

Being aware of the extent of degraded ecosystems and recent international impetus on large-scale restoration (Convention on Biological Diversity 2010), it is also necessary to consider the economic feasibility of restoration. The cost of restoration may be mitigated or even completely offset if the restored ecosystems produce increased ecosystem services with economic value that is lost when the ecosystem is in degraded state (Bullock *et al.* 2011, de Groot *et al.* 2013, Menz *et al.* 2013). More data on the multiple potential ecosystem service benefits provided by peatland restoration is called for (Kimmel and Mander 2010). However, the key issue concerning the effect of peatland restoration in the provisioning of ecosystem services appears to be the balance of C and greenhouse gases and their role in global climate regulation (Kimmel and Mander 2010). Apparently, ecosystem-level C budgets for restored sites cannot be constructed with the data describing the C sequestration in the surface peat only. However, the magnitude of potential economic gains related to C sequestration in restored peatlands can be highlighted with a simple calculation related to my results. The average and the highest prices in the voluntary C market for comparable terrestrial C projects in 2010 were 6 and 136 USD per credit (t CO_2e (carbon dioxide equivalents)), respectively (Peters-Stanley *et al.* 2011). On average 116.3 g C m^{-2} yr^{-1} accumulated into the surface peat of studied sites during the 3-12 years' post-restoration time period corresponding to 426.4 g m^{-2} yr^{-1} of CO_2e. (III). Thus, with the 2010 prices, the surface peat of the restored sites sequesters C at a rate corresponding to 26 – 580 USD ha^{-1} $year^{-1}$ for the 3-12 years' post-restoration time period. In Finland alone there are *ca.* 1 million hectares of forestry drained peatlands where the drainage has not been economically profitable in terms of increasing timber growth. The cost of blocking of ditches (including costs for planning of the measures) in Finland is about 610 USD per ha (Jouni Penttinen, Natural Heritage Services of Metsähallitus, pers. comm.). Therefore, the total one-off cost of restoring the 1 million hectares would be *ca.* 610 million USD. Using above numbers, the market value of surface-peat C of 1 million hectares of restored boreal *Sphagnum* peatlands would amount between 26 to 580 million USD annually over the first decade after restoration. The mechanisms needed for gaining C credits from peatland rewetting are starting to emerge, and the socio-economic importance related to restoration of wetlands has been emphasized (see e.g. Tanneberger and Wichtmann 2011, Alexander and McInnes 2012, Kettunen *et al.* 2012, Reed *et al.* 2013). Indeed, it is suggested that wetland restoration, in general, pays (i.e. provides more benefits than costs) due to increased ecosystem services (de Groot *et al.* 2013). However, long-term experiments e.g. on the changes in greenhouse gas and fluvial DOC fluxes as well as the development of tree stands are needed to reliably estimate if peatland restoration may really produce tradable C-related ecosystem services. The rough and unrealistic calculations above, hopefully, attract scientific and societal interest to establish such studies.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Ennallistamisen vaikutukset metsäojitetun suoekosysteemin rakenteeseen ja toimintaan

Ihmistoimet ovat muuttaneet luontaisia ekosysteemejä lähes kaikkialla maapallolla. Tämä on johtanut lajien kiihtyvään uhanalaistumiseen. Epäillään myös, että lisääntyvä ekosysteemien muokkaaminen heikentää niiden toimivuutta ja kykyä tuottaa ihmisten itsensäkin tarvitsemia hyödykkeitä eli ekosysteemipalveluja. Ennallistamisen tavoitteena on käynnistää ekosysteemien luontaisen rakenteen ja luontaisten toimintojen palautuminen kohti tilaa, jossa ne olivat ennen ihmisen aiheuttamaa häiriötä. Ekosysteemin rakenteilla tarkoitetaan esimerkiksi lajiyhteisöjen koostumusta ja toiminnalla esimerkiksi hiilen ja ravinteiden kiertoa systeemissä. Ennallistamiseen on kohdistettu suuret yhteiskunnalliset odotukset: kansainvälisen sopimuksen mukaan 15 % rakenteeltaan ja toiminnaltaan heikentyneistä ekosysteemeistä tulee ennallistaa vuoteen 2020 mennessä. Näin pyritään turvaamaan monimuotoisuuden ja luonnon ihmisillekin tuottamien palvelujen säilymistä. Ennallistamisen toimivuutta on kuitenkin epäilty. Epäilykset voivat toisaalta olla ennenaikaisia, koska usein käytettävissä on tutkimustietoa vain muutamien ensimmäisten ennallistamisen jälkeisten vuosien ajalta. Monissa tapauksissa ongelmien syynä voi olla myös elinympäristön palauttamiseen tarvittavien ekologisten mekanismien tai ennallistettavan elinympäristön puutteellinen tuntemus.

Suot ovat meille suomalaisille tuttuja. Harva kuitenkaan tietää, että niillä on maailmanlaajuisesti suuri merkitys ilmaston säätelyssä. Tuhansien vuosien aikana soiden kasvillisuus on sitonut ilmakehästä valtavan määrä hiilidioksidia, jonka sisältämä hiili on varastoitunut usein metrien paksuiseen turvepatjaan. Turpeen ja hiilen kertymistä - kuten myös soilla elävän lajiston esiintymistä - säätelevät suurelta osin hydrologiset tekijät kuten veden pinnan syvyys ja suoveden kemiallinen koostumus. Suomessa ja muualla maailmassa on ojitettu soita puuntuotannon lisäämiseksi miljoonia hehtaareja. Ojitus muuttaa suota merkittävästi. Keskeisin muutoksia aiheuttava tekijä on veden pinnan lasku. Se lisää hapekkaisiin oloihin sopeutuneiden pieneliöiden aiheuttamaa turpeen hajotusta suon pintakerroksessa. Turpeen ja suoveden laatu muuttuu. Metsäojituksen on epäilty johtavan turpeeseen varastoituneen hiilivaraston purkautumiseen. Soiden lajistossa tapahtuu suuria muutoksia kosteisiin oloihin sopeutuneiden lajien korvautuessa kuivempiin ja varjoisampiin paremmin sopeutuneilla lajeilla. Aiempien tutkimusten tulokset ovat kuitenkin osin ristiriitaisia, eikä läheskään kaikkia ojituksen pitkän aikavälin vaikutuksia tunneta hyvin. Esimerkiksi vedenpinnan alenemisesta johtuvan häiriön aiheuttama vaihtelu suoekosysteemin sisällä tunnetaan huonosti.

Soita ennallistetaan nostamalla vedenpintaa ojia tukkimalla. Joissain tapauksissa poistetaan lisäksi ojituksen aikana kasvanutta puustoa suon alkuperäisen avoimuuden palauttamiseksi. Tutkin väitöskirjassani, onko lajiston ja toiminnan palauttaminen todella mahdollista näillä suhteellisen yksinkertaisilla menetelmillä. Tarkastelin ekosysteemin rakennetta kasviyhteisöjen lajikoostumuksen ja toimintaa etenkin hiilen sitoutumiseen liittyvien tekijöiden avulla. Muutosten ymmärtämiseksi tutkin myös ojituksen ja ennallistamisen vaikutuksia suoveden syvyyteen ja kemialliseen koostumukseen sekä ennallistamisen vaikutuksia pintaturpeen kemiallisiin ominaisuuksiin. Tarkastelin lisäksi, kuinka ojituksen aiheuttama suon sisäinen vaihtelu kasvilajiston koostumuksessa vaikuttaa lajiston palautumiseen. Käytin tutkimuksessa kahta koeasetelmaa. Ensimmäiseen sisältyi kaksi suota, joiden kasvillisuuden, vedenkorkeuden ja pintaturpeen kemiallisten ominaisuuksien muutoksia oli seurattu niiden ojitetulla ja ennallistetulla osalla ennallistamista lähtien. Toisessa koeasetelmassa vertasin kasviyhteisöjen samankaltaisuutta, suoveden pinnan tasoa sekä suoveden kemiallisia eroja luonnontilaisten, ojitettujen sekä viisi ja 10 vuotta aiemmin ennallistettujen soiden välillä. Lisäksi tarkastelin tällä asetelmalla ojituksen ja ennallistaminen vaikutuksia pintaturpeen kertymiseen sekä turpeen pintakerroksen hiilensidontaan. Molemmat koeasetelmat sijaitsivat Etelä-Suomessa.

Havaitsin suoveden pinnan olevan merkittävästi luontaista matalammalla vielä vuosikymmeniä ojituksen jälkeen. Veden pinnan lasku oli suurin lähellä ojia. Yhdessä ojien kaivamiseen liittyvän fysikaalisen häiriön kanssa tämä saa aikaan häiriön voimakkuutta kuvaavan gradientin, jonka toisessa päässä ovat voimakkaimmin häirityt alueet (ojat) ja toisessa päässä kauimpana ojista sijaitsevat alueet. Havaitsin myös eroja suoveden kemiallisessa koostumuksessa ojitettujen ja luonnontilaisten soiden välillä: esimerkiksi suoveden liukoisen orgaanisen hiilen pitoisuudet ovat huomattavasti korkeampia ojien välisellä saralla kuin luonnontilaisella suolla. Tämä viittaa siihen, että pitkäaikaisen ojituksen seurauksena alapuolisiin vesistöihin voi - valumasuhteista riippuen - huuhtoutua luontaista enemmän vedenlaatua heikentävää liuennutta orgaanista hiiltä. Havaitsin myös merkittäviä eroja ojissa virtaavan veden ja saroilta kerätyn veden laadussa. Ennallistaminen puolestaan palautti vedenpinnan samalle tasolle kuin luonnontilaisilla vertailusoilla. Suoveden ja pintaturpeen kemiallinen koostumus vaikutti palautuvan enemmän luonnontilaista muistuttavaksi ennallistamisen jälkeen. Suon sisäinen vedenlaadun vaihtelu oli merkittävästi vähäisempää ennallistetuilla kuin ojitetuilla soilla. Tulokset viittaavat siihen, että suon rakennetta ja toimintaa säätelevissä tekijöissä tapahtuu merkittävää palautumista jo muutamia vuosia ennallistamisen jälkeen. Suoveden pinnan havaittiin kuitenkin hieman laskeneen tukituissa ojissa suhteessa ympäröivien sarkojen vedenpintaan 10 vuotta ennallistamisen jälkeen. Tämä voi olla merkki vettymiseen liittyvistä ongelmista, jotka voivat haitata suon palautumista tulevaisuudessa. Ennallistajien onkin syytä tarkkailla tilannetta ja tehdä tarvittaessa korjaavia toimenpiteitä. Tulokseni tukevat aiempia havaintoja, joiden mukaan fosforin ja typen huuhtoutuminen voi lisääntyä tilapäisesti ennallistamisen jälkeen. Tämä voi lisätä rehevöitymisriskiä alapuolisissa vesistöissä muutamien ennallistamisen jälkeisten vuosien ajan. Toisaalta 10 vuotta aiemmin ennallistetuilta soilta mitattiin alhaisempia liuenneen orgaanisen hiilen pitoisuuksia kuin ojitettujen soiden vedestä. Tämä viittaa mahdollisuuksiin vähentää alapuolisiin vesistöihin huuhtoutuvan orgaanisen hiilen määrää pidemmällä aikavälillä.

Aiempien tutkimustulosten mukaisesti havaitsin ojituksen vaikuttavan kasviyhteisöihin selvästi. Muutos suhteessa luonnontilaisen suon kasviyhteisöihin oli sitä suurempi mitä voimakkaampi oli pääasiassa vedenpinnan laskusta aiheutunut häiriö suon sisällä. Tulosten perusteella näyttää siltä, että ojitettujen soiden kasviyhteisöjen palautuminen ilman ennallistamista on hidasta ja epävarmaa. Ennallistaminen puolestaan käynnisti kasvillisuuden palautumisen. Ero luonnontilaisten soiden kasvillisuuteen oli kuitenkin vielä selkeä 10 vuotta ennallistamisen jälkeen. Ojituksen aiheuttaman häiriön suuruus vaikutti palautumiseen: heikosti häirityt alueet muistuttivat kasviyhteisöiltään suuresti luonnontilaisia jo 10 vuotta ennallistamisen jälkeen, mutta voimakkaimmin häirityillä alueilla kasvillisuus poikkesi vielä huomattavasti luonnontilaisten soiden kasvillisuudesta.

Havaitsin pintaturpeen kertyvän hitaammin ojitetuilla kuin luonnontilaisilla soilla. Ojitus näytti myös heikentävän hiilen sitoutumista turvekerroksen pintaosaan. Pintaturpeen kertymisnopeus oli puolestaan samankaltainen ennallistetuilla ja luonnontilaisilla soilla. Ennallistamisen jälkeen kertyneeseen pintaturpeeseen ei kuitenkaan sitoutunut hiiltä vielä samalla nopeudella kuin luonnontilaisten soiden pintaturpeeseen. Tulosten perusteella vaikuttaa siltä, että ennallistamalla voidaan palauttaa suoekosysteemin toimintoja luontaiselle tasolle, vaikka ekosysteemin rakenne eli kasviyhteisön koostumus poikkeaa vielä merkittävästi luontaisesta. Rakenteen ja toiminnan suhteen palautuminen vaikuttaa kuitenkin riippuvan tarkastelluista toiminnoista.

Ennallistamiselle asetettujen kansainvälisten tavoitteiden näkökulmasta tutkimukseni tulokset ovat lupaavia. Tulokseni osoittavat kuitenkin, että ennallistamisen vaikutusten ymmärtäminen vaatii kärsivällisyyttä ja pitkäjänteistä seurantaa. Suoveden pinnan nousu sekä suoveden ja turpeen kemiallisten ominaisuuksien palautuminen vaikuttavat luovan hyvät edellytykset lajiston ja ekosysteemin toimintojen palautumiselle. Alkuperäisen rakenteen eli lajikoostumuksen palautuminen käynnistyy ja tärkeitä suoekosysteemin toimintoja palautuu luontaiselle tasolle jo ensimmäisen ennallistamisen jälkeisen vuosikymmenen aikana. On myös huojentavaa havaita, että alkuperäisen lajiston palauttamista edellyttäviä - usein hyvin kalliita - toimenpiteitä ei aina tarvita ihmisen kannaltakin tärkeiden ekosysteemin toimintojen palauttamiseen. Kansainvälisesti on korostettu mahdollisuuksia turvata soiden tuottamia ekosysteemipalveluja ennallistamalla. Tulokseni antavat viitteitä joidenkin hiileen varastointiin liittyvien mekanismien palautumisesta ennallistamisen jälkeen. Tarvitaan kuitenkin merkittävää lisätutkimusta selvittämään näitä taloudellisestikin houkuttelevia mahdollisuuksia.

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ORIGINAL PAPERS

I

THE EFFECTS OF LONG-TERM DRAINAGE AND SUBSEQUENT RESTORATION ON WATER TABLE LEVEL AND PORE WATER CHEMISTRY IN BOREAL PEATLANDS

by

Tuomas Haapalehto, Janne S. Kotiaho, Rose Matilainen & Teemu Tahvanainen
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THE EFFECTS OF LONG-TERM DRAINAGE AND SUBSEQUENT RESTORATION ON WATER TABLE LEVEL AND PORE WATER CHEMISTRY IN BOREAL PEATLANDS

Haapalehto, T.[1,2*], Kotiaho, J.S.[1], Matilainen, R.[3], & Tahvanainen, T.[4]

[1]Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland.
[2]Metsähallitus, Natural Heritage Services, P.O. Box 36, 40101 Jyväskylä, Finland.
[3]Department of Chemistry, P.O. Box 35, 40014 University of Jyväskylä, Finland.
[4]Department of Biology, University of Eastern Finland, P.O.Box 111, 80101 Joensuu, Finland

*Corresponding author; E-mail: tuomas.o.haapalehto@student.jyu.fi, tuomas.haapalehto@metsa.fi, mobile: + 358 40 3532480

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Abstract

Degradation by drainage threatens biodiversity and globally important peatland ecosystem functions such as long-term carbon sequestration in peat. Restoration aims at safeguarding peatland values by recovering natural hydrology. Long-term effects of drainage and subsequent restoration, especially related to within-site variation of water table level and pore water chemistry, are poorly known. We studied hydrological variation at 38 boreal *Sphagnum* peatland sites (pristine, drained and restored) in Finland. Drainage decreased the average water table level especially near the ditches for decades and induced water chemical changes such as increased DOC concentration in peat pore water. There were also large differences in water chemistry between the samples collected from ditches and from the peat strips between the ditches. For example, the ditch water had apparently higher minerogenic influence, while DOC concentrations were highest in peat strips. Restoration was effective in regaining the natural water table level and induced a recovery of pore water chemistry towards the targeted pristine conditions. Restoration also resulted in lessened water chemical differences between ditches and peat strips indicating successful decrease of drainage-induced artificial within-site variation in water chemistry. The water table level in filled ditches was on average slightly lowered compared to surrounding areas 10 years after restoration. While such a difference may be an early warning sign for incomplete recovery of hydrology in long-term, we found no chemical evidence supporting this assumption yet. Our study suggests that restoration can result in significant recovery of peatland hydrology within 10 years, while some deviation from pristine peatlands is still typical. Restoration has a potential to reduce leaching of nutrients and DOC to downstream waters in the long term, but practitioners should be prepared for temporary increase of leaching of N and P for at least five years after restoration of boreal *Sphagnum* peatlands.

1. Introduction

Hydrological factors regulate central ecosystem functions like the flow of nutrients and development of soils. These functions enable the provision of globally important ecosystem services such as food crops, timber and many other biological products (Millennium Ecosystem Assessment 2005). By influence on the carrying capacity and niche formation in ecosystems, hydrology is an important driver of biodiversity thus forming the basis for ecosystem services (Millennium Ecosystem Assessment 2005; Konar *et al.* 2013). The significance of hydrology on ecosystem functions and services is emphasized in northern boreal and subarctic peatlands that cover only 3 % of Earth's land surface but constitute one third of the global terrestrial carbon pool (Yu 2011). Water level fluctuations and water chemistry largely control the accumulation and decomposition of peat and consequent fluxes of carbon as CO_2, CH_4 and as dissolved organic carbon (DOC) in peatlands (Moore and Knowles 1989; Tranvik and Jansson 2002; Belyea and Malmer 2004; Holden 2005; Jungkunst and Fiedler 2007).

Like many other ecosystems (Foley *et al.* 2005), peatlands have been severely degraded. Approximately 50 million hectares (13 %) of peatlands have been directly altered by human land-use (Lappalainen 1996; Strack 2008; Tanneberger and Wichtmann 2011). One major cause of degradation of peatlands is drainage for timber production, affecting approximately 15 million hectares in the northern boreal and subarctic regions (Strack 2008). Drainage of certain peatland areas may also induce significant changes beyond considerable distances within the same catchments to hydrology of undrained peatland areas due to catchment-scale disruption of hydrological connections (Tahvanainen 2011). The total peatland area impacted negatively by drainage and other land-use may, therefore, be much larger than often reported based on the actual drained areas. Drainage lowers the water table level generally by 20-60 cm with typical spatial pattern related to the distance from the ditch (Laine and Vanha-Majamaa 1992; Prévost *et al.* 1999; Price *et al.* 2003). Ditches act as main water flow channels through drained peatlands, and prevent the spread of minerogenic water from the catchment over the peatland surface. Because of the lowered water table level, drainage increases aeration and promotes decomposition and nutrient mineralization in the peat matrix (Niedermeier and Robinson 2007). Subsequently, pH and concentrations of several chemical elements increase in the pore and outflow water shortly after drainage (Prévost *et al.* 1999; Åström *et al.* 2001; Holden *et al.* 2004; Moore *et al.* 2013). In contrast, long-term changes of pore water chemistry after drainage are not well understood (Holden *et al.* 2004). Indeed, understanding the changes in pore water, which is in direct contact to the peat, might help e.g. to explain the apparently contradictory results from studies exploring the effects of drainage and land-use on increased riverine DOC around northern hemisphere (Freeman *et al.* 2004; Sarkkola *et al.* 2009; Räike *et al.* 2012; Huotari *et al.* 2013).

There is an increasing pressure toward ecological restoration in response to anthropogenic degradation of ecosystems. In general, restoration aims at reversing the degradation by partial rehabilitation or complete restoration of original structure (community composition) and function (e.g. cycling and fluxes of nutrients) of ecosystems (Dobson *et al.* 1997; Society for Ecological Restoration International 2004; Suding 2011). Precise aims of peatland restoration may differ due to different causes and varying extent of degradation. Most importantly, however, peatland restoration aims at recovering the original hydrological patterns (water table level, water chemistry, water flow paths), which would allow re-establishment of viable populations of characteristic peatland species (Vasander *et al.* 2003; Aapala *et al.* 2009). The societal expectations for restoration in securing biodiversity and provision of ecosystem services are monumental; a global target to restore 15 % of degraded ecosystems by 2020 was set recently (Convention on Biological Diversity 2010; European Commission 2011). However, recent meta-analyses question the projected positive impacts of restoration in general (Benayas *et al.* 2009), and specifically in the case of peatlands (Moreno-Mateos *et al.* 2012). Possible failures in reaching restoration targets call for better mechanistic understanding of the underlying key-factors for successful restoration, such as hydrological variation in the case of peatlands.

Early results on the hydrological recovery of peatlands are now starting to accumulate, but they seem to be controversial to some extent. For example, both successes and failures of regaining original water table level (Worrall *et al.* 2007; Klimkowska *et al.* 2010; Haapalehto *et al.* 2011; Laine *et al.* 2011; Hedberg *et al.* 2012; Schimelpfenig *et al.* 2013) as well as both intended and unintended effects on water chemistry (Höll *et al.* 2009; Koskinen *et al.* 2011; Wilson *et al.* 2011a, b) have been reported. While bringing urgently needed data on the poorly understood hydrological effects of peatland restoration, most studies have covered only a few sites and only the time period of first few years after restoration. Indeed, properly replicated studies on the hydrological recovery of peatlands are called for (Holden *et al.* 2011; Wilson *et al.* 2011a) to judge the generality and overall impact of restoration in the longer-term. One important but poorly understood hydrological aspect is the recovery of within-site variation in hydrology. Even relatively moderate patterns of peatland surface topography, such as hummocks and hollows, affect water flow paths and the development of plant communities (Bragazza and Gerdol 1999). Subsidence of peat after drainage is typically uneven and depends on the distance from the ditches (van der Schaaf 2012). This leads to a considerable increase of topographic variation in drained peatlands and provides a challenge for restoration practitioners. Insufficient blocking of ditches can, for example, redirect water flow along the artificial flow paths formed by the lines of blocked ditches. This may, in turn, act to sustain hydrological differences (related to water table level and water chemistry) between the blocked ditches and the intervening peat strips. Such uneven hydrological recovery is, indeed, suggested to hamper the recovery of communities (Hedberg *et al.* 2012). Therefore, it is vital for our overarching goal of restoration, to better understand the effects of restoration on the hydrological variation within restored sites.

Here we explore the long-term effects of drainage and subsequent ecological restoration on the hydrology of peatlands with special attention paid to within-site hydrological variation. We use a replicated comparative experimental design in which the 38 study sites on boreal Sphagnum peatlands in southern Finland were divided into four categories according to their management status (pristine, forestry drained, restored five years ago and restored 10 years ago). We asked:

1. What is the long-term effect of drainage on water table level and pore water chemistry?
2. To what extent is ecological restoration effective in reversing the effects of drainage on water table level and pore water chemistry?

We measured water table level five times during one growing season and collected water samples for chemistry analyses once at each site. The effects of drainage and restoration on water table level were determined by comparing average seasonal water table levels and differences in within-site water table level variation between pristine, drained and restored sites. Effects of drainage and restoration on pore water chemistry were studied by analyzing the effects of drainage and restoration as well as sampling location (ditch or adjacent peat strip) on the values derived from principal component analysis and measurements of single chemical variables.

2. Methods

2.1. Study sites

The study area is located in Southern Finland between 61° 53´ and 62° 51´ N and 22° 53´ and 25° 26´ E in the south-boreal climatic-phytogeographical zone, where raised bogs are the main type of greater peatland formations. The mean annual temperature is ca. +4°C and precipitation ca. 650 mm. The elevation above sea level is around 150 meters. The area belongs to the Early Proterozoic bedrock area, characterized by silicaceous granite and granodiorite minerals.

We selected 38 study sites within a 75 km radius (distances between the sites ranged from 200 m - 150 km) and divided them into four categories according to their management status: i) pristine (n = 10), ii) drained (n = 9), iii) previously drained and restored 3-7 years before the study (restored 5 years ago, n = 9), iv) previously drained and restored 9-12 years before the study (restored 10 years ago, n = 10). For simplification, the categories are referred to Pristine, Drained, Res 5 and Res 10 further on. Selection of the sites was based on close examination of old and new aerial photographs accompanied with field observations, such that the vegetation type (weakly minerotrophic pine fen) and tree stands of the drained and restored sites were originally similar to those of the pristine sites. Study sites were located within larger *Sphagnum* dominated peatlands consisting of a mosaic of ombro-mesotrophic peatland vegetation types. The sites were considered independent from each other in their surface water flow based on topographic data and field observations. Average peat depth at the sites ranged from 95 cm to more than 200 cm. The peat was mainly underlain by till i.e. the typical soil type in the region. However, characteristics of the surrounding mineral soils suggest that the underlying soil might be sand at a few sites. The set up may be considered a chronosequence. Such space-for-time substitutions are sometimes problematic in inferring vegetation succession e.g. if the sites differ originally in their properties (Johnson and Miyanishi 2008). We have, however, responded to this challenge by having a number of replicates for each management status. Additionally, special attention is paid to the selection of sites as described above. Significant changes take place in peatland ecosystems after drainage and restoration. Hence, the possibility for slightly larger variation in the original vegetation types of drained and restored sites, when compared to pristine sites, cannot be ruled out. However, we are confident that such marginal differences would not be likely to provide grounds for false interpretation of the results and misleading conclusions.

All of the drained and restored sites were drained for forestry by the state during 1960s and 1970s with ditch interval of 30-50 meters. Fertilization to increase tree growth was a standard procedure at those times, and although no records of the fertilization have been kept, all of the sites were likely fertilized soon after drainage with PK fertilizer. At some of the drained sites ditches had been cleared again in 1990s. Growth of Scotch pine (*Pinus sylvestris*) and downy birch (*Betula pubescens*) at originally sparsely pine covered sites had variably increased after the drainage. In 1980s some of the sites were designated to conservation with a subsequent decision to restore them. The restoration measures included filling in the ditches with peat excavated near the ditches, construction of dams and removal of the tree stands in cases where drainage had significantly increased tree growth. The amount of trees removed was adjusted so that all the sites had more or less the same tree cover in the end, mimicking the pre-disturbance tree cover determined from aerial photographs. Restoration was conducted by Natural Heritage Services of Metsähallitus (governmental institution responsible for management of conservation areas). Due to the compression and decomposition the peat near to the ditches has often been observed to be subsided more than the peat elsewhere in the drainage area. Therefore, the filling was supplemented by peat dams elevating *ca.* 50 cm over the peat surface and extending perpendicularly a few meters at both sides of the ditch to avoid water flow along the subsided areas. For simplification, both the currently active ditches of the drained sites and the in-filled ditches at the restored sites are referred to as 'ditches' further on.

At the Pristine sites, vegetation was characterized by common peatland plants typical to oligotrophic lawn-level peatland vegetation, such as *Eriophorum vaginatum*, tall-sedges (e.g. *Carex rostrata*) and *Sphagnum* mosses (*Sphagnum angustifolium*, *Sphagnum fallax* and *Sphagnum fuscum*). In the Drained sites, common forest plants, such as the dwarf shrubs *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Rhododendron tomentosum* and *Betula nana* dominated the field layer, *Pleurozium schreberi* along with *Sphagnum* mosses (*Sphagnum angustifolium*, *Sphagnum magellanicum* and *Sphagnum russowii*) being the most common species in the ground layer. The vegetation changed towards that of Pristine after restoration, with increased abundance of *Sphagnum* and sedges and decreased abundance of forest shrubs (Kareksela *et al.* 2014).

2.2. Measurements of water table level

Altogether 40 permanent 20-mm polypropylene pipe wells were systematically laid at each study site (Fig. 1). At the drained and restored sites, the wells were placed in five transects running perpendicular to the ditch with each transect having a pair of wells (a sampling unit) at four distances from the ditch (0, 5, 10 and 15 m). As the distance between transects was four meters, the wells formed a rectangular grid with an area of 15 × 20 m. A similar grid of wells was laid on Pristine sites. At all sites, the location of the first transect (laid in the ditch at drained and restored sites) was randomized. The depth of the water table (the distance of water to peat surface) in each well was measured five times (May, June, July, August, and September) in 2008. Each time, the measurements were taken during a two day period with stable climatic conditions.

The peat surface at the location of each well and the lowest peat surface within each sampling unit were leveled in September 2007. Additionally, we leveled the lowest peat surface at three locations along each transect (5, 10 and 15 m from the ditch) at the opposite side of the ditch. Thus, we had altogether 35 leveling values for the lowest peat surface (15 from both sides of the ditch and five from the ditch) at Drained, Res 5 and Res 10 sites. Only the lowest peat surfaces of each sampling unit were leveled at Pristine sites giving altogether 20 leveling values for each Pristine site.

We converted the measurements of water table depth in each well to the absolute level of water table throughout the site by subtracting the measured water table depths from the level of peat surface at the location of each well. Most peatlands have a naturally sloping surface and, consequently, a sloping water table. Since we were interested in the effects of drainage and restoration on within-site variation in the water table level, the variation in water table level caused by the ditch needed to be separated from the variation caused by the natural slope in the water table. Therefore, we corrected the water table level calculated for each sampling unit in two directions (coaxial and perpendicular to the ditch) to gain comparable horizontal values of water table level throughout the site. To correct for the natural slope coaxial to the ditch we firstly calculated the average level of the lowest peat surface at the transects furthest away from each other in the direction coaxial to the ditch. To exclude the possible effect of surface subsidence near the ditches, only the values of the levelings 10 and 15 m from the ditch at both sides of the ditch were used. Secondly, the difference in elevation (in cm) between the first and the last transects was calculated and divided by the distance between the transects (20 m) to gain the difference in elevation per meter of distance. Thirdly, we calculated a correction term for each transect by multiplying the difference in elevation per meter by the distance to the first transect. The water table levels in each well were then corrected by adding the correction term to the water table levels. For example, the water table level in the wells with a five meter distance from the first transect was corrected by dividing the total difference in the elevation by 20, multiplying the product by five and adding the resulted correction term to the original water table levels. The water table levels were thereafter corrected similarly for the natural slope perpendicular to the ditch. However, instead of using the levelings from the transects furthest away from each other in direction coaxial to ditch (as described above), the levelings at 15 m distance from the ditch at both sides of the ditch (altogether 10 values) were used. At pristine sites, the correction was calculated using the values at the opposite sides of the sampling unit grid.

2.3. Water sampling for chemical analyses

To study changes in water chemistry, 32-mm diameter polypropylene pipe wells with 2 mm slits and polypropylene filter gauges were laid at study sites (Fig. 1). At the Drained and restored sites, three wells with 10-m intervals to each other were laid to the distance of 15 m from the ditch (sampling location "Peat strip"; Fig. 1). Additionally, one and three more wells were laid into the ditch at the Drained and restored sites (sampling location "Ditch"; Fig. 1), respectively. Altogether three wells were laid in central parts of the sampling grid at Pristine sites (Fig. 1). The 100 cm long wells penetrated to 90 cm depth into peat. Water samples were collected in August 2007 with a plastic vacuum pump in 250-ml plastic bottles and kept cool with ice coolers during the transport. For analyses, the samples were divided in seven categories (subgroups) according to their management status and sampling location: (1) Drained ditch, 2) Drained peat strip, 3) Res 5 ditch, 4) Res 5 peat strip, 5) Res 10 ditch, 6) Res 10 peat strip, 7) Pristine).

We analysed pH, electrical conductivity (EC), redox potential (E_{h7}) and concentrations of Ca, Fe, Na, N, P, and dissolved organic carbon (DOC) from the water samples. Measurements of pH, EC and E_{h7} were conducted after 2 to 5 hours of collection using a Consort SP50X meter and electrodes SP10B, SK10T, SP50X. Temperature compensation was automated to reference temperature +25°C. The samples were then stored in +4°C, dark before analyses. The concentrations of cations (Ca, Fe, Na) and total organic carbon (TOC, hereafter referred to as DOC due to filtration) were analyzed from all collected samples after filtration with 0.45 µm membrane filters with PerkinElmer Optima 4300 DV inductively coupled plasma optical emission spectrometer and Shimadzu TOC-5000 analyzer, respectively. The analyses of cations were performed in the laboratory of Inorganic and Analytic Chemistry of the University of Jyväskylä and the analyses of N, P and DOC in the Ecology Research Institute laboratory of the University of Eastern Finland, Joensuu. The concentrations of N and P were analyzed from two samples per site (one sample per sampling location) except for three Drained sites for which only samples from strips were analyzed, and Pristine sites for which only one sample per site was analyzed.

2.4. Data analysis

The focus of our study is in the effects of degradation (drainage) and recovery (restoration) on different hydrological aspects (water table level, water chemistry) of peatlands. However, for the clarity of presentation, the analytical methods and results are divided according to hydrological aspect studied.

2.4.1. Water table level

To study the effects of drainage and restoration on water table level, we analyzed the effect of management status (Pristine, Drained, Res 5, Res 10) and distance from the ditch on the water table level with linear mixed model analysis. The analysis was chosen because it allows the use of data with unequal variances and data from a nested hierarchy like ours with several sampling units and wells with different distances to ditch within each site. Management status, distance from the ditch (0, 5, 10, 15 m), and their interaction were used as fixed factors in the analyses. Site identity, distance from the ditch (subject to site) and month (subject to site) were used as random factors. Water table differences between different management statuses and between different distances from the ditch within each management status category were examined with Fisher's Least Significant Difference (LSD) tests. Two sites (one from Res 5 and another from Pristine) were excluded from the water table level analyses due to insufficient leveling results. Average over values for two wells per sampling unit was calculated before the analysis.

2.4.2. Water chemistry

We needed altogether four analytical steps to study changes in water chemistry. First, we analyzed if drainage and restoration had affected water chemistry in general. We measured a large number of possibly correlated water chemical variables, and therefore we performed a principal component analysis (PCA). PCA reduces the dimensionality of the data set, retains as much of the variation as possible and defines the most important principal components (PCs) of the data. To see if management status had an overall effect on water chemistry, we calculated Euclidean distances (ED) between samples belonging to different subgroups (1) Drained ditch, 2) Drained peat strip, 3) Res 5 ditch, 4) Res 5 peat strip, 5) Res 10 ditch, 6) Res 10 peat strip, 7) Pristine) in the three dimensional PCA solution and tested the differences with MRPP (Multi-Response Permutation Procedures). Three first PCs were selected for comparisons since they showed a significant or nearly significant difference from random solution while for rest of the components the p-value of permutations was 1.000 (Table 3).

Secondly, to study if restoration had, in addition to having a general impact on water chemistry, induced a change of overall water chemistry towards original chemistry, we compared the average ED between Pristine and other sites separately for ditches and peat strips. This was done by calculating an average ED between each Pristine sample and other subgroups (for each Pristine sample average over all EDs between the sample and samples in a certain subgroup). The differences between Drained and restored samples in EDs to Pristine samples were tested with independent samples t-test.

Thirdly, we assessed how drainage and restoration affected pore water chemistry. For that we interpreted the correlations between water chemical variables used in the PCA (pH, EC, Ca, Na, Fe, P, N, DOC) and most important water chemical gradients PC1-PC3 (Table 3). To study how the changes in water chemistry induced by drainage and restoration were related to PCs or more detailed single water chemical variables (pH, EC, Ca, Na, Fe, P, N, DOC, E_{h7}), we calculated the average value of each PC and chemical variable for each site. The overall effect of management status was tested with ANOVA and differences between management statuses were examined with LSD tests.

Fourthly, to assess the within-site variation in water chemistry we determined whether there were differences in water chemistry between ditches and peat strips at Drained and restored sites. For that we analyzed the effects of management status and sampling location (ditch/peat strip) on PCs and water chemical variables with repeated measures ANOVA using sampling location as a within-subject factor and management status as a between-subject variable. Pristine sites were excluded from the analysis because they did not have the same sampling location variable due to absence of ditches. Differences between ditches and peat strips for each management status were examined with LSD tests.

Averages of values of analyzed variables for each site were calculated for ditches and peat strips before the analyses. Because pH (hydrogen ion concentration) affects water conductivity, EC was corrected by subtracting the conductivity of H^+ in each sample from EC detected from samples. Original redox potential (E_{h7}) values were also pH corrected according to calculation $E_{h7} = E_h - 59*(7\text{-pH})$ where E_h is the redox potential measurement in the field. Furthermore, the meter readings were corrected for the Ag/AgCl reference electrode (Consort SP50X) by adding 200 mV. Since we only analyzed N and P concentrations from ditches at three drained sites we excluded other samples collected from ditches at Drained sites from PCA and subsequent analyses based on PCA scores.

Linear mixed models, ANOVA, LSD comparisons, t-tests and repeated measures ANOVA were calculated with IBM SPSS statistics 20.0 and PCA and MRPP with PC-Ord 5.33 (McCune and Mefford 2006).

3. Results

3.1. Water table level

Management status and distance from the ditch had a significant effect on the average seasonal water table level (Table 1). Pairwise comparisons showed a lower water table level for Drained than for Pristine, Res 5 and Res 10, whereas there were no differences between Pristine and either of the restored groups (Table 2, Fig. 2). The significant management status by distance interaction effect suggests that the effect of management status was different at different distances from the ditch (Table 1). There were no differences in water table level between different distances from the ditches at Pristine or at Res 5 sites (LSD comparison, df = 96, $p > 0.271$ for all), but water table level at Drained sites differed between all distances from the ditch (LSD comparison, df = 96, $p < 0.001$ for all, Fig. 2) except between the 10-m and 15-m distances (LSD comparison, df = 96, $p = 0.303$). At Res 10 sites there seemed to be a tendency for lower water table level at the 0-m than at the 10-m and 15-m distances from the ditch (LSD comparison, df = 96, $p < 0.019$ for both), whereas there were no differences between other distances (LSD comparison, df = 96, $p > 0.099$ for all). Thus, the water table level seems to have lowered in the infilled ditches 10 years after the restoration (Fig. 2).

3.2. Pore water chemistry

The PC1 explained 33 % of variation and correlated most strongly with pH, Ca and EC (Table 3), representing therefore the minerogenic influence in pore water. The PC2 explained 27 % of variation and correlated most strongly with concentrations of N, P and DOC (Table 3). Consequently, PC2 is interpreted to represent the release of nutrients from peat matrix. The PC3 explained an additional 16 % of variation and correlated with concentrations of Fe and Na. Unlike the first two PCs, PC3 was not quite statistically significant (Table 3).

The PCA and subsequent MRPP analysis showed a significant difference between Pristine and Drained sites (Fig. 3, Table 4). Additionally, there was a difference between Pristine and Res 5 and between Pristine and Res 10 in the cases of both ditches and peat strips (Fig. 3, Table 4). However, for both ditches and peat strips the pore water chemistry of Res 10 was closer to Pristine chemistry than the chemistry of Drained (independent samples t-test between Drained and Res 10, equal variances assumed; ditches: $t = 3.005$, df = 18, $p = 0.008$; peat strips: $t = 2.747$, df = 18, $p = 0.013$; Fig. 3). Although the ED to Pristine sites was smaller for Res 5 than for Drained, the differences were not statistically significant (independent samples t-test between drained and Res 5, equal variances assumed; ditches: $t = 1.059$, df = 18, $p = 0.303$; peat strips: $t = 1.850$, df = 18, $p = 0.081$; Fig. 3).

Examination of the PCs and individual chemical variables with ANOVA showed that management status had a significant overall effect on PC2 and on the concentrations of Ca, N and P (Table 5). Differences were indicated also for EC, pH and DOC (Table 5). Pairwise comparisons showed that drainage clearly raised the overall values for Ca and pH when compared to pristine conditions (Table 6, Fig. 4). Furthermore, there was an apparent tendency towards that for DOC and EC also. Despite apparently higher N and P concentrations at peat strips when compared to pristine sites, the overall effect of drainage was not statistically significant due to low concentrations in ditch water (Fig. 4). Average Ca and pH decreased already five years after restoration to pristine level but for Ca there seemed to be a slight difference again between Pristine and Res 10 (Table 6, Fig 4). Also DOC decreased after restoration when compared to Drained sites. Whereas the average DOC was still slightly higher in Res 10 than Pristine, the difference between the groups was not statistically significant (Table 6, Fig 4). The average values of PC2, N and P were clearly higher for Res 5 than Pristine (Table 6, Fig 4). Furthermore, a statistically significant but less clear difference was found between Res 5 and Drained (Table 6, Fig. 4). There were no differences between Drained and Res 10 for PC2, N and P (Table 6, Fig 4). N and P seemed to, furthermore, be lower for Res 10 than for Res 5. Whereas the average P was still slightly higher in Res 10 than Pristine, the difference between the groups was not statistically significant (Table 6, Fig 4). Restoration did not affect the average EC raised by drainage and, in fact, the average EC rise after drainage was largely driven by high ditch water EC (Table 6, Fig 4). There was a tendency towards lower Na concentration for Res 10 than Drained, but we did not find a difference between the Pristine and any other management status (Table 6, Fig 4). There was a clear tendency towards higher average Fe concentration at Res 10 than at Pristine, but there were no differences between Drained and Res 5 or between Drained and Res 10 (Table 6, Fig 4). For PC1 and E_{h7} there was a slight tendency towards a difference between Drained and Pristine, but neither Res 5 nor Res 10 differed from Pristine (Table 6, Fig 4). E_{h7} seemed to be, furthermore, lower at Res 5 and Res 10 than Drained (Table 6, Fig 4).

According to the PCA and MRPP, the overall water chemistry at Drained sites differed between ditches and strips but there were no differences between ditches and strips for either Res 5 or Res 10 (Table 4, Fig 3). A significant sampling location effect in the repeated measures ANOVA performed without Pristine sites suggests an overall clear difference between the samples collected from ditches and peat strips for DOC and pH, and a clear tendency towards a difference for PC1 (Table 7, Fig. 4). Furthermore, a significant sampling location×management status interaction suggests that the effect differed between Drained, Res 5 and Res 10 for PC1, N, DOC and pH (Table 7, Fig. 4). Pairwise comparisons showed that at the Drained sites values for PC1 and pH were clearly higher in the samples collected from the ditches than from the peat strips and, that there was an apparent tendency towards such a difference for EC as well (Table 8). In contrast, PC1 and DOC were lower in the ditches than in the peat strips (Table 8, Fig 4). However, we found no differences for PC1, pH, EC and DOC between the ditches and peat strips at Res 5 and Res 10 (Tables 7 and 8, Fig. 4). N was higher in the ditches than in peat strips for Res 5, but there was no difference between the ditches and peat strips for Drained and Res 10 (Table 8, Fig. 4). Similarly, PC3 values differed between ditches and strips at Res 5 but no difference could be seen at Res 10 or Drained (Table 8, Fig. 4).

4. Discussion

We show that significant lowering of the average water table level by peatland drainage is sustained for decades and that the draw down remains largest near the ditches. The natural pattern of high and even water table level was regained five years after restoration but increased within-site unevenness of the water table level was observed again 10 years after restoration. Also drainage-induced changes in water chemistry were significant still several decades after drainage. Overall elevation of pH and EC as well as increased average concentrations of Ca and DOC were observed at Drained sites when compared to Pristine, but there were large differences between the samples collected from ditches and adjacent peat strips. For example, increased pH and EC after drainage were driven by significantly higher values in ditches when compared to peat strips. Furthermore, despite higher N and P concentrations at peat strips, the overall effect of drainage when compared to the concentrations at Pristine sites was not significant due to low concentrations in ditch water. Restoration induced a recovery of pore water chemistry towards pristine chemistry. Especially the water chemical factors related to minerogenic influence of pore water had recovered and for Ca, pH, DOC, E_{h7} values close to pristine levels were reached during the first few years after restoration. Restoration could also remove most of the water chemical differences (especially related to pH and DOC) between ditches and peat strips. The concentrations of N (especially in the ditches) and P increased in pore water five years after restoration, decreasing again 10 years after restoration. Fe showed an increasing pattern after restoration especially in the filled ditches.

The greatest hydrological change caused by drainage is the decadal drawdown of water table observed in our study. This drawdown affects not only peatland structures, such as above and below ground communities (Laine *et al.* 1995; Jaatinen *et al.* 2007), but also ecosystem functions such as soil respiration, nutrient circulation and accumulation of peat and C (Braekke 1987; Martikainen *et al.* 1995; Mäkiranta *et al.* 2009; Kareksela *et al.* 2014). As the average water table level could be re-established and maintained for 10 years, restoration of studied peatlands was successful in regaining the single most important condition needed for further recovery of ecosystem. Together with water table level, changes of pore water chemistry may influence peatland community composition and peatland functions (Tahvanainen *et al.* 2002; Price *et al.* 2005; Bragazza *et al.* 2005). Our results show that differences between Pristine and Drained sites in chemistry are significant still after several decades. However, the recovery of overall pore water chemistry towards targeted pristine conditions after restoration is promising and may act to promote e.g. the recovery of plant communities (Haapalehto *et al.* 2011; Laine *et al.* 2011; Hedberg *et al.* 2012).

In addition to clear within-site differences in water table level after drainage, we expected to see water chemical differences between samples from ditches and adjacent peat strips in Drained sites. The flow of mineral-rich water from catchment is directed along the artificial flow paths formed by ditches, and hence mineral element concentrations and pH are often higher in ditches than in peat strips. Secondly, increased DOC was expected in peat strips when compared to ditches due to potentially higher DOC production and diminished flushing rate allowing DOC to accumulate in pore water in peat strips (Tahvanainen *et al.* 2002). Such differences were, indeed, evident in our data.

Even slight changes in water table level or water chemistry may affect the development of peatland ecosystems (Tahvanainen 2011). Restoration should, therefore, aim to eliminate the unnatural within-site hydrological differences and artificial water flow paths. After the initial recovery of even within-site water table level five years after restoration, the water table level seemed to have lowered at infilled ditches when compared to surrounding areas 10 years after restoration. Such a lowering might be due to erosion of dams and ditch-fillings resulting in redevelopment of flow paths along the infilled ditches and the subsided areas close to them. With time, such development could lead to insufficient rewetting of areas further away from the ditches. This, in turn, could hamper the recovery of peatland species communities (Haapalehto *et al.* 2011; Hedberg *et al.* 2012). Similarly to the Drained sites, the concentration of water flow along the infilled ditches should, most likely, result in increased mineral concentrations and decreased DOC at the infilled ditch areas when compared to pore water elsewhere. We did not find such pore water differences between the infilled ditches and peat strips at Res 5 and Res 10 sites, however. This suggests that the slightly decreased water table level in the infilled ditches would not have influenced the hydrological recovery of the restored sites. We find, however, that the increased within-site differences in water table level may hamper the recovery of hydrology in the future, and the possible long-term deterioration of ditch blocking structures should not be ignored by restoration practitioners.

The major nutrients N and P are generally scarce in the studied peatlands and they are effectively taken up by living organisms (Silvan *et al.* 2003, 2004b). Large hydrological disturbances such as drainage and restoration result in turnover of species and provide new substrate for decomposers. Subsequently, increased N in pore water has been observed a few years after drainage (Prévost *et al.* 1999). We did not find general increase of N and P in drained peatlands, due to lower levels observed in ditch water, but pore water concentrations at Drained sites were many-fold higher compared to pristine pore water still decades after drainage (Fig. 4). At restored sites, we found an increase of N and P similar to those observed earlier in pore water of rewetted temperate alkaline fens (Zak and Gelbrecht 2007; Zak *et al.* 2010) and outflow waters of more acidic boreal peatlands (Koskinen *et al.* 2011). Such an increase may be due to increased amounts of redox sensitive substances and, parallel to the effects of drainage, enhanced availability of decomposable organic matter in the upper highly decomposed peat horizon (Zak and Gelbrecht 2007). Whereas increased P concentrations were observed for both ditches and strips five years after restoration, significant increase of N was found only at the infilled ditches. Ground level vegetation and trees are very effective in retaining N after altered nutrient conditions in the studied type of peatlands (Silvan *et al.* 2004b; Vikman *et al.* 2010). Abundance of *Eriophorum vaginatum*, a key species in terms of nutrient immobilization in boreal peatlands (Silvan *et al.* 2004a), and growth of tree saplings increase significantly for a few years after restoration (Kuuluvainen *et al.* 2002; Haapalehto *et al.* 2011) especially when restoration measures include removal of tree stand (Hedberg *et al.* 2012). Increased N concentration in the infilled ditches may therefore be related to higher physical disturbance during restoration followed by slower recovery of vegetation after restoration in ditches when compared to peat strips.

Increased release of nutrients after restoration is suspected to cause eutrophication of downstream waters especially in nutrient rich wetlands (Niedermeier and Robinson 2007, 2009; Zak *et al.* 2008). Like earlier results focusing on runoff waters from similar nutrient poor peatlands (Koskinen *et al.* 2011), we found the highest post-restoration pore water P concentrations approximately five years after rewetting. Furthermore, we found a decline close to the pristine level at the sites restored 10 years ago. In contrast to high P mobilization over decades taking most likely place in rewetted calcareous fens with agricultural history (Zak *et al.* 2008), our results suggest that the risk of eutrophication of downstream waters diminishes after five to ten years after restoration of nutrient-poor peatlands drained for forestry. The peatlands studied by Koskinen *et al.* (2011) were of similar nutrient poor type and also located in Southern Finland. Similar temporal P release pattern observed in pore water concentrations (our study) and in outflow water (Koskinen *et al.* 2011) after restoration suggest that pore water measurements, which are often much easier and cheaper than outflow monitoring, could provide a proxy for the estimation of nutrient outflux patterns after restoration. The quantification of fluvial fluxes would, however, require discharge monitoring.

The effects of drainage on DOC have been controversial for a long time (see review by Holden *et al.* 2004). Recent studies have found increased leaching and pore water concentrations of DOC soon after excavation of ditches (Wallage *et al.* 2006; Strack *et al.* 2008) and drainage has been suggested to increase leaching of DOC to downstream watercourses (Huotari *et al.* 2013). The increased pore water concentrations may be due to elevated net DOC production under lower water table conditions driven by increased decomposable biomass after vegetation change and larger water table fluctuations (Wallage *et al.* 2006; Strack *et al.* 2008). It is surprising, therefore, that drainage has not been clearly connected to increased DOC concentrations and export in long-term monitoring of downstream waters (Lepistö *et al.* 2008; Sarkkola *et al.* 2009; Rantakari *et al.* 2010; Räike *et al.* 2012). The effect of restoration on fluvial carbon export is, perhaps, even more contradictory. Increased TOC release especially at nutrient rich sites (Koskinen *et al.* 2011) and increased TOC and DOC in blocked ditches shortly after restoration (Worrall *et al.* 2007; Gibson *et al.* 2009; Wilson *et al.* 2011a) have been observed. In parallel, severe natural droughts followed by natural rewetting could destabilize C stocks causing DOC losses to downstream waters (Fenner and Freeman 2011). In contrast, decreased DOC concentration in soil water perhaps due to increased flushing of DOC from upper peat layers in short term (Wallage *et al.* 2006) and decreased decomposition (Höll *et al.* 2009) decades after restoration have been found. These apparent controversies may partly reflect methodological differences arising from e.g. whether ditch or pore water concentrations were studied and whether discharge rates were considered or not (Wilson *et al.* 2011a). Furthermore, large differences in time-scale of studies (from a couple of years to decades), different focal peatland types (blanket bogs, fens, boreal *Sphagnum* peatlands) and difficulties in separating the effects of drainage or restoration from other land-use within the studied catchments complicate comparisons between studies.

Here, we took a snapshot on DOC concentrations of originally similar boreal *Sphagnum* peatlands decades after drainage. Ditch water DOC at Drained sites was close to the pore water DOC of Pristine. When interpreting the results one should, however, notice that the sampled ditches were not systematically selected to drain entire peatlands. It is therefore likely that a large share of DOC produced in studied drained peatlands is not present in the sampled ditches, and our ditch water DOC estimates are not comparable to studies reporting effects of drainage on DOC outflux in runoff. Instead, it is more relevant to compare pore water from Pristine sites to the pore water from peat strips at Drained sites. Such a comparison describing the impact of drainage on pore water DOC (within the peat where the actual production and decomposition of DOC take place) shows 1.6 times (36 mg/l) higher DOC for Drained than Pristine on average. DOC may be flushed to downstream aquatic ecosystems (Worrall *et al.* 2002) during peak flow periods, where the increased DOC loading can alter physical and chemical conditions such as acidity, light penetration and bioavailability of metals and nutrients or contribute to food webs as carbon source to microbes (Evans *et al.* 2005). Although it is not possible to estimate the extra DOC load due to elevated concentrations in pore water after drainage without discharge data, the order of magnitude of potential load may be approached by a simple calculation concentrating, say, in Finland where forestry-drainage has been perhaps most extensive. Assuming that the peatland sites and the snap-shot DOC concentrations measured here are representative of average conditions of the five million ha of drained peatlands in Finland and that annually all DOC of uppermost 30-cm pore water layer is exported from surface peat with average water content of 0.9 (270 mm runoff), we arrive in an estimate of a capacity of Finnish peatlands to lose DOC at an increased rate of 486 000 t per year due to drainage. Although this is a very rough figure produced by a simplified multiplication, it can be compared e.g. with the total DOC export by Finnish rives to the Baltic Sea, estimated at 900 000 t C yr^{-1} (Räike *et al.* 2012). We do not suggest half of Finnish river DOC export would be caused by drainage of peatlands, but we point out that pore waters in surface peat strata of drained peatlands do contain excess DOC in this comparably high order of magnitude that may be exported as depending on hydrological conditions.

In contrast to increased DOC concentration due to drainage, we found a decreasing trend of DOC concentrations after restoration in both ditch and pore water, with average concentration close to pristine level 10 years after restoration. Hence, the 22 mg/l lower average DOC concentration 10 years post-restoration when compared to the average DOC in peat strips of Drained sites suggests that restoration could result in significant reduction in leaching of fluvial carbon from drained peatlands. Thereby, peatland restoration has the potential to improve downstream water quality in long-term. This might be especially important in heavily drained areas such as Finland where meeting the global target of restoring 15 % of degraded ecosystems suggests restoring 0.75 million ha peatlands (Convention on Biological Diversity 2010). It must, however, be noted that the DOC concentration in pore water changes seasonally (Tahvanainen *et al.* 2003) and is dependent on peat quality (Zak and Gelbrecht 2007). Because the export of DOC depends also on discharge rates and drainage may decrease the amount of water passing through the peat matrix, it may be that some of the excess DOC observed in pore water after drainage will not be flushed to downstream waters. On the other hand, even slightly increased concentrations of DOC in ditch water may result in significantly decreased outflux of DOC due to decreased water flow from the drains after restoration (Gibson *et al.* 2009; Wilson *et al.* 2011a). Since we did not measure discharge rates and studied only one type of peatlands with nonrecurring pore water sampling, our results only describe potential mobile pools of DOC as affected by drainage and restoration.

DOC loss may approach 2/3 of the annual carbon sink of boreal peatlands (Roulet *et al.* (2007), but see Gažovič *et al.* (2013) for lower estimates). The significantly increased pore water DOC after drainage may, therefore, partly explain recent studies that have found large losses of carbon from peat after decades of drainage (Simola *et al.* 2012; Pitkänen *et al.* 2013; Kareksela *et al.* 2014). On the other hand, rapid re-establishment of surface peat accumulation rate was recently found after peatland restoration (Kareksela *et al.* 2014). Together with our results this suggests the potential of restoration to recover some important components of peatland carbon cycle. Given the global importance of fluvial carbon fluxes from peatlands and the results presented here and in previous studies, DOC dynamics after drainage and restoration certainly deserve further long-term studies.

The elevated Fe concentrations at Res 5 when compared to Pristine and the tendency towards higher Fe in ditches than peat strips may be related to differences in redox conditions. Filled ditches have often small ponds and areas lying topographically lower than adjacent areas. Due to accumulation of water in these areas, anaerobic, reductive conditions would favor reduction of Fe (III) to Fe (II) increasing Fe solubility and hence elevate concentrations of Fe in pore water (Küsel *et al.* 2008). The high total Fe concentrations (and wide range of variation) in filled ditches should, thus, be connected to low redox. Indeed, while no overall difference of E_{h7} was found between ditches and peat strips at Res 5 and Res 10, the hypothesis is supported by a significant negative Pearson correlation (-0.66, $p < 0.01$) between Fe and E_{h7} at restored sites suggesting that highest Fe was found in most reductive environments. Fe reduction is linked to circulation of C, S, P and N in anaerobic soils and hence to several peatland functions such as methanogenesis and DOC production (Lovley 1991; Knorr 2012). Our results suggest that even though we did not observe water chemical differences between the ditches and strips in nonrecurring measurements of pH and DOC in restored sites, further research is needed to draw a clear picture on the behavior of Fe and the recovery of peatland functions related to pore water Fe. This is especially true, since Fe is suggested to be one key chemical component for the recovery of rewetted peatlands (Kemmers *et al.* 2003). In addition to affecting the biogeochemical cycles of peat it may for example hamper the establishment of specialist species after restoration (Aggenbach *et al.* 2013).

In conclusion, drainage for forestry has long-lasting effects on boreal peatland hydrology resulting in drawdown of water table level and substantial changes of pore water chemistry. Moreover, drainage causes increased small scale spatial variation in water table level and water chemistry within peatlands. Restoration, in contrast, recovers the water table level and initiates a gradual recovery in the pore water chemistry towards values typical to pristine peatlands. However, we observed a re-emerging drawdown of water table level at the infilled ditches lines at the sites studied 10 years after restoration. Even though we did not find evidence in pore water chemistry to show that such a drawdown would hamper further recovery of restored ecosystems, this may be an early warning sign of failure of hydrological recovery in the future. This should not be ignored by restoration practitioners and scientists responsible for monitoring the effects of restoration. While restoration has the potential to reduce leaching of DOC to downstream waters in the long term, practitioners should be prepared for excess leaching of N and P from boreal *Sphagnum* peatlands for at least five years after restoration.

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Table 1. The fixed effects of the linear mixed model analysis for water table level.

Source	Num. df	Denom. df	F	p
Intercept	1	32.00	397.483	<0.001
MS	3	32.00	35.679	<0.001
Distance	3	96.03	61.253	<0.001
MS*Distance	9	96.03	37.184	<0.001

MS = Management status

Table 2. Pairwise LSD comparisons between management statuses for water table levels.

Management status 1	Management status 2	Mean difference (1-2)	SE	p
Pristine	Drained	30.782	3.761	<0.001
	Res 5	-3.322	3.761	0.384
	Res 10	0.993	3.761	0.794
Drained	Res 5	-34.104	3.761	<0.001
	Res 10	-29.789	3.761	<0.001
Res 5	Res 10	4.315	3.761	0.260

for all comparisons df = 32, Res 5 = Restored 5 years ago, Res 10 = Restored 10 years ago

Table 3. The summary of principal component analysis of water chemistry. Three first principal components (PC) and their correlations with studied water chemical variables (eigenvectors) are shown.

	PC1	PC2	PC3
Eigenvalue	2.625	2.157	1.271
% of variance explained	32.8	27.0	15.9
cumulative % of variance explained	32.8	59.8	75.7
Monte Carlo p	<0.001	<0.001	0.081
Eigenvectors			
pH	-0.932	0.070	-0.103
EC	-0.733	0.451	-0.049
Ca	-0.580	0.511	0.215
Na	-0.420	0.134	0.805
Fe	-0.392	0.407	-0.676
P	0.400	0.670	0.230
N	0.404	0.745	-0.200
DOC	0.479	0.706	0.114

Table 4. Euclidean distances (ED) and results of MRPP analysis between subgroups in the principal component analysis of water chemistry. First three axes (principal components) were included in the calculation.

Subgroups			ED	T	A	p
1	vs.	2	5.172	-3.831	0.239	0.003
1	vs.	3	5.290	-5.234	0.274	0.001
1	vs.	4	4.597	-2.801	0.168	0.017
1	vs.	5	4.308	-3.035	0.143	0.012
1	vs.	6	4.041	-2.805	0.144	0.018
1	vs.	7	4.143	-3.156	0.152	0.009
2	vs.	3	3.044	-1.061	0.035	0.142
2	vs.	4	3.174	0.977	-0.034	0.864
2	vs.	5	3.396	-1.189	0.034	0.120
2	vs.	6	3.124	-1.523	0.042	0.080
2	vs.	7	3.658	-5.001	0.170	0.001
3	vs.	4	2.988	-1.252	0.038	0.112
3	vs.	5	2.892	-1.383	0.040	0.095
3	vs.	6	2.677	-1.761	0.050	0.059
3	vs.	7	3.763	-9.011	0.327	<0.001
4	vs.	5	3.017	0.705	-0.018	0.737
4	vs.	6	2.729	0.668	-0.016	0.722
4	vs.	7	3.174	-3.390	0.089	0.007
5	vs.	6	2.156	1.387	-0.038	0.997
5	vs.	7	3.047	-3.915	0.111	0.004
6	vs.	7	2.893	-5.829	0.157	<0.001

Subgroups: 1 = Drained, ditch, 2 = Drained, peat strip, 3 = Restored 5 y ago, ditch, 4 = Restored 5 y ago, peat strip, 5 = Restored 10 y ago, ditch, 6 = Restored 10 y ago, peat strip, 7 = pristine.
T = test statistic of MRPP, A = chance-corrected within-group agreement of MRPP

Table 5. ANOVA for principal components (PC1-PC3) and water chemical variables. Average of values for each site are used for calculations over all four management statuses (Pristine, Drained, Res 5, Res 10).

	MS	F	p
PC1	3.061	1.992	0.138
PC2	11.538	13.303	<0.001
PC3	1.061	1.421	0.257
Ca	3.781	4.976	0.006
Fe	9.916	1.796	0.166
Na	0.331	2.046	0.126
N	1.040	10.269	<0.001
P	0.076	6.252	0.002
DOC	926.984	3.026	0.043
EC	298.1	2.889	0.05
E_{h7}	1532.919	2.276	0.097
pH	0.307	3.737	0.02

df (treatment) = 3, df (error) = 34 for other variables than N, P, PC1, PC2, PC3 for which df (error) = 28

Table 6. Pairwise LSD comparisons between management statuses for principal components (PC1-PC3) and water chemical variables. Average of values for each site are used for calculations.

	(I) Management status	Pristine	Pristine	Pristine	Drained	Drained	Res 5
	(J) Management status	Drained	Res 5	Res 10	Res 5	Res 10	Res 10
PC1	Mean Diff. (I-J)	1.538	-0.441	0.257	-1.979	-1.281	0.698
	SE	0.816	0.569	0.554	0.826	0.816	0.569
	p	0.070	0.446	0.646	0.024	0.128	0.231
PC2	Mean Diff. (I-J)	-1.111	-2.548	-1.940	-1.438	-0.829	0.608
	SE	0.613	0.428	0.416	0.621	0.613	0.428
	p	0.081	<0.001	<0.001	0.028	0.187	0.166
PC3	Mean Diff. (I-J)	0.749	0.307	0.739	-0.442	-0.010	0.431
	SE	0.569	0.397	0.386	0.576	0.569	0.397
	p	0.199	0.446	0.066	0.450	0.986	0.287
Ca	Mean Diff. (I-J)	-1.542	-0.665	-0.800	0.876	0.741	-0.135
	SE	0.401	0.401	0.390	0.411	0.401	0.401
	p	<0.001	0.106	0.048	0.040	0.073	0.738
Fe	Mean Diff. (I-J)	-0.201	-1.072	-2.204	-0.871	-2.003	-1.132
	SE	1.080	1.080	1.051	1.108	1.080	1.080
	p	0.853	0.328	0.043	0.437	0.072	0.302
Na	Mean Diff. (I-J)	-0.151	0.216	0.247	0.367	0.399	0.032
	SE	0.185	0.185	0.180	0.189	0.185	0.185
	p	0.418	0.251	0.178	0.061	0.038	0.865
N	Mean Diff. (I-J)	-0.262	-0.793	-0.487	-0.531	-0.225	0.306
	SE	0.209	0.146	0.142	0.212	0.209	0.146
	p	0.221	<0.001	0.002	0.019	0.292	0.046
P	Mean Diff. (I-J)	-0.145	-0.021	-0.077	-0.196	-0.062	0.134
	SE	0.073	0.051	0.049	0.074	0.073	0.051
	p	0.843	<0.001	0.132	0.013	0.401	0.014
DOC	Mean Diff. (I-J)	-17.589	-22.976	-13.921	-5.387	3.668	9.055
	SE	8.042	8.042	7.827	8.251	8.042	8.042
	p	0.036	0.007	0.084	0.518	0.651	0.268
EC	Mean Diff. (I-J)	-12.441	-10.368	-9.628	2.072	2.813	0.741
	SE	4.668	4.668	4.543	4.789	4.668	4.668
	p	0.012	0.033	0.041	0.668	0.551	0.875
pH	Mean Diff. (I-J)	-0.382	0.002	-0.066	0.385	0.316	-0.069
	SE	0.132	0.132	0.128	0.135	0.132	0.132
	p	0.006	0.986	0.609	0.007	0.022	0.606
E_{h7}	Mean Diff. (I-J)	-22.035	6.519	3.596	28.554	25.631	-2.923
	SE	11.924	11.924	11.606	12.234	11.924	11.924
	p	0.073	0.588	0.759	0.026	0.039	0.808

Res 5 = Restored 5 years ago, Res 10 = Restored 10 years ago

Values are given as mg/l for Ca, Fe, Na, N, P and DOC, as µS/cm for EC and as mV for E_{h7}

Table 7. Between subject effects of repeated measures ANOVA for principal components (PC1-PC3) and water chemical variables over sampling locations (ditch/peat strip) and management statuses (Drained, Res 5 and Res 10).

	Location (factor 1)			Location*Management status		
	MS	F	p	MS	F	p
PC1	8.427	5.418	0.031	12.929	8.312	0.003
PC2	0.431	0.472	0.500	1.235	1.353	0.282
PC3	1.103	4.326	0.051	0.588	2.306	0.127
Ca	0.034	0.050	0.824	1.889	2.831	0.078
Fe	12.485	2.804	0.107	1.625	0.365	0.698
Na	0.011	0.119	0.733	0.076	0.807	0.457
N	0.064	0.297	0.592	2.463	11.485	0.001
P	0.012	0.542	0.470	0.001	0.06	0.942
DOC	2202.333	11.613	0.002	3950.822	20.832	<0.001
EC	252.118	2.261	0.145	282.926	2.537	0.099
E_{h7}	765.824	1.042	0.317	194.661	0.265	0.769
pH	1.632	14.877	0.001	1.910	17.408	<0.001

df (Location) = 1, df (Location*Management status) = 2,
df (error) = 25 for other variables than N, P, PC1, PC2, PC3 for which df (error) = 19

Table 8. Pairwise LSD comparisons between sampling locations (ditch/peat strip) for principal components (PC1-PC3) and water chemical variables for different management statuses.

	Drained			Res 5			Res 10		
	MD (Ditch-Strip)	SE	p	MD (Ditch-Strip)	SE	p	MD (Ditch-Strip)	SE	p
PC1	-3.938	1.018	0.001	0.790	0.588	0.195	0.118	0.558	0.835
PC2	-0.190	0.780	0.811	0.897	0.450	0.061	-0.022	0.427	0.960
PC3	-0.103	0.412	0.806	-0.820	0.238	0.003	-0.173	0.226	0.453
Ca	0.660	0.385	0.099	-0.606	0.385	0.128	-0.201	0.365	0.587
Fe	0.374	0.995	0.710	0.920	0.995	0.364	1.543	0.944	0.115
Na	0.088	0.145	0.548	-0.169	0.145	0.255	-0.005	0.138	0.974
N	-0.743	0.378	0.064	1.067	0.218	<0.001	-0.060	0.207	0.775
P	-0.056	0.122	0.652	-0.043	0.071	0.549	-0.016	0.067	0.814
DOC	-46.390	6.492	<0.001	3.004	6.492	0.648	5.709	6.159	0.363
EC	13.312	4.978	0.013	-0.056	4.978	0.991	-0.510	4.723	0.915
pH	1.086	0.156	<0.001	-8.88E^{-16}	0.156	1.000	-0.060	0.148	0.689
E_{h7}	-3.363	12.777	0.795	-4.122	12.777	0.750	-14.730	12.121	0.236

Res 5 = Restored 5 years ago, Res 10 = Restored 10 years ago, MD = mean difference
Values are given as mg/l for Ca, Fe, Na, N, P and DOC, as µS/cm for EC and as mV for E_{h7}

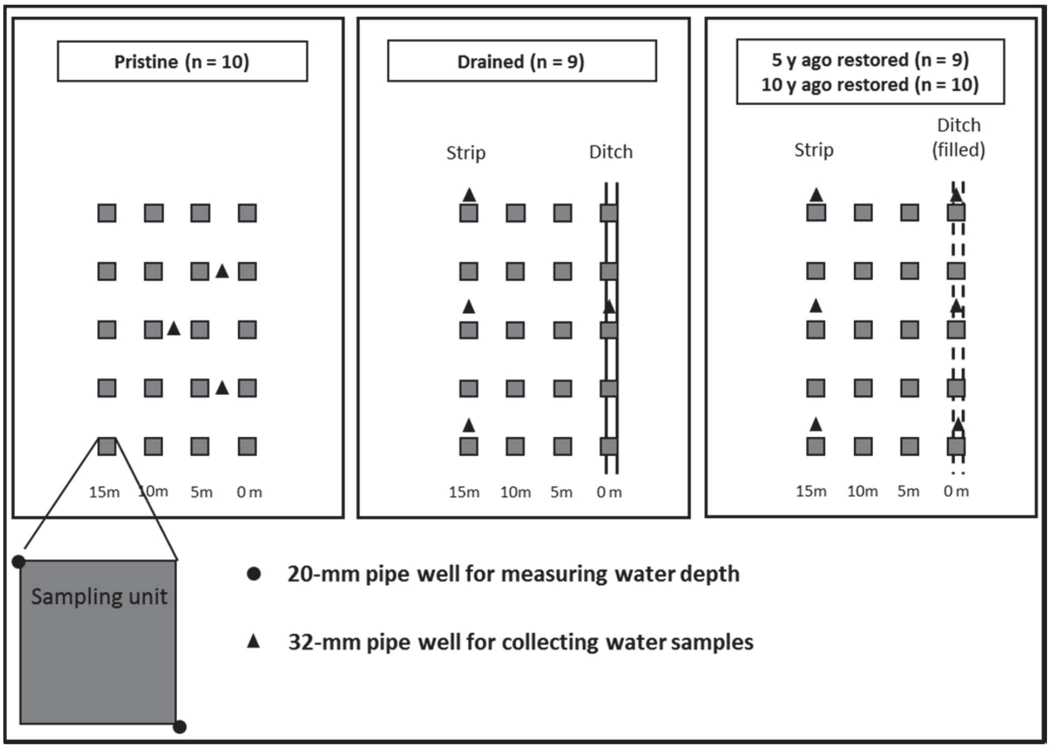

Fig. 1. Study set ups for measuring water table depth and collecting water samples at pristine, drained and restored sites. Distances (m) refer to distance of sampling units to ditches at restored and drained sites. A similar grid of sampling units was laid at pristine sites.

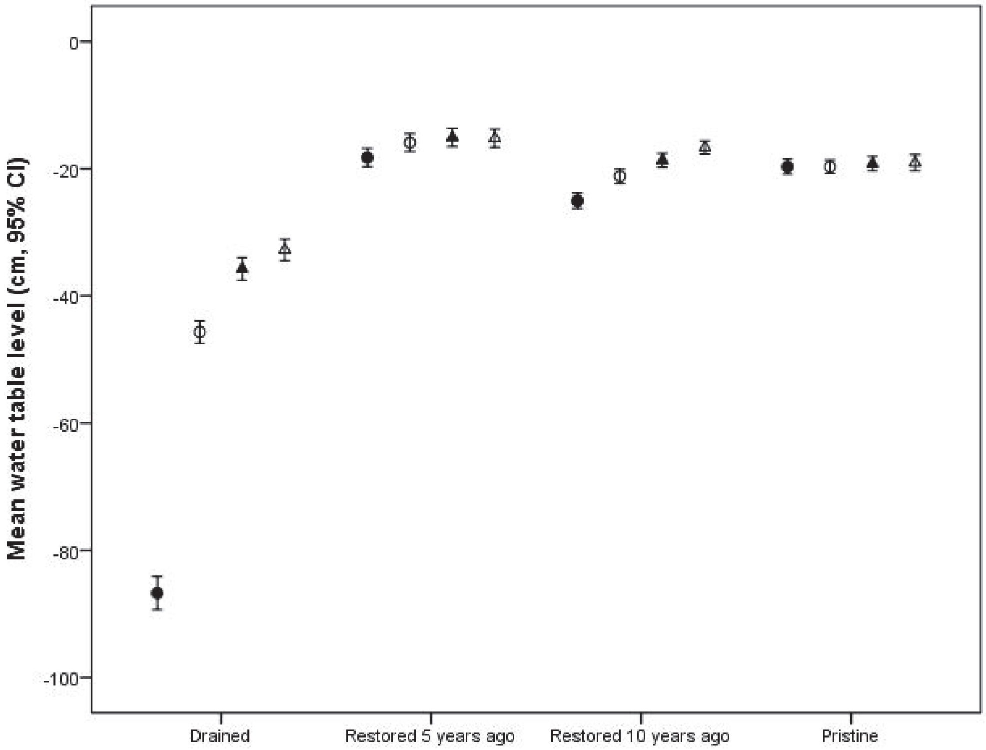

Fig. 2. Mean water table levels with 95 % CI at different distances to the ditch during summer. Symbols: filled circle = 0 m from the ditch, open circle = 5 m from the ditch, filled triangle = 10 m from the ditch, and open triangle = 15 m from the ditch. The figures consist of five measurements (May-September) from five wells at each distance to ditch.

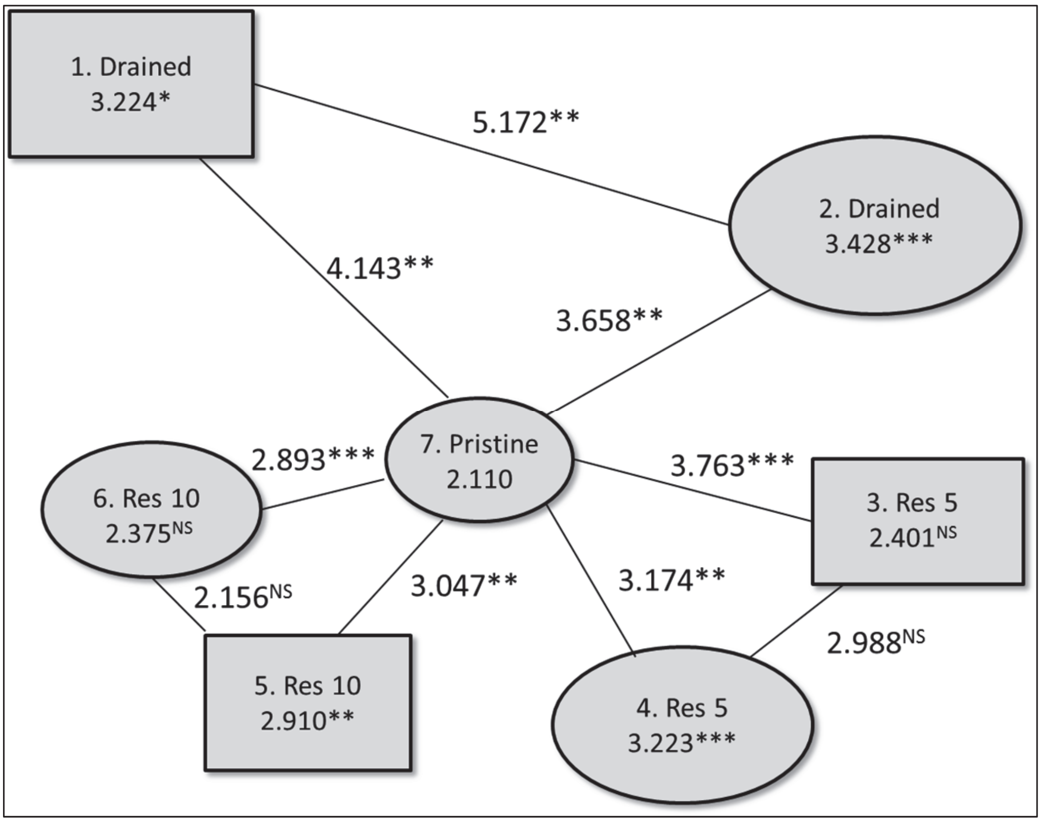

Fig. 3. Average Euclidean distances (ED) and their statistical significances between subgroups 1-7 for the three dimensional resolution of principal component analysis (PCA) of water chemistry. The values next to a line joining two subgroups show the average ED between the groups, and the symbols thereafter refer to the statistical difference from MRPP test between the subgroups. To allow more comprehensive utilization of the results than discussed in the text, average EDs within subgroups are shown inside boxes (samples from ditches) and ellipses (samples from peat strips). The symbols following the average within subgroup ED refer to the statistical significance from independent samples t-tests comparing the average EDs within a given subgroup to the average ED within pristine subgroup. Statistical significance of results: ***: $p < 0.001$, **: $p < 0.01$, * $p < 0.05$, ns: non-significant. A complete list of distances between subgroups is given in Table 4.

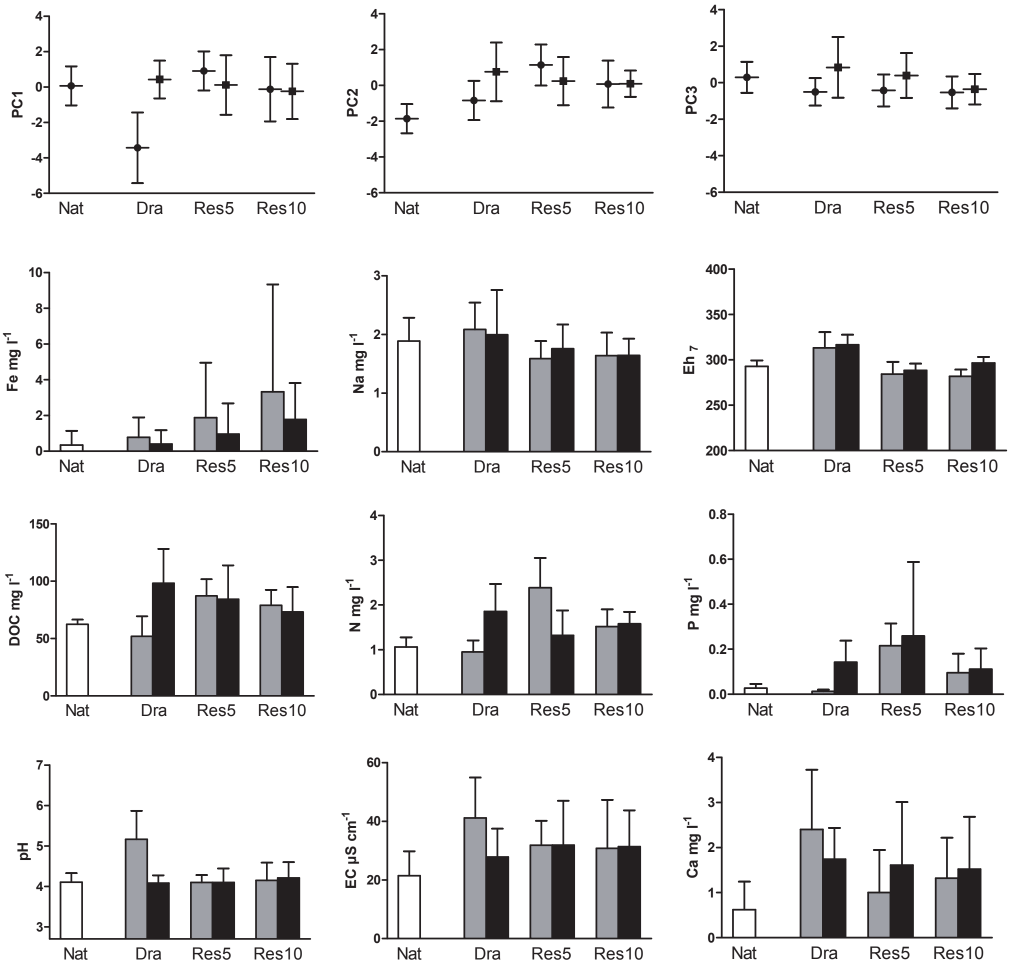

Fig. 4. Average values (+- 1 SD) of PC1-PC3 and water chemical variables for different management statuses from samples collected from ditches (gray bars) and peat strips (black bars). Note that for PC1, PC2, PC3, N and P, figures show the average values over all sites in each group (n = 10, 9, 9 and 10 for Pri, Dra, Res 5 and Res 10, respectively). However, only the sites with N and P analyzed both from ditch and peat strip at each site were included in the ANOVA and subsequent pairwise tests.

II

THE EFFECTS OF PEATLAND RESTORATION ON WATER-TABLE DEPTH, ELEMENTAL CONCENTRATIONS, AND VEGETATION: 10 YEARS OF CHANGES

by

Tuomas Haapalehto, Harri Vasander, Sinikka Jauhiainen, Teemu Tahvanainen &
Janne S. Kotiaho 2011

Restoration Ecology 19: 587-598.

III

DEGREE OF DEGRADATION AND EFFECTIVENESS OF RESTORATION: TRAJECTORIES OF PLANT COMMUNITY RECOVERY IN DRAINED PEATLANDS

by

Tuomas Haapalehto, Santtu Kareksela, Riikka Juutinen, Markku Kuitunen,
Teemu Tahvanainen, Hilja Vuori & Janne S. Kotiaho 2014

Submitted manuscript

Degree of degradation and effectiveness of restoration: trajectories of plant community recovery in drained peatlands

Tuomas Haapalehto[1,2], Riikka Juutinen[1,3], Santtu Kareksela[1], Markku Kuitunen[1], Teemu Tahvanainen[4], Hilja Vuori[1] and Janne S. Kotiaho[1]

[1] Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland.

[2] Metsähallitus, Natural Heritage Services, P.O. Box 36, 40101 Jyväskylä, Finland

[3]Current address: Metsähallitus, Natural Heritage Services, P.O. Box 8016, 96101 Rovaniemi, Finland

[4] Department of Biology, University of Eastern Finland, P.O.Box 111, 80101 Joensuu, Finland.

Abstract

Extensive degradation of natural landscapes has led to the appraisal of ecological restoration as a major strategy to mitigate biodiversity loss. The goal of restoration is to recover ecosystem structures and functions, but most empirical evaluations of the effectiveness of restoration are still based on studies spanning only few post restoration years. We studied the effects of long-term degradation and subsequent restoration on plant communities with a set up consisting of 38 boreal peatland sites. Degradation (drainage for forestry) had a strong effect on plant communities. However, the effect was dependent on the degree of degradation within sites, i.e. water table drawdown and physical destruction of peatland surface. Restoration was effective in initiating a recovery of the community composition within 10 years. The development of community composition and the trajectories of recovery were, however, dependent on the degree of degradation. Least degraded communities recovered nearly completely, while communities with greater degree of degradation showed only weak development towards target composition. The observed recovery was driven by changes in species abundances rather than by changes in species identities. Overall, our results are promising, but highlight the need for patience in drawing conclusions on the efficiency of restoration in recovering ecosystem structures. We discuss our results from the perspective of ecosystem resistance and resilience. We find that the large within-site variation observed in plant communities after restoration may, in fact, be desirable for the adaptive capacity of communities in the future. It appears, however, that the expectations of restoration regarding the resistance and resilience may be difficult to fulfil. This highlights the need for careful consideration of restoration targets in the rapidly changing world.

Keywords: ecological resilience, ecosystem structure, disturbance, mire, spatial variation, vegetation

Introduction

Almost everywhere around the globe, human land use has caused extensive degradation of natural landscapes accompanied with extinctions of species and loss of ecosystem services to an extent that it already poses a threat to the long-term sustainability of humanity itself (Millennium Ecosystem Assessment 2005; Foley *et al.* 2005; Halpern *et al.* 2008; Rockström *et al.* 2009; Ellis 2011; Cardinale *et al.* 2012). This has caused ecological restoration to be raised to a major strategy for reversing the biodiversity losses and increasing the provision of ecosystem services (Bullock *et al.* 2011; Halme *et al.* 2013; Wortley *et al.* 2013). The importance of restoration as a fundamental conservation strategy is further highlighted by its entry to the premier transnational political convention according to which 15 % of the degraded ecosystems should be restored by 2020 (Convention on Biological Diversity 2010). In addition, ecological restoration is also increasingly being called upon to compensate for the biodiversity values lost in development projects by restoring degraded sites elsewhere (Maron *et al.* 2012). The goal of ecological restoration is the recovery of ecosystems' structures and functions, for example species community composition and carbon sequestration capacity respectively (Dobson *et al.* 1997; Society for Ecological Restoration International 2004; Shackelford *et al.* 2013; Kareksela *et al.* 2014). However, while some encouraging empirical evidence exists that ecological restoration succeeds in recovering some of the degraded biodiversity and ecosystem services, values of both often remain lower in restored than in the targeted reference ecosystems (Benayas *et al.* 2009; Wortley *et al.* 2013). Moreover, in many cases there is still much uncertainty as to how effective ecological restoration really is (Suding 2011), and the number of empirical evaluations about the true effectiveness of ecological restoration has only recently started to increase (Wortley *et al.* 2013). Indeed, serious doubts have been cast for example on the ability of ecological restoration to really be able to recover the ecosystem services (Palmer and Filoso 2009) and to deliver biodiversity offsets such that losses at the impact site would be genuinely compensated by restoring a degraded site elsewhere (Maron *et al.* 2012).

Ecological restoration is still a young discipline, and thus most of the empirical evaluations of the effectiveness of restoration are by necessity based on relatively short term investigations. Hence, to some extent, the concerns about not achieving the restoration goals (Benayas *et al.* 2009; Suding 2011; Wortley *et al.* 2013) may reflect the time constraint combined with the impatience due to urgency of the matter. In other words, our expectations sometimes appear to be based on high hopes rather than profound understanding of the expected development of the degraded ecosystems after restoration. Therefore, even when restoration has been successful in initiating a true process of recovery, the possibility that the recovery towards the target is following an unanticipated trajectory, may lead to unjustified concerns. To be able to judge whether the goal of restoration is likely to be achieved, we need to understand the trajectories, i.e. the development of the community composition over time towards the target (Matthews *et al.* 2009).

Ecosystem’s resistance and resilience are key attributes in determining success of restoration (Society for Ecological Restoration International 2004). Resistance and resilience should be understood as the ability of the structures and functions of the ecosystem to resist changes imposed by external disturbances, and the ability of the structures and functions of the ecosystem to recover from the external disturbance, respectively (Holling 1973; Pimm 1991; Tilman and Downing 1994; Society for Ecological Restoration International 2004). Understanding the resistance and resilience in the framework of ecological restoration is, however, challenging because we need to simultaneously consider the communities of the targeted reference ecosystems, degraded ecosystems and restored ecosystems. The resistance and resilience can be considered from the perspective of each: what is the resistance and resilience of the target ecosystem to the initial disturbance, what is the resistance and resilience of the degraded ecosystem to the restoration, and what is the resistance and resilience of the restored ecosystem to future environmental changes. It is also notable that resilience and resistance can be viewed from the perspective of different attributes of ecosystem structure and function (Society for Ecological Restoration International 2004). To be effective, restoration needs i) to overcome the resistance and resilience in the degraded community in order to facilitate the recovery of the pristine community composition, and ii) to strengthen the resistance and resilience in the recovered community in order to facilitate its long term persistency (Suding *et al.* 2004; Harris *et al.* 2006; Suding 2011). The importance of addressing resistance and resilience when judging the efficiency of restoration in the face of rapidly changing environment has been emphasized (e.g. Suding 2011) but these issues are seldom addressed with respect to results of field studies.

One factor potentially influencing the effectiveness of ecological restoration is the degree of degradation. For example, the probability of restoration measures to reach the targets when prioritizing the restoration sites - which is likely to be affected by the degree to which the site has been degraded - should be considered when allocating resources for restoration (Hobbs and Kristjanson 2003; Alday and Marrs 2013). One aspect of the degree of degradation, that has seldom been considered, is within-site variability in the degree of degradation. Indeed, disturbances typically increase environmental heterogeneity e.g. variation in the biogeophysical environmental factors within the impacted site (Sousa 1984). Moreover, restoration measures themselves are likely to cause temporary disturbance and possibly even further degradation of varying degree (Ilmonen *et al.* 2013). It is conceivable that the variability in the degree of degradation may affect the outcome of restoration. Hence, the within-site variation in degraded and restored communities should be understood e.g. when estimating the efficiency of and setting the targets for restoration.

Boreal and subarctic peatlands are ecosystems that store one third of global soil carbon, but cover only 3 % of the global land-area (Yu 2011). In addition to sequestering CO_2, peatlands impact the global climate by emitting CH_4 and N_2O (Juszczak and Augustin 2013; Gong *et al.* 2013). Each of these important ecosystem functions are closely related to the characteristics of peatland plant communities (Ward *et al.* 2013). Like many other ecosystems, also peatlands have been severely degraded. Approximately 50 million hectares (13 % of peatlands) have been directly altered by human land-use (Lappalainen 1996; Strack 2008; Tanneberger and Wichtmann 2011). One major cause of degradation is drainage for timber production affecting approximately 15 million hectares of peatlands (Strack 2008). Drainage alters hydrology, which is the primary biogeophysical factor shaping the structure and functions in peatlands, by lowering the water-table level typically by 20–60 cm (Laine and Vanha-Majamaa 1992), with marked effects on plant community composition (Laine *et al.* 1995; Mälson *et al.* 2008). Drainage also causes unnatural within-site spatial gradients in water table level connected to distance from the ditches (Price *et al.* 2003; Haapalehto *et al.* 2014). The water table drawdown together with the uneven destruction of peatland surface during the excavation of ditches creates a complex gradient in the degree of degradation within the drained sites. In the severe degradation end of the gradient are the ditches where the original vegetation has been almost completely destroyed, bare peat exposed to erosion, and fluctuation of water level intensified. In the other end of the gradient are the areas furthest away from the ditches where, in general, the only degrading factor is the much less decreased water table level. The within-site spatial heterogeneity in the effects of drainage is clearly reflected in the functionality of peatlands such as production of methane (Minkkinen and Laine 2006). However, the effect of such within-site variation in the degree of degradation on plant community composition is still poorly understood (see also Urbanová *et al.* 2012).

The methods of ecological restoration of peatlands drained for timber production comprise mainly of recovering the original hydrology by blocking the water flow along the ditches (Vasander *et al.* 2003; Aapala *et al.* 2009). Some promising results on the recovery of plant species community composition after peatland restoration exist (e.g. Malson *et al.* 2008; Haapalehto *et al.* 2011; Laine *et al.* 2011; Hedberg *et al.* 2012), but there are also concerns on the effectiveness of restoration in recovering the targeted plant community composition (Moreno-Mateos *et al.* 2012). Results from recent studies indicate that such problems might be related to failures in recovering the original hydrology evenly within the restored sites (Haapalehto *et al.* 2011, 2014; Hedberg *et al.* 2012).

Here we report results from a replicated comparative field study, with the broad aim of understanding the dynamics of the plant species community composition of boreal peatlands after drainage and restoration in relation to within-site variation in the degree of degradation. More specifically we determine i) to what extent the plant community composition is changed after drainage and does the change depend on the within-site gradient in the degree of degradation (i.e. the distance from the ditch), ii) to what extent ecological restoration is effective in recovering the pristine plant community composition, and is the recovery dependent on the within-site degree of degradation, and iii) what are the within-site successional trajectories of the restored plant communities in relation to the degree of degradation. Finally, we discuss the changes in plant community composition after disturbance and restoration from the perspective of resistance and resilience of degraded and restored peatland ecosystems.

Materials and methods

Study sites and the comparative study setup

We selected altogether 38 study sites in southern Finland within a radius of 75 km (with a range of 200 m - 150 km between the sites) between 61° 53´ and 62° 51´ N and 22° 53´ and 25° 26´ E. The sites are in the south-boreal climatic-phytogeographical zone, where raised bogs are the main type of greater peatland formations. The mean annual temperature is ca. +4°C, precipitation ca. 650 mm and elevation above the sea level ca. 150 meters. The study sites are located to the Early Proterozoic bedrock area, where the bedrock is granites and loose minerals typical for granodiorites.

Each of the 38 study sites falls into one of four different management classes: i) pristine (n = 10), ii) drained (n = 9), iii) previously drained and restored 3-7 years before the study (restored 5 years ago, n = 9), iv) previously drained and restored 9-12 years before the study (restored 10 years ago, n = 10). For simplification, from here on the classes are referred to as Pristine, Drained, Res 5 and Res 10. Study sites were selected based on close examination of old and new aerial photographs combined with field observations to ensure that the sites in their pristine condition represented roughly the same vegetation type (weakly minerotrophic *Sphagnum* dominated pine fens). Based on topographic data and field observations, the selected sites were determined to be independent from each other in their surface water flow. The size of the patches of roughly similar vegetation was not recorded in detail. The sizes, however, ranged from a few hundred square meters to a few hectares within each management status category. Average peat depth at the sites ranged from 95 cm to more than 200 cm. The underlying soil type beneath the peat layer was till or sand. The set up may be considered a chronosequence. Such space-for-time substitutions are sometimes problematic in inferring vegetation succession e.g. if the sites differ originally in their properties (Johnson and Miyanishi 2008). We have responded to this challenge by having a number of replicates for each management status. Additionally, special attention was paid to the selection of sites as described above. Significant changes take place in peatland ecosystems after drainage and restoration. Hence, the possibility for slightly larger variation in the original vegetation types of drained and restored sites, when compared to pristine sites, cannot be ruled out.

All of the drained and restored sites were drained for forestry by the state during 1960s and 1970s with ditch interval of 30-50 meters. At the time, application of PK fertilizer to increase tree growth was a standard post-drainage procedure, and although no records of the fertilization have been kept, it is likely that all of the sites have been fertilized. In 1980s some of the sites were designated to conservation with a subsequent decision to restore them. The restoration was conducted by Natural Heritage Services of Metsähallitus which is a governmental institution responsible for management of conservation areas. Restoration measures included filling in the ditches with peat excavated near the ditches, construction of dams and removal of the tree stands in cases where drainage had increased the growth of Scotch pine (*Pinus sylvestris*) and downy birch (*Betula pubescens*). Removal of tree cover was adjusted to mimick the pre-disturbance tree cover. Decomposition and compression of the peat near the ditches causes subsidence of peat surface and therefore, the filling of the ditches was supplemented by peat dams. The dams elevate ca. 50 cm over the peat surface and extend a few meters at both sides of the ditch to prevent water flow along the subsided ditch line. The restoration measures form pits and bare peat surfaces around the filled ditches and thus result in a variable surface structure at the exact site of restoration, while peatland surfaces right outside the ditches remain largely intact. At some of the drained sites ditches had been cleared again in 1990s. To keep it simple, the currently active ditches of the drained sites as well as the infilled ditches at the restored sites are referred to as ditches from here on.

In an earlier paper on hydrology and pore water chemistry (Haapalehto *et al.* 2014) we determined the effects of drainage and restoration on the water table level of current study sites. Drainage had lowered the water table level on average by 31 cm. Important for the current study is the strong water table level gradient determined by the distance from the ditch within drained sites: compared to the pristine reference sites, the water table level at 0, 5, 10 and 15 meters from the ditch was on average ca. 65, 25, 15 and 10 cm lower at the drained than pristine sites, respectively. In comparison, the average water table did not differ any longer from the pristine level at Res 5 and Res 10 sites. Furthermore, the within-site variability in the water table level caused by drainage (as explained above) was evened out five years after restoration. It should be noted that the disturbance was further increased at 0 m distance by physical destruction of peatland ecosystem when the ditches were excavated and again when the restoration was carried out: during restoration the communities at 0 m distance from the ditch are largely destroyed due to filling the ditches with peat, whereas elsewhere within the restored sites the changes are less remarkable. This gradient creates spatial variability in the degree of degradation, the influence of which on the plant community composition is on the focus of the current study.

Sampling of plant community composition

A grid of 20 1-m^2 plots was established at each study site for the determination of the plant community composition (Fig. 1). At the Drained and restored sites, the plots were placed in five parallel transects four meters apart running perpendicular to the ditch. At each transect there was a plot at 0, 5, 10 and 15 meters from the ditch. A similar 15 m x 20 m grid of plots was laid at the Pristine reference sites. Within each of the study sites, the location of the first plot (laid on the ditch at drained and restored sites or on random surface on pristine sites) was randomized. At each plot the abundance (percentage cover) of all species of vascular plants and bryophyte species (Bryophyta, Marchantiophyta) as well as some species of lichens was estimated to the nearest 1%. Plant community composition data was collected between June and August 2007 by the same two people (SK and RJ) at each site. Nomenclature follows Ulvinen *et al.* (2002) for bryophytes and (Hämet-Ahti *et al.* 1998) for vascular plants.

Data analysis

To better understand changes in species community composition in relation to different management classes and to the variable degree of degradation, it is useful to use and compare several diversity measures (see e.g. Miller *et al.* 2011). We were interested in if the changes in community composition were related to changes in species identities or rather to changes in species abundances. Therefore, we calculated dissimilarities of plant communities between all studied vegetation plots using the Bray-Curtis dissimilarity measure calculated separately for species presence/absence data and species abundance data. Comparison of the results from these two calculations allow us to infer whether changes are more due to alteration in species pool or by changes in species abundances. For example, if a significant difference between two management statuses is observed only using abundance data, we can infer that the changes are more due to alteration in the species abundance, not due to changes in species identities. Bray-Curtis dissimilarity D based on the species abundance data between plant communities i and h was calculated as

$$Dih = \frac{\sum_{j=1}^{p} |aij - ahj|}{\sum_{j=1}^{p} aij + \sum_{j=1}^{p} ahj}$$

where p is the number of the species and a the abundance of each of the j species. The Bray-Curtis measure calculated with presence/absence data is also known as the Sörensen or Sörensen-Dice index. Therefore, the Bray-Curtis index calculated here with presence/absence data is referred to as Sörensen-Dice from further on.

To determine the effect of drainage on plant community composition we calculated the dissimilarity of each drained 1-m^2 plot to all of the pristine reference plots. We then calculated the average of the dissimilarities to pristine plots for each drained plot. Similarly, to determine the effect of restoration, we firstly calculated the dissimilarity of each restored plot to all of the pristine reference plots and thereafter calculated the average for each restored plot to pristine plots. The dissimilarity of each plot thus expresses the dissimilarity of the plant community composition of the focal plot from the "average" plant community composition of the pristine reference plots. From now on we use the term dissimilarity-from-pristine to remind the reader that the dissimilarity is calculated from the pristine site and the comparisons among the management statuses are comparisons of the differences between management statuses in their dissimilarity-from-pristine. The indices were calculated in PC-Ord 5.3 (McCune and Mefford 2006).

The effect of management status (Pristine, Drained, Res 5, Res 10), distance from the ditch (0 m, 5 m, 10 m, 15 m) and their interaction on the dissimilarity-from-pristine of plant community composition were analysed with linear mixed models. Management status, distance from the ditch and their interaction were entered as fixed factors and the study site and distance from the ditch (subject to study site) as random factors. Fisher's Least Significant Difference (LSD) tests were used for pairwise comparisons. All dissimilarities-from-pristine between the plots within a study site were excluded from the analyses. Linear mixed models and LSD tests were performed in IBM SPSS Statistics 20.

To further describe and illustrate the interaction between the management status and the distance from the ditch on the plant species community composition and to examine the trajectories of recovery after restoration we performed a NMS ordination with PC-Ord 5.3. Development and within-site differences in the plant community compositions after restoration at different distances from the ditch were visually inspected from NMS ordination using centroids of sites of each management status in a given distance from the ditch. To relate the plant community composition patterns shown in the panels 3a-d to the ecology of the observed species, we calculated the weighted average scores for the species in the NMS analyses and plotted them along the NMS axes 1 and 2 (Fig. 3e). To relate the development of community composition to species ecology, we subjectively divided the species in the NMS plot into five categories (wet poor peatlands, wet minerotrophic peatlands, dry poor peatlands (hummocks), forests, disturbed surfaces with bare peat and flowing water) according to their characteristic habitat type (Fig. 3e). The data on the ecology and characteristic habitats of species was derived from Ulvinen *et al.* (2002) and Eurola *et al.* (1995) for bryophytes and vascular plants, respectively. Furthermore, we depicted the trajectories of community composition development for each management status at each distance from the ditch by joining the centroids with a line (Fig. 3f). Species with only one observation were excluded from the ordination analysis. Before the analysis, the data consisting of relative abundances of species within 1 m^2 plots was relativized by rows (plots) and columns (species) and arcsine square root transformed. The analysis was performed using Bray-Curtis dissimilarity measure, originally six possible axes, 500 iterations in maximum, 250 runs with real and randomized data. As suggested by the analysis software, the 2D solution with a final stress of 21.35 was selected. This resulted in a cumulative r^2 of 0.75 for the two axes.

The number of sites with an observation of a species and the average abundance of each species per plot at each distance from the ditch for each of the management statuses were tabulated in Supplement 1.

Bray-Curtis (as well as the Sörensen-Dice) is a semimetric index (e.g. Wilson 1931; McArdle and Anderson 2001). This implies that the dissimilarities do not, strictly, fulfil all metric assumptions for testing the differences with ANOVA style linear models (see e.g. McArdle and Anderson 2001). Consequently, non-parametric multivariate analyses relying on permutations for achieving p-values are suggested for testing multivariate data derived from semimetric indices (Legendre and Anderson 1999; Anderson 2001; McArdle and Anderson 2001). Even after deep consideration of possible options we could not find a non-parametric analysis that permutes the data from this type of complex and hierarchical design correctly. Because Bray-Curtis provides a more ecologically meaningful interpretation of the data than metric indices (see McArdle and Anderson 2001), we chose to use Bray-Curtis and linear mixed models as explained above. We are confident that our analyses, supported by visual interpretation of figures, are not likely to provide grounds for false interpretation of the results and misleading conclusions. This was further verified by running PERMANOVA+ and PERMDISP (Anderson *et al.* 2008) with the most suitable analysis parameters available for this kind of data, and comparing the results (not shown here) to the results obtained by linear mixed models.

Results

Management status and the distance from the ditch both had a significant main effect and there was an interaction between the two in dissimilarities-from-pristine on both Sörensen-Dice and Bray-Curtis measures (Table 1, Fig. 2).

Effect of drainage

With both measures, the dissimilarities-from-pristine of the Drained communities were overall greater than the dissimilarities-from-pristine of the Pristine communities (Table 2, Fig. 2). However, the difference in the dissimilarities-from-pristine was dependent on the distance from the ditch such that the difference decreased with increasing distance from the ditch (Table 2, Fig. 2). At 15 meters from the ditch it appears that there was no significant difference in the dissimilarities-from-pristine between Drained and Pristine communities (Table 2) suggesting that drainage had not influenced the species community composition. However, from the NMS ordination it can be seen that even at the 15 meters distance from the ditch the communities of the plots at the Drained and Pristine sites did not really overlap (Fig. 3). Therefore, we re-ran the above mixed model analysis of variance and the pairwise comparisons with data from which we excluded one of the Pristine sites that in the NMS ordination appeared to have a relatively deviant point at one of the distances from the ditch (at the bottom left corner of the plot in Fig. 3). This exclusion had no effect on any of the other results, but it confirmed our interpretation of the NMS ordination that there indeed is a small but significant difference in the dissimilarities-from-pristine between the plots at the Drained and Pristine sites also at the 15 meters distance from the ditch (for Sörensen-Dice MD = -0.069, p = 0.035 and for Bray-Curtis MD = -0.163, p = 0.017).

Based on the ecology of species present in the NMS analysis (Fig. 3e), there appear to be two patterns in the ordination data. The first is a gradient that runs from bottom left to top right corner of the ordination. Species along this gradient are changing from species characteristic to wet and open hollow level habitats in the bottom left end (e.g. *Sphagnum tenellum*, *Sphagnum balticum*, *Cladopodiella fluitans*) through species characteristic to hummock habitats in the middle (e.g. *Sphagnum fuscum*, *Rubus chamaemorus*, *Aulacomnium palustre*) to species characteristic to dry and closed forest habitats in the top right end (e.g. *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Pleurozium schreberi*, *Dicranum polysetum*) (Fig. 3e). The other pattern is the clustering and separation of species of highly disturbed bare peat and flowing water habitats to the bottom right corner of the ordination (e.g. *Polytrichastrum longisetum*, *Carex canescens*) (Fig. 3e).

The communities at Drained sites were characterized by increased relative abundance of species mainly found from closed forests (e.g. above mentioned species typical to unnaturally dry and forested habitats) and decreased relative abundance of species typical to bogs and fens (e.g. *Vaccinium microcarpum/oxycoccos*, *Drosera rotundifolia*, *Andromeda polifolia* and *Carex rostrata*, *Carex pauciflora*, *Dactylorhiza maculata*, *Sphagnum fallax*, respectively) (Fig. 3, Supplement 1). A few species occasionally found from the wettest surfaces of Pristine sites (e.g. *Carex limosa*, *Scheuchezeria palustris*) were not present at the Drained sites at all (Supplement 1). Moreover, some typical peatland species (e.g. *Carex rostrata*, *Sphagnum fallax*) were almost exclusively found in the ditches at the Drained sites, albeit in very low abundances. However, most species typical to targeted Pristine sites (e.g. *Sphagnum angustifolium*, *Sphagnum magellanicum*) were nevertheless present in low abundances at most Drained sites at the 5-15 m distances from the ditch (Supplement 1).

Effect of restoration

Dissimilarities-from-pristine of the Res 5 communities did not differ overall, or at any of the distances from the ditch, from those of the Drained communities (Table 2, Fig. 2). Thus, it appears that restoration was not effective in changing the plant community towards the target community composition during the first five years post restoration. However, at the Res 10 sites, the Bray-Curtis dissimilarities-from-pristine were overall reduced relative to those of Drained sites (Table 2). While there were no changes at 0 m from the ditch, the reductions in the dissimilarities-from-pristine at other distances from the ditch were evident (Table 2; Figure 2). With Sörensen-Dice similar clear reduction in dissimilarity-from-pristine was not observed (Table 2, Fig. 2). Thus, restoration appeared to be effective in initiating a recovery of the community composition during five to 10 years post restoration. Since it was mostly Bray-Curtis measure that was influenced with no or smaller effects observed in Sörensen-Dice measure, the recovery of the community composition was mainly driven by the changes in species abundances rather than in their identities.

Overall, dissimilarities-from-pristine of Res 5 and Res 10 communities were significantly greater than those of the Pristine communities with both of the dissimilarity measures, but the differences were dependent on the distance from the ditch (Table 2, Figure 2). The plots at the Res 5 sites had greater dissimilarity-from-pristine than the Pristine plots at all distances with both measures, but the dissimilarity-from-pristine seems to be decreasing with increasing distance to the ditch (Table 2). The plots at the 10 years ago restored sites show similar pattern, but importantly, there no longer was a significant difference in the dissimilarity-from-pristine between Res 10 plots at the 10-15 meters distance from the ditch and the pristine plots (Table 2). Thus, already 10 years after the restoration the plant communities furthest away from the ditches seem to be as similar to Pristine communities as the Pristine communities are themselves.

Judged from the NMS (Fig. 3e) and species specific changes (Supplement 1), during the first 10 years post restoration at 5-15 meters distance from the ditch, the recovery of community composition was mainly driven by decreased relative abundance of forest species (especially *Pleurozium schreberi*) and increased relative abundance of some peatland species with wide ecological niches (e.g. *Sphagnum angustifolium* and *Sphagnum magellanicum*). At the 0 m distance from the ditch, the relative abundance of species capable of utilizing the bare peat surfaces and released nutrients (e.g. *Carex magellanica*, *Eriophorum vaginatum*; Silvan *et al.* 2004) seemed to increase five years after restoration (Supplement 1). This was followed by a decreased relative abundance of species typical to bare peat (*Carex magellanica*, *Dicranella cerviculata*, *Polytrichastrum longisetum*, *Eriophorum vaginatum*) and increased relative abundance of species typical to wet fens (*Carex rostrata*, *Sphagnum fallax*, *Straminergon stramineum*; Supplement 1). Hence, even though both of the dissimilarity measures suggested that the communities at 0 m distance from the ditch were still significantly more dissimilar-from-pristine than the pristine communities (Table 2), there apparently were some changes in the plant communities also within the infilled ditches. This can also be seen when Table 2 is closely inspected: the mean difference (MD) in the dissimilarity-from-pristine between Res 10 and Pristine is somewhat smaller than that with Res 5 and Drained with both dissimilarity measures.

When we depicted the trajectories of community composition development for each management status at each distance from the ditch by joining the centroids with a line, a roughly similar pattern of development was seen almost irrespective of the distance from the ditch. After an initial loop towards communities characterized by increased abundance of species typical to heavily degraded habitats (right to bottom-right, see above), all of the trajectories change track more or less towards the pristine sites (bottom-left, Fig. 3f). Although the overall shape of the trajectories was roughly similar, there appeared to be a magnitude gradient in the curvature of the trajectory relative to the distance from the ditch such that the curvature increased with decreasing distance from the ditch (Fig. 3f). In contrast to other distances from the ditch, the trajectory of communities at 0 m distance does not point directly towards the Pristine sites. It is also notable that certain peatland species that were not recorded from the drained sites (e.g. *Carex limosa*, *Scheuchzeria palustris*) were not found from the restored sites either (Supplement 1).

Discussion

We set up to determine i) to what extent the plant community composition has changed after drainage and does the change depend on the within-site degree of degradation, ii) to what extent ecological restoration is effective in recovering the original plant community composition, and is the recovery dependent on the degree of degradation, and iii) what are the within-site successional trajectories of the restored plant communities in relation to the degree of degradation. Our main findings can be summarized as follows: Drainage had a strong effect on species community composition. This was heavily dependent on the degree of degradation related to differential drawdown of water table level and physical disturbance during drainage period. Restoration was effective in initiating a recovery of community composition within 10 years post restoration. According to our analyses the recovery was dependent on the degree of degradation: plant communities in the plots with less degradation at 10 and 15 meters from the ditch appeared to be very similar to the target communities after the first 10 post restoration years, while plots with greater degree of degradation at 0 and 5 meters from the ditch showed no, or only some recovery, respectively, and were still significantly different from the plots at the Pristine sites. Finally, the NMS ordination showed that while the post restoration community development trajectories at all distances from the ditch were fairly similar and indicate initiation of recovery, it appears that the restoration is causing further albeit transient disturbance. Moreover, even though largely similar shaped with all other distances, the trajectory of the plots subject to most severe disturbances during both drainage and restoration measures (nearly complete destruction of plant communities and opening of bare peat surfaces) appeared not to point towards pristine target communities 10 years post restoration.

Our results provide strong support for some earlier studies suggesting that the impact of drainage in peatland ecosystems can still be seen after several decades since the original water table drawdown (Laine *et al.* 1995; Laiho *et al.* 2003; Mälson *et al.* 2008; Pellerin *et al.* 2009). Drainage causes a gradient of water table draw down (Haapalehto *et al.* 2014). Accompanied by the higher physical disturbance within and close to the ditches this results in a variable degree of degradation in these ecosystems. This variable degree of degradation was strongly visible in our community composition data: the dissimilarity-from-pristine of the community composition between the Drained and the Pristine sites decreased with increasing distance from the ditch i.e. with decreasing degree of degradation. Indeed, the community compositions of the plots with the least degree of degradation at 15 meters from the ditch were only slightly altered by drainage. However, some deviation from the Pristine communities was apparent, and thus even the water table drawdown of 10 cm (Haapalehto *et al.* 2014), should be considered a threat to the pristine peatland plant communities. In some cases, spontaneous recovery may be sufficient in re-establishing target communities (Hobbs and Cramer 2008; Jones and Schmitz 2009). Our results, however, support earlier hypothesis suggesting that a recovery of the targeted plant communities in drained peatlands due to overgrowth and thus slow natural blockage of the ditches is unlikely in a time scale relevant for halting the loss of biodiversity (Haapalehto *et al.* 2011).

Concerns have been expressed on the ability of ecological restoration to recover the original ecosystem structures and functions (Benayas *et al.* 2009; Palmer and Filoso 2009; Suding 2011; Wortley *et al.* 2013). However, due to the young age of the discipline, most of the observations are based on relatively short term investigations and in many cases only on individual unreplicated case studies. Moreover, our understanding on the development of the restored ecosystem characteristics like successional trajectories after restoration is typically imperfect (Hobbs and Cramer 2008). Such concerns may, therefore, be premature. Our results support earlier studies (Mälson *et al.* 2008; Haapalehto *et al.* 2011; Laine *et al.* 2011; Hedberg *et al.* 2012) suggesting that the recovery of forestry drained peatland ecosystem structure, measured as plant community composition, may, indeed, be initiated by restoration. It, however, took five to 10 years post restoration even for the least degraded plots to show clear initiation of recovery towards the target, and there was only weak if any indication of recovery in the most degraded plots. In fact, even the least degraded communities appeared to show development towards a direction other than the target community composition still five years post restoration. The time needed for judging the efficiency of restoration measures depends on studied ecosystem attributes, but in many cases it may be much longer than practitioners have anticipated (e.g. Matthews *et al.* 2009; Moreno-Mateos *et al.* 2012). The observed relatively slow recovery suggests that there, indeed, is a risk of drawing premature conclusions about the effectiveness of restoration in achieving the recent global expectations laid on restoration (Convention on Biological Diversity 2010; Bullock *et al.* 2011; Maron *et al.* 2012; Halme *et al.* 2013; Wortley *et al.* 2013). The development of communities towards the direction opposite to the target composition (Fig. 3f) and the decreased abundances of some typical peatland species especially in the infilled ditches five years after restoration (e.g. *Andromeda polifolia*, *Drosera rotundifolia*, *Sphagnum fuscum*; Supplement 1) suggests that the deviation from target communities is partly due to further disturbance in the plant communities during the restoration. Our results, hence, support earlier studies suggesting that the disturbance by the restoration measures themselves may be one factor delaying the re-establishment of target communities (Ilmonen *et al.* 2013).

Looking at our results at the species level, we can see that in accordance to earlier studies, the recovery of wetland communities seems to be driven by changes in species abundances rather than in their identities (Moreno-Mateos *et al.* 2012). Furthermore, most of the original peatland species were still present in low abundances at most of the drained sites at the 5-15 m distances from the ditch (Supplement 1). Hence, it appears that it is not only the least degraded areas (see Urbanová *et al.* 2012) within drained sites that can provide refugia for the original peatland species. Interestingly, while many original peatland species were present in low abundances outside the most degraded plots, there were a few species typical to pristine peatlands (e.g. *Carex rostrata*, *Sphagnum fallax*) that could only be found in the most degraded plots i.e. in the ditches at the Drained sites. Their presence in the ditches, even though in very low abundances, may be important for the recovery of plant communities after restoration, as it is probable that these novel habitat refugia contributed to the highly increased abundance of these species in the filled in ditches after restoration (Supplement 1). It should, however, be noted that there were some specialised peatland species, growing typically in the wettest areas of studied pristine peatlands (*Carex limosa*, *Scheuchzeria palustris*), which could not be found from either drained or restored sites (Supplement 1). This is in line with earlier studies suggesting that the species once disappeared due to drainage re-establish poorly (Hedberg *et al.* 2012). Active transplantations of target species are suggested as a measure to completely restore target vegetation (e.g. Hedberg *et al.* 2012). We feel, however, that it should also be carefully considered what else we could do with the resources that re-establishing the complete original communities by transplantations would take (see e.g. Bottrill *et al.* 2008; Gilbert 2011; Game *et al.* 2013). For example, if the intention is not to bring back a strictly defined set of target species, partial recovery of plant community composition may still be sufficient to recover some important peatland ecosystem functions like surface peat growth in these nutrient and species poor habitats (Kareksela *et al.* 2014).

The concepts of ecosystem resistance and resilience are intimately linked to successful restoration (Society for Ecological Restoration International 2004; Suding 2011). To be effective restoration needs i) to overcome the resistance and resilience of the degraded ecosystem state (Suding *et al.* 2004; Alday and Marrs 2013; Alday *et al.* 2013), and ii) to strengthen the resilience (and resistance) of the restored system in order to facilitate its long term persistency (Suding 2011). Despite the relatively slow rate of recovery, we, indeed, found a development of plant communities towards the target. This suggests that restoration was efficient in overcoming the resistance of the ecosystem in its degraded state, and that the original ecosystem still shows some resilience despite significant changes after drainage (see also Lake 2013). Additionally, we found no reversal of the trajectories of community development towards the degraded state. Hence the degraded ecosystem appears not be resilient to restoration within the studied time-scale (see Suding *et al.* 2004). In general, ecosystem may be resistant or resilient to restoration measures, if the magnitude of intervention was not great enough, intervention was incorrect, or because intervention was imposed at inappropriate spatial or temporal scale (Lake 2013). The persistence of the degraded state may also be enforced by such factors as species that alter the biogeochemical cycling, trophic interactions, lack of original species or their propagules and long-term changes in environmental factors (Suding *et al.* 2004). We suggest that the successful overcoming of resistance and resilience in the degraded ecosystem was possible in our case especially because the most important environmental factor affecting community composition, i.e. water table level, was successfully re-established (Haapalehto *et al.* 2014). Furthermore, most of the original species were apparently present also at the sites in their degraded state (Supplement 1). Judged from the pore water chemistry (Haapalehto *et al.* 2014), drainage did not result in such irreversible changes in the biogeochemical cycling of studied sites that would strongly favour the maintenance or re-establishment of the degraded ecosystem state.

Our data showed interesting results related to the within-site variability in the degree of degradation due to drainage. From Table 2 it can be inferred that the variability in the degree of degradation (as a function of the distance from the ditch) is increasing the within-site variability in the community compositions: at least degraded drained plots (15 meters from the ditch) the communities are only slightly more dissimilar-from-pristine than the pristine sites but the dissimilarity-from-pristine increased with increasing degree of degradation at 10, 5 and 0 meters from the ditch. Thus drainage appears to increase heterogeneity in the community composition when compared to the Pristine communities. When we focus on the effects on restoration we can see that the restoration was effective in decreasing the heterogeneity among the plots of 5, 10 and 15 meters from the ditch 10 years post restoration (Table 2). However, the dissimilarity-from-pristine at 0 meters from the ditch was still much larger than at other distances and, consequently, significant heterogeneity still remains in the restored ecosystems when compared to pristine ecosystems.

Overall, our results are encouraging from the perspective of ecological restoration, because restoration was clearly effective in initiating the recovery of community composition towards the pristine target. However, whether the target of restoration should be a recovery of the original communities (Society for Ecological Restoration International 2004) or something else can be speculated (Hobbs *et al.* 2006, 2009, 2011). For example, would it be desirable to manage communities such that they would be more tolerant for climate change? If this is the target, then some increased heterogeneity in the community compositions, which was indeed apparent in our data, might actually be desirable. This is because more heterogeneous communities are more likely to be able to adapt to the changing environments of the future (see e.g. Vellend 2005, 2010). If the target is the original or pristine community composition, then restoration needs to overcome the resistance and resilience of the degraded system, and to strengthen the resistance and resilience of the recovered system in order to facilitate its long term persistency. However, if we set the target to be a community that can adapt to the changing environments in the future, then it appears that a completely contradictory goal of restoration emerges: restoration should facilitate systems not to be too resistant to the changing environment but rather to be fast to adapt. Similarly, it appears that with this target the systems should not be resilient so that they would not aim towards the previous community composition that would in the new conditions be less adapted. Arguments in favour of both can be made, but for restoration practitioners, that will very soon have to decide what to do when restoring the 15% of all degraded habitats (Convention on Biological Diversity 2010), and measure what they have achieved, it really matters which one is the target.

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Table 1. The fixed effects of the linear mixed model analysis for Sörensen-Dice and Bray-Curtis dissimilarity-from-pristine of plant community composition with management status (MS; pristine, drained, restored 5 y ago, restored 10 y ago) and distances from the ditch (0, 5, 10, 15 m) and their interaction.

Source	Sörensen-Dice			Bray-Curtis		
	Denom. df	F	p	Denom. df	F	p
Intercept	34.0	3835.190	<0.001	34.0	1412.054	<0.001
MS	34.0	17.758	<0.001	34.0	12.104	<0.001
Distance	102.2	44.114	<0.001	102.0	17.186	<0.001
MS*Distance	102.2	5.683	<0.001	102.0	4.182	<0.001

Numerator df's are 1, 3, 3 and 9 for Intercept, MS, Distance and MS*Distance, respectively.

Table 2. Mean difference (MD) and significance (p) of pairwise LSD comparisons for Sörensen-Dice and Bray-Curtis dissimilarity-from-pristine of plant community composition between management statuses overall, and between management statuses at different distances from the ditch.

		Overall		0 m		5 m		10 m		15 m	
MS(I)	MS(J)	MD (I-J)	p	MD (I-J)	p	MD (I-J)	p	MD (I-J)	p	MD (I-J)	p
		Sörensen-Dice									
Pri	Dra	-0.130	<0.001	-0.223	<0.001	-0.157	<0.001	-0.086	0.009	-0.053	0.100
	Res5	-0.163	<0.001	-0.270	<0.001	-0.176	<0.001	-0.129	0.000	-0.075	0.021
	Res10	-0.098	<0.001	-0.214	<0.001	-0.087	0.007	-0.068	0.031	-0.023	0.459
Dra	Res5	-0.033	0.184	-0.047	0.154	-0.019	0.564	-0.044	0.189	-0.022	0.503
	Res10	0.031	0.194	0.009	0.791	0.070	0.032	0.017	0.589	0.030	0.351
Res5	Res10	0.064	0.010	0.056	0.086	0.089	0.007	0.061	0.061	0.052	0.107
		Bray-Curtis									
Pri	Dra	-0.259	<0.001	-0.361	<0.001	-0.355	<0.001	-0.209	0.002	-0.109	0.102
	Res5	-0.240	<0.001	-0.394	<0.001	-0.255	<0.001	-0.175	0.009	-0.137	0.041
	Res10	-0.124	0.014	-0.333	<0.001	-0.151	0.021	-0.022	0.738	0.009	0.883
Dra	Res5	0.018	0.717	-0.033	0.632	0.100	0.143	0.034	0.622	-0.028	0.683
	Res10	0.135	0.009	0.028	0.669	0.204	0.003	0.187	0.006	0.119	0.076
Res5	Res10	0.116	0.023	0.061	0.359	0.104	0.120	0.154	0.022	0.147	0.029

MS = management status, Pri = Pristine, Dra = Drained, Res5 = Restored 5 y ago, Res10 = Restored 10 y ago

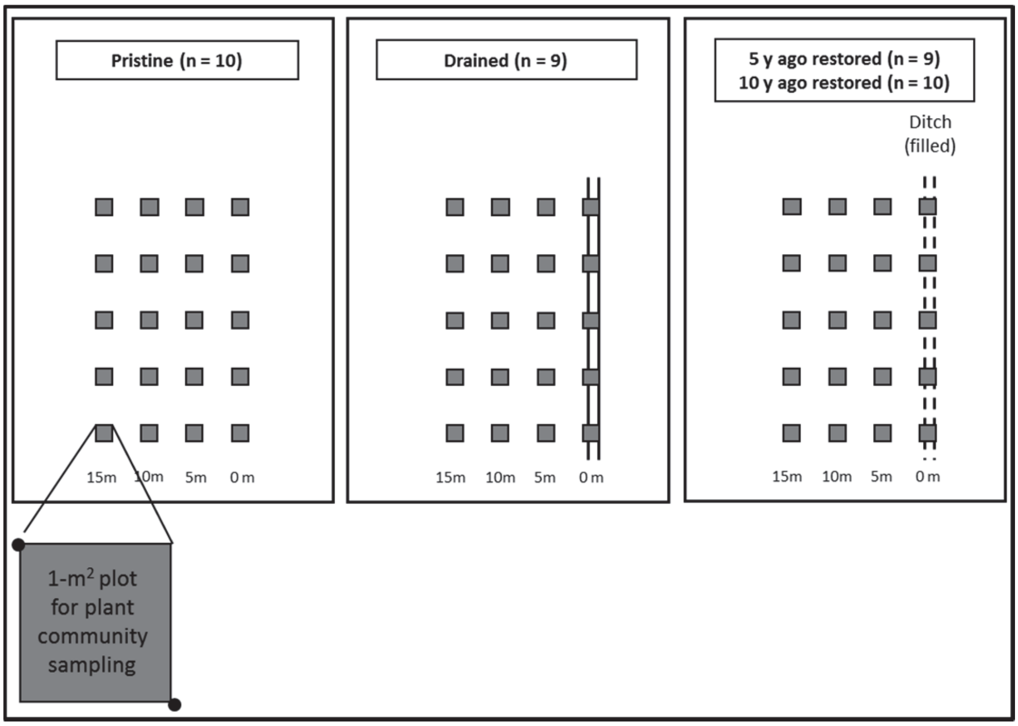

Figure 1. Study set-ups for sampling the vegetation at pristine, drained and restored sites. Distances (m) refer to distance of 1-m^2 plots to ditches at restored and drained sites. A similar grid of plots was laid at pristine sites.

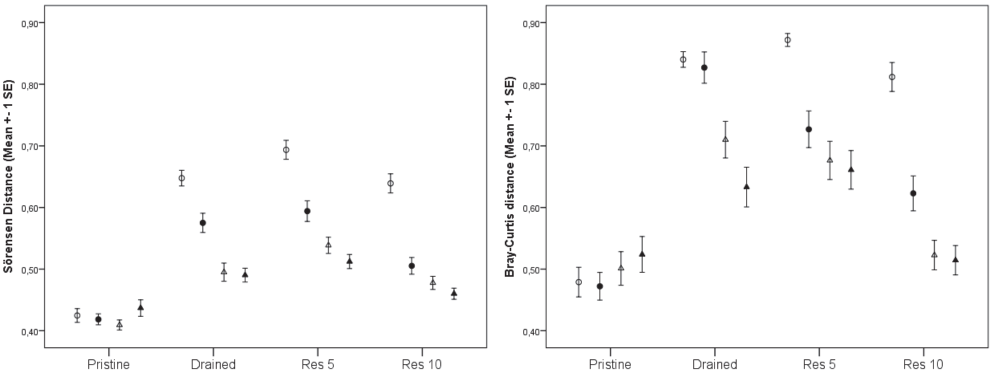

Figure 2. The average a) Sörensen-Dice and b) Bray-Curtis dissimilarities-from-pristine of plant communities at different distances from the ditch. The lower the distance (dissimilarity), the more similar to pristine the communities are. Open circles, filled circles, open triangles and filled triangles represent 0, 5, 10 and 15 m distance from the ditch, respectively. Res 5 = restored five years ago, Res 10 = restored 10 years ago.

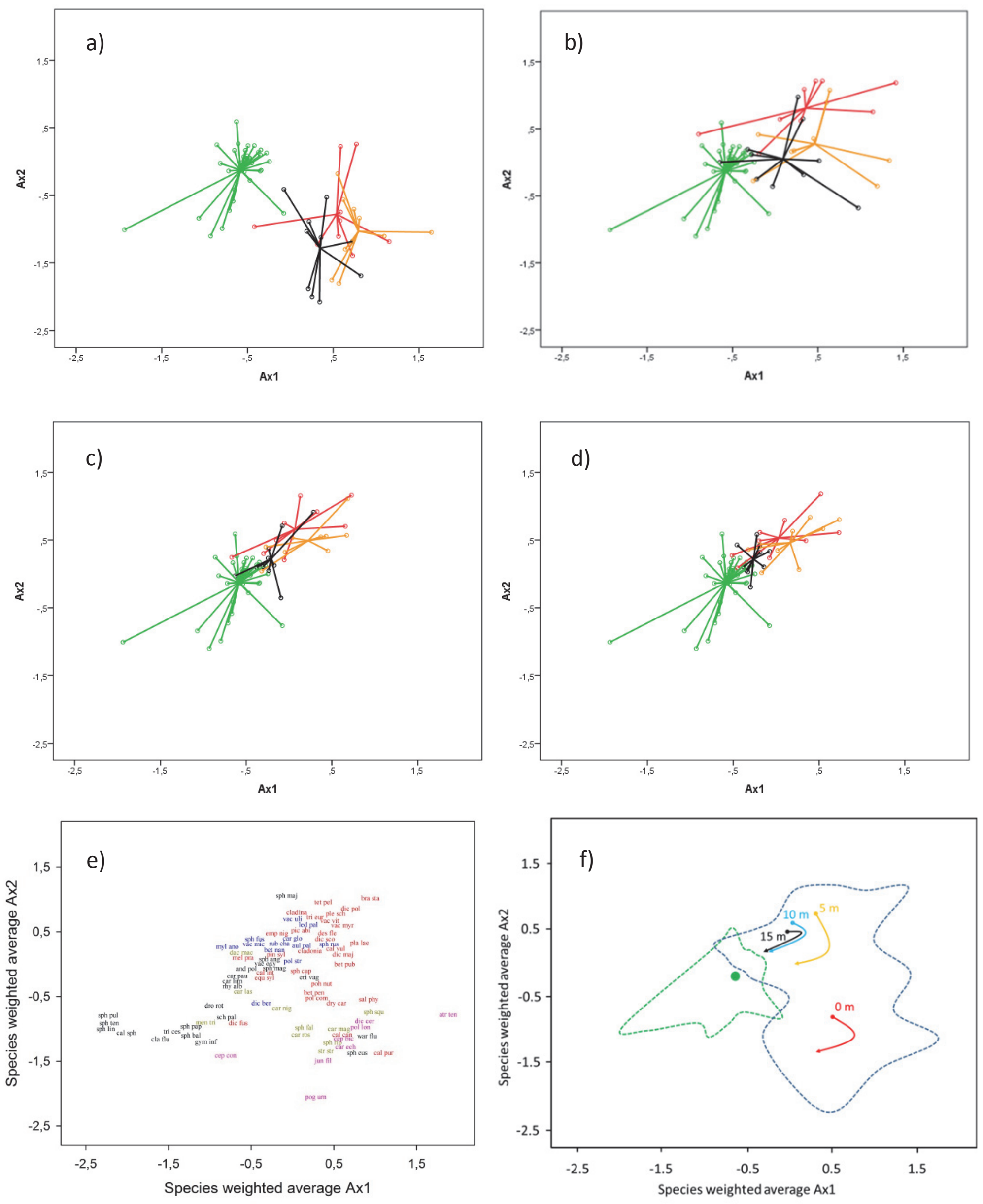

Figure 3. The position of the sites of different management statuses (panels a-d), species typical to different habitat types (panel e) and trajectories of recovery of plant communities in the ordination space (NMS, axes 1 and 2; panel f). Panels a-d correspond to 0, 5, 10 and 15 m distance from the ditch, respectively. Green, red, orange and black circles indicate weighted average scores for management statuses pristine, drained, 5 years ago restored and 10 years ago restored, respectively. The centroids represent the average of sample scores for each management status, i.e. the average position of each management status in the ordination space. As for other management statuses, each pristine circle represents the average of scores over the

five 1-m^2 plots at a given distance from the ditch. As a separation from other management statuses we, however, show the average scores from all four distances from the ditch in every panel a-d. This is done to illustrate the variance within the pristine sites. Note that even though presented in separate panel, the axes scores for different distances from the ditch are derived from one NMS analysis. Panel 3e represents the weighted average scores for species in the NMS analysis. The species were divided in groups according to their ecology: black = wet poor peatlands, yellow = wet minerotrophic peatlands, blue = dry poor peatlands (hummocks), red = forests, purple = disturbed surfaces with bare peat and flowing water. In panel 3f red, yellow, light blue and black arrows highlight the trajectories of the recovery i.e. changes in the community composition at different distances from the ditch in the NMS space. The arrows have been created by joining the centroids of drained, 5 years ago restored and 10 years ago restored sites at each distance from the ditch. For comparison, the scattering of communities of Pristine and other management statuses are illustrated with green and dark blue dotted lines, respectively. Green dot represents the centroid of Pristine communities.

Supplement 1. Species relative abundance and the number of sites a species has been observed with the management status and distance from the ditch. Also the weighted average scores (W.A.) for each species in the NMS analysis are given with the abbreviated names used in Fig. 3e.

				Pristine								Drained							
		NMS		0 m		5 m		10 m		15 m		0 m		5 m		10 m		15 m	
Species	Short name	W.A. Ax1	W.A. Ax2	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency
Andromeda polifolia	And pol	-0,51	-0,03	2,4	9	3,5	10	4,7	10	4,5	10	0,0	3	0,2	8	0,2	8	0,4	8
Betula nana	Bet nan	-0,22	0,22	3,7	8	2,6	9	2,0	9	2,4	9	0,3	4	2,9	6	3,5	8	3,0	8
Betula pendula	Bet pen	0,26	-0,51	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,2	1	0,0	0	0,0	0
Betula pubescens	Bet pub	0,63	0,00	1,2	0	0,0	0	0,0	1	0,0	0	4,9	9	5,0	8	1,5	5	2,4	6
Calamagrostis purpurea	Cal pur	1,10	-1,37	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Calluna vulgaris	Cal vul	0,46	0,27	0,0	0	0,0	0	0,0	0	0,0	0	0,2	3	0,6	1	0,0	1	0,0	1
Carex canescens	Car can	0,62	-1,12	0,0	0	0,0	0	0,0	0	0,0	1	1,8	8	0,0	0	0,0	0	0,1	1
Carex chordorrhiza	Car cho			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Carex echinata	Car ech	0,64	-1,24	0,0	0	0,0	0	0,0	1	0,0	1	0,6	4	0,0	1	0,0	0	0,0	0
Carex globularis	Car glo	0,00	0,39	0,1	2	0,1	2	0,1	2	0,2	2	0,0	0	0,0	0	0,0	0	0,4	1
Carex lasiocarpa	Car las	-0,60	-0,42	0,0	1	0,0	2	0,2	1	0,1	1	0,1	1	0,1	1	0,1	1	0,0	1
Carex limosa	Car lim	-0,73	-0,26	0,0	1	0,0	2	0,0	3	0,1	2	0,0	0	0,0	0	0,0	0	0,0	0
Carex magellanica	Car mag	0,59	-1,00	0,0	2	0,0	1	0,0	1	0,0	0	0,3	1	0,0	0	0,0	0	0,0	0
Carex nigra	Car nig	-0,14	-0,61	0,1	1	0,1	1	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0
Carex pauciflora	Car pau	-0,67	-0,22	0,0	8	0,3	10	0,2	9	0,2	7	0,0	1	0,0	0	0,0	2	0,0	1
Carex rostrata	Car ros	0,10	-1,09	0,5	10	2,6	8	2,4	7	1,1	5	2,4	2	0,0	1	0,0	0	0,0	0
Chamaedaphne calyculata	Cha cal			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dactylorhiza maculata	Dac mac	-0,62	0,13	0,0	2	0,0	1	0,0	2	0,0	3	0,0	0	0,0	0	0,0	0	0,0	0
Deschampsia flexuosa	Des fle	0,38	0,50	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Drosera rotundifolia	Dro rot	-0,95	-0,64	0,0	7	0,2	6	0,1	8	0,1	5	0,0	3	0,0	0	0,0	0	0,0	0
Dryopteris carthusiana	Dry car	0,51	-0,53	0,1	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Empetrum nigrum	Emp nig	-0,19	0,37	3,6	8	2,5	8	2,5	10	2,3	9	0,1	8	2,6	8	4,7	9	2,3	9
Epilobium angustifolium	Epi ang			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Eriophorum vaginatum	Eri vag	0,20	-0,20	5,9	10	6,5	10	6,3	10	5,3	10	4,8	9	2,0	9	2,8	9	3,1	9
Equisetum sylvaticum	Equ syl	-0,34	-0,21	0,0	1	0,1	1	0,1	1	0,2	1	0,0	1	0,0	0	0,0	0	0,0	0
Juncus filiformis	Jun fil	0,37	-1,49	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Ledum palustre	Led pal	0,19	0,58	1,8	3	1,0	4	0,6	4	1,0	3	0,0	2	0,4	3	1,2	3	0,9	3
Melampyrum pratense	Mel pra	-0,41	0,10	0,0	1	0,0	0	0,0	0	0,0	2	0,0	0	0,0	2	0,0	2	0,0	1
Menyanthes trifoliata	Men tri	-1,14	-0,95	0,0	2	0,5	3	0,2	1	0,2	1	0,0	1	0,0	0	0,0	0	0,0	0
Picea abies	Pic abi	0,10	0,53	0,0	0	0,0	2	0,0	0	0,0	0	0,5	3	1,5	6	0,0	2	0,7	6
Pinus sylvestris	Pin syl	-0,20	0,18	0,9	7	0,1	7	0,6	6	0,1	4	0,1	7	0,2	8	0,2	5	0,2	7
Rhyncospora alba	Rhy alb	-0,73	-0,31	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Rubus chamaemorus	Rub cha	-0,07	0,38	6,1	9	2,9	8	3,7	8	4,4	9	0,2	2	2,9	7	3,9	9	3,9	8
Salix aurita	Sal aur			0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0
Salix phylicifolia	Sal phy	0,92	-0,54	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Scheuchzeria palustris	Sch pal	-0,80	-0,82	0,0	2	0,0	3	0,0	3	0,0	2	0,0	0	0,0	0	0,0	0	0,0	0
Trientalis europaea	Tri eur	0,36	0,72	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Trichophorum cespitosum	Tri ces	-1,46	-1,04	0,0	2	0,3	2	0,1	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Vaccinium microcarpum	Vac mic	-0,46	0,32	0,1	5	0,1	6	0,1	5	0,0	4	0,0	1	0,0	4	0,1	5	0,1	4
Vaccinium myrtillus	Vac myr	0,54	0,60	0,2	1	0,0	0	0,0	1	0,0	0	1,3	5	1,2	6	0,9	7	1,8	5
Vaccinium oxycoccos	Vac oxy	-0,33	0,01	1,9	10	3,8	10	3,1	10	3,5	10	0,2	6	1,1	7	1,4	9	1,4	9
Vaccinium uliginosum	Vac uli	0,08	0,61	3,5	8	1,8	5	1,5	7	1,5	6	0,6	6	8,6	6	10,0	8	9,2	7
Vaccinium vitis-idaea	Vac vit	0,45	0,69	0,8	1	0,0	2	0,1	2	0,2	2	1,1	2	5,1	8	2,8	5	1,9	4
Atrychium tenellum	Atr ten	1,88	-0,78	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Aulacomnium palustris	Aul pal	0,10	0,31	0,4	5	0,2	5	0,1	6	0,2	8	0,0	3	0,2	8	0,8	9	1,1	8
Brachythecium reflexum	Bra ref			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Brachythecium starkei	Bra sta	0,94	1,02	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Brachythecium spp.	Brachyth	0,11	0,35	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	2	0,0	1	0,0	1
Callliergon cordifolium	Cal cor			0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Calypogeia integristipula	Cal int	-0,33	-0,11	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	1	0,0	0
Calypogeia sphagnicola	Cal sph	-2,01	-1,06	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Calypogeia spp.	Calypoge	0,16	-0,55	0,0	0	0,0	0	0,0	0	0,0	0	0,0	3	0,0	0	0,0	0	0,0	0
Cephalozia bicuspidata	Cep bic	0,62	-1,15	0,0	0	0,0	0	0,0	0	0,0	0	0,0	2	0,0	0	0,0	0	0,0	0
Cephalozia connivens	Cep con	-0,81	-1,41	0,0	0	0,0	0	0,0	1	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Cephalozia spp.	Cephaloz	0,66	-0,25	0,0	1	0,0	0	0,0	0	0,0	2	0,0	1	0,0	0	0,0	2	0,0	0
Cladina spp.	Cladina	0,05	0,80	0,0	0	0,0	2	0,1	1	0,0	1	0,0	1	0,3	4	0,0	2	0,1	3
Cladonia spp.	Cladonia	0,22	0,26	0,0	0	0,0	1	0,0	1	0,0	0	0,0	5	0,2	7	0,0	3	0,1	4
Cladopodiella fluitans	Cla flu	-1,42	-1,09	0,0	1	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranella cerviculata	Dic cer	0,83	-0,96	0,0	0	0,0	0	0,0	0	0,0	0	1,6	6	0,0	3	0,0	0	0,0	1
Dicranum bergeri (D. undulatum)	Dic ber	-0,38	-0,60	0,0	0	0,0	0	0,0	1	0,0	0	0,0	1	0,0	0	0,0	0	0,0	1
Dicranum fragillifolium	Dic fra			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranum fuscescens	Dic fus	-0,66	-0,91	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranum majus	Dic maj	0,61	0,15	0,0	0	0,0	0	0,0	1	0,0	0	0,0	2	0,0	2	0,0	1	0,0	0
Dicranum polysetum	Dic pol	0,65	0,77	0,0	0	0,0	0	0,0	0	0,0	1	0,0	4	1,5	7	0,7	7	0,4	7
Dicranum scoparium	Dic sco	0,39	0,36	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	1	0,0	0	0,0	0
Ditrichium pusillum	Dit pus			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0
Gymnocolea inflata	Gym inf	-1,05	-1,15	0,0	2	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Lophozia heterophylla	Lop het			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Mylia anaomala	Myl ano	-0,79	0,29	0,0	2	0,0	2	0,1	1	0,0	1	0,0	1	0,0	1	0,0	1	0,0	0
Ochrolecia androgyna	Ochrolec			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Placiothecium laetum	Pla lae	0,81	0,33	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Pleurozium schreberi	Ple sch	0,46	0,75	6,8	3	0,0	2	0,0	4	0,1	4	1,5	7	34,0	9	26,2	9	24,6	9
Pohlia nutans	Poh nut	0,35	-0,23	0,0	3	0,0	2	0,0	4	0,0	0	0,0	3	0,0	4	0,0	2	0,0	5
Pogonatum urnigerum	Pog urn	0,28	-2,05	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Polytrichastrum longisetum	Pol lon	0,78	-0,97	0,0	0	0,0	0	0,0	0	0,0	0	0,7	5	0,0	0	0,0	0	0,0	0
Polytrichum commune	Pol com	0,30	-0,51	2,0	4	0,6	4	2,3	2	0,1	1	3,7	8	0,1	1	0,0	1	0,0	1
Polytrichum strictum	Pol str	0,00	0,05	1,2	7	0,4	8	0,4	9	0,6	8	2,3	9	1,7	9	1,0	9	1,2	8
Ptilidium pulcherrimum	Pti pul			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Ptilidium ciliare	Pti cil			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum angustifolium	Sph ang	-0,28	0,08	65,7	9	61,5	10	66,3	10	77,8	10	8,8	9	14,7	9	30,7	9	44,4	9
Sphagnum annulatum	Sph ann			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum balticum	Sph bal	-1,23	-1,10	0,0	2	0,1	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Sphagnum capillifolium	Sph cap	0,10	-0,10	0,0	1	0,1	0	0,0	0	0,0	0	0,1	3	0,0	0	0,0	0	0,0	2
Sphagnum cuspidatum	Sph cus	0,78	-1,28	0,0	0	0,0	0	0,0	0	0,0	0	0,2	2	0,0	0	0,0	0	0,0	0
Sphagnum fallax	Sph fal	0,14	-1,03	0,4	9	10,2	9	7,5	9	8,9	7	13,8	8	0,0	0	0,0	0	0,0	0
Sphagnum fimbriatum	Sph fim			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum fuscum	Sph fus	-0,46	0,36	7,3	5	6,5	4	5,8	5	5,0	6	0,6	4	0,1	3	1,7	4	2,0	7
Sphagnum lindbergii	Sph lin	-2,22	-0,89	0,0	1	0,4	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum magellanicum	Sph mag	-0,22	-0,06	5,7	10	8,9	10	9,2	10	5,3	10	5,6	9	4,9	7	4,7	8	2,3	9
Sphagnum majus	Sph maj	-0,07	1,06	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum papillosum	Sph pap	-1,23	-0,96	0,0	3	8,7	2	5,7	0	0,0	0	2,7	1	0,0	0	0,0	0	0,0	0
Sphagnum pulchrum	Sph pul	-2,23	-0,79	0,0	1	0,5	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum riparium	Sph rip	0,53	-1,21	0,0	0	0,0	1	1,1	1	0,0	0	5,7	6	0,0	0	0,0	0	0,0	0
Sphagnum rubellum	Sph rub			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum russowii	Sph rus	0,43	0,31	3,8	3	0,0	1	0,0	7	0,2	2	3,2	7	0,1	5	0,6	6	0,7	4
Sphagnum squarrosum	Sph squ	0,98	-0,74	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum tenellum	Sph ten	-2,22	-0,91	0,0	1	0,1	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Straminergon stramineum	Str str	0,40	-1,34	0,0	3	0,0	6	0,0	5	0,0	2	0,0	2	0,0	0	0,0	0	0,0	0
Tetraphis pellucida	Tet pel	0,37	0,96	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1
Trapeliopsis granulosa	Trapelio			0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Warnstorfia fluitans	War flu	0,86	-1,11	0,0	1	0,0	0	0,0	0	0,0	1	0,0	1	0,0	0	0,0	0	0,0	0

	Restored 5 y ago								Restored 10 y ago							
	0 m		5 m		10 m		15 m		0 m		5 m		10 m		15 m	
Species	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency	Mean cover	Frequency
Andromeda polifolia	0,0	1	0,0	6	0,1	6	0,2	7	0,0	3	0,5	7	0,7	10	0,7	8
Betula nana	0,2	2	1,2	7	2,0	9	1,8	9	0,3	4	5,6	9	6,3	10	5,7	10
Betula pendula	0,1	2	0,3	1	0,0	0	0,0	0	0,8	2	1,9	2	1,4	2	0,8	1
Betula pubescens	5,5	9	5,8	6	3,4	5	1,5	6	2,0	4	3,8	5	0,8	3	1,7	5
Calamagrostis purpurea	0,0	1	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Calluna vulgaris	0,0	1	0,4	4	0,8	3	0,4	4	0,0	1	0,2	2	0,0	0	0,4	1
Carex canescens	1,7	7	0,0	1	0,0	1	0,0	0	0,3	6	0,0	0	0,0	0	0,0	0
Carex chordorrhiza	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1
Carex echinata	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Carex globularis	0,0	3	0,2	2	0,2	3	0,3	3	0,0	0	0,1	2	0,1	1	0,1	2
Carex lasiocarpa	0,1	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,2	1	0,0	2
Carex limosa	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Carex magellanica	1,2	6	0,1	4	0,0	0	0,0	0	0,1	2	0,0	1	0,0	1	0,0	0
Carex nigra	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Carex pauciflora	0,0	0	0,0	1	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	1
Carex rostrata	3,4	3	0,1	1	0,1	1	0,0	0	16,5	7	0,9	5	0,0	1	0,0	1
Chamaedaphne calyculata	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,1	1	0,0	0
Dactylorhiza maculata	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	1	0,0	1
Deschampsia flexuosa	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0
Drosera rotundifolia	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dryopteris carthusiana	0,2	4	0,0	0	0,0	1	0,0	1	0,0	1	0,0	1	0,0	0	0,1	1
Empetrum nigrum	0,0	2	0,8	8	1,2	9	2,1	9	0,0	0	2,0	10	1,9	10	2,4	10
Epilobium angustifolium	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Eriophorum vaginatum	22,3	9	8,6	9	4,2	9	4,0	9	16,3	10	9,4	10	8,3	10	7,2	10
Equisetum sylvaticum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Juncus filiformis	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Ledum palustre	0,0	1	2,9	6	2,2	8	2,1	6	0,0	1	1,1	2	0,2	2	0,2	1
Melampyrum pratense	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0
Menyanthes trifoliata	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,1	1
Picea abies	0,0	0	0,7	3	0,6	5	0,1	2	0,0	1	0,2	3	0,6	3	0,6	4
Pinus sylvestris	0,1	7	0,0	5	0,1	5	0,2	5	0,1	2	0,2	8	0,7	8	0,9	9
Rhyncospora alba	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	1
Rubus chamaemorus	0,9	3	3,1	8	5,8	8	6,4	8	0,5	3	4,8	7	5,6	8	6,8	10
Salix aurita	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Salix phylicifolia	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Scheuchzeria palustris	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Trientalis europaea	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Trichophorum cespitosum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Vaccinium microcarpum	0,0	0	0,0	0	0,0	3	0,0	1	0,0	0	0,0	4	0,0	3	0,0	3
Vaccinium myrtillus	0,1	6	2,1	7	3,0	6	1,5	5	0,0	0	0,2	3	0,1	4	0,1	2
Vaccinium oxycoccos	0,0	6	0,5	7	0,8	8	0,8	7	0,4	9	2,5	10	1,9	10	1,9	9
Vaccinium uliginosum	0,1	3	3,5	9	5,0	9	5,2	9	0,1	1	3,2	7	2,6	8	2,5	5
Vaccinium vitis-idaea	0,0	2	2,7	6	2,6	7	2,2	7	0,0	0	1,0	4	1,2	5	3,3	5
Atrychium tenellum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Aulacomnium palustris	0,0	4	0,7	9	0,9	8	0,6	9	0,2	4	0,6	10	1,2	10	0,3	10
Brachythecium reflexum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Brachythecium starkei	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Brachythecium spp.	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0
Callliergon cordifolium	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Calypogeia integristipula	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Calypogeia sphagnicola	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Calypogeia spp.	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Cephalozia bicuspidata	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Cephalozia connivens	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Cephalozia spp.	0,0	1	0,0	1	0,0	1	0,0	0	0,0	0	0,0	2	0,0	0	0,0	0
Cladina spp.	0,0	0	0,1	3	0,0	1	0,0	0	0,0	0	0,0	0	0,1	4	0,0	0
Cladonia spp.	0,0	1	0,0	2	0,0	0	0,0	2	0,0	1	0,0	0	0,1	4	0,0	0
Cladopodiella fluitans	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranella cerviculata	0,9	2	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranum bergeri (D. undulatum)	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranum fragillifolium	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0
Dicranum fuscescens	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Dicranum majus	0,0	0	0,0	1	0,0	0	0,0	0	0,0	1	0,0	2	0,0	3	0,0	0
Dicranum polysetum	0,0	1	0,2	6	0,4	7	0,6	6	0,0	2	0,2	5	0,1	3	0,1	4
Dicranum scoparium	0,0	0	0,0	1	0,0	0	0,0	1	0,0	1	0,0	4	0,0	2	0,0	0
Ditrichium pusillum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Gymnocolea inflata	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Lophozia heterophylla	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0
Mylia anaomala	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Ochrolecia androgyna	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0
Placiothecium laetum	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0
Pleurozium schreberi	0,5	7	15,3	9	13,4	9	20,0	9	0,6	6	12,6	9	11,7	9	10,7	9
Pohlia nutans	0,1	6	0,0	4	0,0	3	0,0	2	0,0	8	0,0	7	0,0	3	0,0	4
Pogonatum urnigerum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Polytrichastrum longisetum	0,4	6	0,0	3	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Polytrichum commune	3,2	8	1,5	6	0,8	2	0,6	2	1,2	6	2,6	4	0,6	5	1,6	5
Polytrichum strictum	1,8	6	0,9	8	1,0	7	0,7	9	0,6	7	0,5	9	1,3	9	1,1	10
Ptilidium pulcherrimum	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Ptilidium ciliare	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Sphagnum angustifolium	4,2	8	28,3	9	37,9	9	39,7	9	13,7	10	44,6	10	61,3	10	64,2	10
Sphagnum annulatum	0,0	0	0,0	0	0,0	0	0,0	0	0,4	1	0,0	0	0,0	0	0,0	0
Sphagnum balticum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum capillifolium	0,0	2	0,0	1	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,1	1
Sphagnum cuspidatum	1,2	3	0,1	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum fallax	22,4	9	2,3	4	0,3	1	0,4	1	34,4	10	5,1	8	1,8	3	0,2	5
Sphagnum fimbriatum	0,0	0	0,0	0	0,0	0	0,0	0	0,1	1	0,0	0	0,0	0	0,0	0
Sphagnum fuscum	0,0	0	0,6	1	1,1	1	1,3	4	0,2	3	0,5	3	2,0	4	0,9	6
Sphagnum lindbergii	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum magellanicum	0,7	8	7,6	7	7,2	7	10,0	7	2,7	7	7,7	10	7,0	10	10,0	10
Sphagnum majus	2,3	4	0,0	0	0,0	0	0,0	0	0,0	1	0,0	1	0,0	1	0,0	0
Sphagnum papillosum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum pulchrum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Sphagnum riparium	1,1	3	0,0	2	0,0	0	0,0	0	12,7	5	0,2	3	0,0	0	0,0	0
Sphagnum rubellum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0
Sphagnum russowii	1,4	4	3,5	6	6,2	7	7,4	4	0,6	5	0,8	5	0,6	6	2,3	5
Sphagnum squarrosum	2,0	4	0,0	0	0,0	0	0,0	0	0,0	1	0,0	1	0,0	0	0,0	0
Sphagnum tenellum	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Straminergon stramineum	0,0	4	0,0	0	0,0	0	0,0	0	0,1	5	0,0	1	0,0	1	0,0	1
Tetraphis pellucida	0,0	0	0,0	1	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0
Trapeliopsis granulosa	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,0	0
Warnstorfia fluitans	0,1	2	0,0	0	0,0	0	0,0	0	0,0	3	0,0	3	0,0	0	0,0	0

IV

FIGHTING CARBON LOSS OF DEGRADED PEATLANDS BY JUMP-STARTING ECOSYSTEM FUNCTIONING WITH ECOLOGICAL RESTORATION

by

Santtu Kareksela, Tuomas Haapalehto, Riikka Juutinen, Rose Matilainen, Teemu Tahvanainen & Janne S. Kotiaho 2014

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Fighting carbon loss of degraded peatlands by jump-starting ecosystem functioning with ecological restoration

Santtu Kareksela[1*], Tuomas Haapalehto[1,2*], Riikka Juutinen[1,3] Rose Matilainen[4],
Teemu Tahvanainen[5] & Janne S. Kotiaho[1,6]

[1] University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland.

[2] Metsähallitus, Natural Heritage Services, P.O. Box 36, 40101 Jyväskylä, Finland

[3]Current address: Metsähallitus, Natural Heritage Services, P.O. Box 8016, 96101 Rovaniemi, Finland

[4] University of Jyväskylä, Department of Chemistry, P.O. Box 35, 40014 University of Jyväskylä, Finland.

[5]University of Eastern Finland, Department of Biology, P.O.Box 111, 80101 Joensuu, Finland.

[6] Natural History Museum, P.O. Box 35, 40014 University of Jyväskylä, Finland.

* Shared first authorship.

Corresponding author: E-mail santtu.kareksela@jyu.fi; Tel +358 40 835 2084; Fax +358 (0)14 617 239

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Abstract

Degradation of ecosystems is one of the greatest concerns on the maintenance of biodiversity and ecosystem services. Ecological restoration fights degradation aiming at the recovery of ecosystem functions such as carbon (C) sequestration and ecosystem structures like plant communities responsible for the C sequestration function. We selected 38 pristine, drained and restored boreal peatland sites in Finland and asked i) what is the long term effect of drainage on the surface peat C storage, ii) can restoration recover ecosystem functioning (surface peat growth) and structure (plant community composition) and iii) is the recovery of the original structure needed for the recovery of ecosystem functions? We found that drainage had resulted in a substantial net loss of C from surface peat of drained sites. Restoration was successful in regaining natural growth rate in the surface peat already within 5 years after restoration. However, the regenerated surface peat sequestered C at a rate of 116.3 g m^{-2} yr^{-1}, when a comparable short-term rate was 178.2 g m^{-2} yr^{-1} at the pristine sites. The plant community compositions of the restored sites were considerably dissimilar to those of pristine sites still 10 years after restoration. We conclude that ecological restoration can be used to jump-start some key peatland ecosystem functions even without the recovery of original ecosystem structure (plant community composition). However, the re-establishment other functions like C sequestration may require more profound recovery of conditions and ecosystem structure. We discuss the potential economic value of restored peatland ecosystems from the perspective of their C sequestration function.

Introduction

We are living an era of ecosystem manipulation. The development of human population has influenced ecosystems almost everywhere around the Earth (Foley *et al.*, 2005; Millennium Ecosystem Assessment, 2005). Ecological restoration aims at the rehabilitation of ecosystem functions and structures, such as C sequestration and species communities, respectively, in order to respond to the threats of habitat and ecosystem level degradation (Vanha-Majamaa *et al.*, 2007; Dobson, 1997; Bradshaw, 1996). Results of restoration, like increase of biodiversity or revival of populations of individual species, are promising (e.g. Benayas *et al.*, 2009) and new targets for restoration of ecosystem functions and services (profitable and/or needed ecosystem functions) are being developed (Aerts & Honnay, 2011; Bullock *et al.*, 2011; Suding, 2011; Benayas *et al.*, 2009; Hobbs & Cramer, 2008). Still, it seems unlikely that restored ecosystems will ever be exactly similar to their pristine targets and there are serious doubts concerning the recovery of ecosystem functions after restoration (Benayas *et al.*, 2009; Zedler & Kercher, 2005). The recovery of ecosystem functions is generally thought to depend on the recovery of original structures, but the relationship of ecosystems' functions and structure is still far from well understood (Cardinale, 2012; Cortina *et al.*, 2006; Bradshaw, 1996).

Current ecological restoration frameworks face two major questions: i) can we return vital ecosystem functions and structures that are partially or totally lost and ii) if we can, is it economically feasible? The answer to the first question is dependent on the degree of ecosystem complexity and on our understanding of ecologically effective restoration practices (Pocock *et al.*, 2012; Cortina *et al.*, 2006). The second question is related to the complexity and thus cost of restoration actions needed, the opportunity costs (i.e. the value of current land use if not restored) and possible economic gains of restoration outcome. Increased ecosystem services, like societal benefits of C sequestration (Russi *et al.*, 2013; Kettunen *et al.*, 2012; Alexander & McInnes, 2012; Nelson *et al.*, 2009), is one example of possible economic gain. Being able to answer these questions is increasingly important because recently a global target was set to fight climate change and biodiversity loss by restoration of 15 % of degraded ecosystems by 2020 (Convention on Biological Diversity, 2010). Restoration is also increasingly being called upon to compensate for the biodiversity values lost in development projects by restoring degraded sites elsewhere (Maron *et al.*, 2012). Cost effective and rather straightforward restoration methods are most likely needed to reach such demanding targets (Perrings *et al.*, 2010).

Increasing attention is paid to the ability of ecosystems to absorb CO_2 and store C (Davidson & Janssens, 2006; Feng, 2005). Compared to other ecosystems, peatlands are the largest reserves of organic C in the soil (e.g. Page *et al.*, 2011; Zedler & Kercher, 2005; Page *et al.*, 2002; Gorham, 1991): boreal and subarctic peatlands alone comprise *circa* 30 % of the global soil C pool (547 Pg C) (Yu, 2011). In natural peatlands, C sequestration results from the deposition of plant biomass to form raw humus in the acrotelm (oxic surface peat layer) and its subsequent transition to long-term storage in the catotelm (anoxic stratum below water level fluctuation range) (e.g. Clymo 1984). However, wide-scale degradation caused by land-use threatens the C pool of peatlands on a global scale (Moore *et al.*, 2013; Pitkänen *et al.*, 2013; Simola *et al.*, 2012; Hooijer *et al.*, 2010; Minkkinen *et al.*, 2008; Oleszczuk *et al.*, 2008). For example, *ca*. 15 000 000 hectares of peatlands have been drained for forestry in the boreal region alone (Minkkinen *et al.*, 2008), possibly causing emissions of C to the atmosphere especially due to increased aerobic decomposition (Hooijer *et al.*, 2010; Silvola *et al.*, 1996). There are contradictory results on effects of drainage to peat C storage, however. Indeed, both negative and positive C balances are reported in drained boreal peatlands (Pitkänen *et al.*, 2013 Simola *et al.*, 2012; Lohila *et al.*, 2011; Ojanen *et al.*, 2010, 2012, 2013; Minkkinen *et al.*, 2008; Minkkinen & Laine, 1998). A part of the controversy may be due to different time scales; many studies have measured current C balance (e.g. Lohila *et al.*, 2011) while others have estimated total changes in C storage (e.g. Simola *et al.*, 2012) during longer drainage periods. In addition, variation between different peatlands can be large (e.g. Ojanen *et al.*, 2012), while the number of independent study sites is often small.

As a response to the overall degradation of peatlands, and potential effects on global C balance, a globally increasing trend towards peatland restoration has arisen (European Commission, 2011; Parish *et al.*, 2008; Erwin, 2009; Ramchunder *et al.*, 2009; Thiele *et al.*, 2009; Worrall, 2009). In general, restoration actions have hierarchical aims. Re-establishment of natural water table level is expected to restore abiotic conditions needed to restart succession towards original species communities (Gorham & Rochefort, 2003). The regained high water table level and development of typical peatland vegetation is expected to result in the re-establishment of the natural acrotelm-catotelm stratification of peat and restart the original ecosystem function of C sequestration. Despite the recognized and increasing importance of peatland restoration the efficiency of the current methods in re-establishing the C sequestration function has not been studied much and research is concentrated mainly on peat mining areas (e.g. Strack & Zuback, 2013; Moreno-Mateos *et al.*, 2012; Soini *et al.*, 2010; Waddington *et al.*, 2010; Cagampan & Waddington, 2008) that globally cover only a minor fraction of degraded peatlands (Strack *et al.*, 2008). In general, the recovery of biological structure has been found to precede the recovery of ecosystem functions in restored wetland ecosystems (Moreno-Mateos *et al.*, 2012). Still, the relationship between the recovery of vegetation and C sequestration in boreal peatland ecosystems remains unexplored.

In this study, we address three questions related to degradation and restoration of C sequestration function of boreal peatlands. First, what is the long term effect of drainage on surface peat C storage? Second, are restored peatlands recovering the targeted pristine ecosystem function and structure? And third, is the recovery of the structure needed for the recovery of ecosystem function? To answer our questions, we examined the recovery of the surface peat, i.e. the peat forming acrotelm layer including the living plant biomass, where the C fixation, most of the decomposition of organic C, and transition of biomass to anaerobic storage layer catotelm take place (Gunnarsson *et al.*, 2008; Francez & Vasander, 1995; Clymo, 1984). We first quantify the change of surface peat C storage due to drainage by using the C to ash and C to Al ratios of surface peat in pristine peatlands to determine the expected C mass for the surface peat of drained peatlands. Then, to determine whether ecosystems regain their original peat growth function after restoration, we compare the peat growth rate between pristine, drained and restored peatlands using data of age and rooting depth of pine seedlings. We also determine the recent apparent rate of C accumulation (RERCA) in surface peat of restored sites and compare it to the RERCA of pristine sites. To determine the recovery of the ecosystem structure, we compare the similarity of plant community composition between pristine, drained and restored peatlands. Finally, we discuss the question if recovery of the original ecosystem structures is needed for the ecosystem functions to recover.

Materials and methods

Study sites

For the study we selected 38 sites on previously unstudied *Sphagnum* peatlands in southern Finland, Europe. The average annual precipitation of the region is 675 mm and the annual mean temperature is +3.4ºC. We selected the sites so that they fell into one of four categories (treatments): i) drained peatlands (n = 9), ii) previously drained and restored 3-7 years before the study (hereafter restored 5 years ago, n = 9), iii) previously drained and restored 9-12 years before the study (hereafter restored 10 years ago, n = 10) and iv) pristine peatlands (n = 10) (see example pictures of the categories in Supporting information: Appendix 1). Distances between the study sites ranged from 200 m to 150 km. The study sites were independent from one other in their surface water flow (based on topographic data and field observations). Based on close examination of old and new aerial photographs accompanied with field observations, the original vegetation types and tree stands of the disturbed sites were roughly similar to those of the chosen pristine control sites. All of the disturbed sites were drained for forestry by the state *ca*. 40 years before the study with ditch interval of 30-50 meters. Tree growth (mainly *Pinus sylvestris* and *Betula pubescens*) had variably increased after the drainage. In 1980s some of the sites were designated to conservation with a subsequent decision to restore the drained sites within the conservation areas. Information on restoration year was available from the habitat database of the state owned land. Restoration measures included filling in the ditches with peat excavated near the ditches, construction of peat dams and removal of trees in cases where drainage had significantly increased tree growth. The amount of trees removed varied slightly so that all the restored sites had more or less the same tree cover in the end, mimicking the pre-disturbance tree cover determined from aerial photographs. The restoration measures may be considered rough and straightforward in the sense that they relied on natural re-establishment of populations of the target species from nearby relict sources. This means that the often laborious and costly transplantations of species or fine scale habitat engineering (e.g. for individual target species) were not applied. Restoration of the sites was conducted by Natural Heritage Services of Metsähallitus (governmental institution responsible for management of conservation areas).

At the pristine sites, vegetation was dominated by common peatland plants typical of oligotrophic lawn-level peatland (peatlands dominated by the intermediate surface between drier hummocks and the wettest level) vegetation, such as *Eriophorum vaginatum*, tall sedges (e.g. *Carex rostrata*) and *Sphagnum* mosses (*Sphagnum angustifolium*, *Sphagnum fallax* and *Sphagnum fuscum*). At the drained sites, common forest plants, such as the dwarf shrubs *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Rhododendron tomentosum* and *Betula nana* dominated the field layer, *Pleurozium schreberi* along with *Sphagnum* mosses (*Sphagnum angustifolium*, *Sphagnum magellanicum* and *Sphagnum russowii*) being the most common species in the ground layer.

Sampling of surface peat and vegetation

The sampling was conducted using a systematic design of 15 1-m^2 vegetation plots in a 10 × 20 meter area at each site. The sampling plots were placed in three transects running parallel to the ditch line 5, 10 and 15 meters from the ditch. The plots were located at 4 meter intervals along each transect forming a grid (Fig. 1). The location of the grid was randomized within the area of the focal habitat type at each site.

We focused our peat sampling on the uppermost 20-25 cm surface peat layer (hereafter simply surface peat) that cover the main range of water table level fluctuation in natural sites and most of the surface layer exposed to increased aeration in drained sites. Six cores of surface peat were collected with a side-cutting box sampler (sampler area: 8.3 × 8.4 cm) at each site. Samples were collected close to the vegetation plots, at the 5, 10 and 15 m distances from the nearest ditch in drained and restored sites (three samples at each distance). Samples were divided into two segments (0-10 cm and 10-20 cm layers from the surface) in the field, sealed into plastic bags and stored frozen prior to analyses. The force needed to employ the box sampler typically causes compaction of surface peat samples and avoiding this requires careful operation in the field

(Pitkänen *et al.* 2011). In addition, we carefully examined the peat samples in the laboratory and adjusted for the compaction by measuring the sample dimensions after reconstructing the erect posture of the *Sphagnum* mosses, whenever an evident compaction was observed. The corrected average depths of the pristine and drained 0-10 cm samples were 14.2 cm (+-2.1 SD) and 10.7 cm (+-1.0 SD), respectively.

Vegetation was sampled at the 15 1-m^2 vegetation plots at each site (Fig. 1). From each plot we recorded relative abundance as a % cover for all plant species based on visual estimation.

Carbon loss

To answer our first question about the effect of drainage on the amount of C in the surface peat, we estimated the C loss from the 0-20 cm peat samples during the approximately 40-year drainage period relative to the pristine sites. Decomposition leads to the loss of C, increase of bulk density and enrichment of ash content of peat. We calculated the expected mass of C for the surface peat samples of drained peatlands by multiplying their observed ash content with the average C to ash ratio obtained from the pristine peatlands (see Appendix 2 for detailed description of the chemical analyses). The loss of C (ΔC_{ASH}) for each sample was then estimated as the difference between the expected and the observed mass of C of the samples from the drained sites (Leifeld *et al.*, 2011; Grønlund *et al.*, 2008). The estimated C loss per m^2 for each drained site was then calculated by multiplying the average C loss of each sample with 1/sampler area (m^2) (see Appendix 3). However, drainage may result in increased leaching of mineral cations (e.g. Prevost *et al.*, 1999; Pitkänen *et al.*, 2013), thus reducing the mass of ash. This causes a potential bias in ΔC_{ASH} estimates towards underestimation of C loss as the decrease of mineral concentration results in higher C to ash ratio. Among the main cations, Al^{3+} is retained relatively strongly at cation exchange sites (Wieder *et al.*, 1988) due to its trivalent charge and high charge to size ratio, i.e. ionic potential. Therefore, we modified the method by using aluminum concentration in place of total ash to yield ΔC_{AL}. Our modification revealed considerably higher estimates of C loss than ΔC_{ASH} (see results). For comparison, we also calculated ΔC estimates using other elements (Appendix 3). These calculations indicated the lowest ΔC in relation to readily leaching cations (Mn < Mg < Fe < Ca) and intermediate ΔC in relation to main nutrients (K < N < P) that are effectively retained by living organisms in the surface peat. The residual ash concentration (total ash – known mineral elements) most likely represented mainly silica (Si) and it indicated the highest ΔC. However, we did not use residual-ash in our estimate of C loss because of the uncertainty of its exact mineral constituents.

Surface peat growth rate

To study the surface peat growth rate we constructed empirical age-depth models of the surface peat layers of the study sites by the pine method (e.g. Ohlson & Dahlberg, 1991; Borggreve, 1889) and estimated the annual growth rate of the surface peat for each site. For this we collected 25-35 small (< 1.5 m) Scotch pines at each study site at the 10 x 20 meters sampling area. In cases where there were not enough pines in the actual sampling area, we extended the collection to similar area in the immediate vicinity. At each site, half of the pines were collected from hummocks and another half from lower-lying surfaces. At one 5 years ago restored site no pines were found and the site was excluded from this analysis. We determined the vertical distance from the root collar (root to shoot transition) of the trees to the peat surface to estimate rooting depth of each pine. The ages of pines were determined by counting the annual rings close to the root collar under a stereomicroscope. We then calculated the apparent annual vertical growth of surface peat as a linear regression coefficient between the rooting depth and age of the pines for each site and used analysis of variance (ANOVA, IBM SPSS Statistics 20) and appropriate post-hoc test to compare the coefficients between the treatments. We limited the age-depth data to the first 10 years, where the age-depth curve was close to linear. For further linearization, the data were first log transformed and regression curves were forced to pass through the origin, i.e. zero peat depth corresponded to zero age.

Recent apparent rate of carbon accumulation in surface peat

We determined the recent apparent rate of carbon accumulation (RERCA) in surface peat after restoration and for comparable period for the pristine sites. By definition, RERCA only includes C bound in peat above a dated horizon and it is the net result of biomass production and decomposition (g C m^{-2} yr^{-1}). Since decomposition continues with material of all ages, the accumulation rate will be the lower the older the material is and thus the accumulation pattern of C is nonlinear with time. However, within the 3-12 year time-scale of our study, we observed that the age-depth pattern and C accumulation was still nearly linear. Since the post-restoration time period varied among the sites in the 5 and 10 years ago restored categories, we used here linear regression to model the cumulative C mass with time (years since restoration) and interpreted the slope as RERCA, i.e. increase of C store with one year increase of age (g m^{-2} yr^{-1}). The post-restoration peat was separated from the older layer that represented the drainage period in the laboratory. The separation was based on visual inspection: there was typically a clear difference in the degree of humification and typical presence of bark and needles of trees and remains of species typical to drained peatland forests such as *Pleurozium schreberi* and *Vaccinium myrtillus*. Additionally, the post restoration peat layer was verified in all sites and with most of the individual cores by dating with annual increments of *Polytrichum* *strictum* and *Eriophorum vaginatum*, and in few cases *Trichophorum cespitosum* (data not shown). The post-restoration surface peat samples were dried to constant weight at 70 °C for the determination of dry weight. The mass of C in each sample was calculated by multiplying dry mass with the measured C concentration. The linear regression was forced through origo (i.e. zero peat depth corresponded to zero age) and the slope was tested against the expected slope (Extra sum-of-squares F test, GraphPad Prism 5 for Windows), i.e. the average 10-year RERCA of pristine sites, which was calculated according to the depth of 10-year old strata based on the pine method (see above).

Plant community composition

To study changes in vegetation, which is an essential element of ecosystem structure and vital for the recovery of the C sequestration function, we compared the similarity of the composition of the plant communities between drained, 5 and 10 years ago restored and pristine sites. For each of the 38 study sites we compiled plant community samples by calculating average relative abundances for each plant species over the 15 1-m^2 vegetation sampling plots. We used average values for each site, because we wanted to assess general patterns of vegetation with respect to surface peat growth rate and C sequestration. Both the identities and the abundances of the species were apparently affected by drainage as well as restoration. Therefore, we used Bray-Curtis community similarity measure considering both species identities and relative abundances (e.g. Magurran, 2004). Effect of treatment on plant community composition was studied by comparing the Bray-Curtis community similarity of the study sites within and between the treatment groups with Non-Parametric MANOVA in PAST 2.17b (PERMANOVA, Anderson 2001; McArdle & Anderson, 2001). For visual inspection we performed NMS (Non-metric Multidimensional Scaling) ordination in PCORD 5, using again the Bray-Curtis similarity as the distance measure, random starting points, 250 runs with the real data and 500 iterations for the final result. For the main purpose and comparisons of the current paper the vegetation analysis was kept simple, while a more detailed analysis of the plant community changes of these sites is under preparation.

Results

Carbon loss

The comparison of expected and observed C masses in surface peat of drained sites showed substantial loss of C due to drainage. The estimates for average C loss from the 0-20 cm surface peat samples were ΔC_{ASH} 5172 g m^{-2} (SE 2339 g m^{-2}) and ΔC_{AL} 6714 g m^{-2} (SE 2908 g m^{-2}). The focal peatlands were drained *ca.* 40 years prior to the study and thus the average per annum C loss (for the 40 years' drainage period) were 129.3 g m^{-2} (SE 58.5) and 167.8 g m^{-2} (SE 72.7) for ΔC_{ASH}

and ΔC_{AL} (Fig. 1) respectively. In CO_2 equivalents these estimates equal to 474.5 and 615.8 g CO_2e m^{-2} yr^{-1}. See Supporting information for derived ΔC estimates for the other elements (Appendix 3) and total mineral concentrations (Appendix 2).

Surface peat growth rate

According to the peat age-depth models peatlands in all treatments accumulated some peat (Appendix 4), but there was a significant difference in the net growth rate (mm yr^{-1}) of surface peat among the treatments (ANOVA $F_{3, 33} = 6.06$, $p = 0.002$). Growth rate at the drained sites was significantly retarded when compared to the pristine, 5 years ago and 10 years ago restored sites (LSD pairwise comparison, for all $p < 0.003$), while there were no differences between the pristine and the 5 years or 10 years ago restored sites (LSD pairwise comparison, $p > 0.760$ for both). Full untransformed age-depth data for all treatments is depicted in appendix 4.

Recent apparent rate of C accumulation in surface peat

We observed a roughly linear rate of C accumulation into surface peat of restored sites after restoration. According to the slope of the regression model the regenerated surface peat layer of restored sites accumulated C with an average rate of 116.3 g m^{-2} yr^{-1} for the 3-12 years period (SE 12.7). In comparison, the RERCA for 10 years period for pristine sites was 178.2 g m^{-2} yr^{-1} (SE 13.3). The difference of the slope was statistically significant against the null-hypothesis of no deviance from the pristine RERCA ($F = 23.73$, $P < 0.001$), but the variation of the accumulation rate at the restored sites was large, and some of the restored sites had even higher post-restoration surface peat C accumulation than predicted by the pristine reference estimate (Fig. 2).

Plant community composition

The ecosystem structure measured as plant community composition was significantly different between the treatments (PERMANOVA $F = 4.719$, $p < 0.001$). Most substantial differences were between pristine sites and all the other sites i.e. drained, 5 years ago restored, and 10 years ago restored sites (pairwise comparisons of pristine to all others, for all $p < 0.006$). There was no difference in the community composition between drained and 5 years ago restored sites (pairwise comparison $p = 0.231$) but the sites restored 10 years ago already showed dissimilarity to the drained sites (pairwise comparisons $p = 0.024$). By visual inspection, the effect of the treatment can be seen on Axis 2 of the ordination (Fig. 3).

Discussion

Our analyses indicate that drainage-induced degradation of the peatland ecosystems results in significant net loss of carbon from surface peat when compared to the undisturbed state of the ecosystem. However, we also learned that the straightforward restoration by filling ditches can jump-start the ecosystem function of surface peat growth, which is an essential step towards re-establishing the long term carbon storage function of peatland ecosystems: already within few years after restoration the surface peat growth rates had recovered on average close to the level of pristine peatlands. Furthermore, the rate was essentially maintained over the post-restoration time span covered by our data. Elsewhere, the recovery of ecosystem structure has been suggested as a prerequisite to the recovery of ecosystem functions in wetlands (Moreno-Mateos *et al.*, 2012). However, our analysis suggests that the employed restoration methods were successful in returning the surface peat growth function although the original ecosystem structure (plant community composition) was not yet recovered. This suggests a relatively loose relationship between these structural and functional ecosystem components. On the other hand, C sequestration rate to the newly formed surface peat was lower than at the pristine sites suggesting that some functions of these peatlands may need more profound recovery of the original structure and conditions to reach the targeted level.

There are several earlier estimates on C balance of similar drained ecosystems as studied here, but there is still no consensus on whether drained boreal peatlands function as sinks or sources of C (e.g. Pitkänen *et al.*, 2013; Ojanen *et al.*, 2012, 2013; Simola *et al.*, 2012; Lohila *et al.*, 2011; Hooijer *et al.*, 2010; Ojanen *et al.*, 2010; Minkkinen *et al.*, 2008; Minkkinen & Laine, 1998; Silvola *et al.*, 1996,). Although environmental conditions undoubtedly add variance on drained peatlands' C balance (e.g. Ojanen *et al.*, 2010, 2012), it appears likely that the lack of consensus stems in part from differences in approach and methodology. Peat core analyses and gas exchange measurements focus on different temporal scales: the gas exchange measurements focus on the real-time gas exchange of the ecosystem, and thus measure only the contemporary fluxes of the disturbed ecosystem. Peat core analyses, on the other hand, cover the cumulative effects on C storage since the beginning of the disturbance (e.g. Simola *et al.*, 2012). We observed considerable loss of C from surface peat due to drainage, while some gas exchange studies have indicated only moderate C loss or in some cases even slightly positive net C balance at similar sites (e.g. Ojanen *et al.*, 2010, 2012, 2013; Lohila *et al.*, 2011; Minkkinen *et al.*, 2008). We suggest that when the aim is to understand the cumulative long term effects of disturbance on C storage of peatland ecosystems, the peat core analyses with undisturbed controls for calculating the net effects should be the preferred methodology. However, when the aim is to capture the current situation then gas exchange measurements can be preferable. In both cases, it is imperative to include also undisturbed reference sites into the study design to understand the net effects of degradation or restoration. Much of the extant literature has not done so, and thus it is difficult if not impossible to draw conclusions of the real net effects of the disturbances on global C balance. It should also be noted that our estimates derived from the surface peat layer only are not directly comparable to studies examining complete peat profiles. However, they are in line with recent studies that have observed reduced accumulation of biomass in the surface peat (Pitkänen *et al.* 2012) and a large net loss of C due to drainage from entire peat column (Pitkänen *et al.*, 2013, Simola *et al.*, 2012).

The reduced surface peat increment rate observed at the drained sites when compared to pristine sites is in line with a recent study, where a significant reduction in the biomass accumulation induced by increased decomposition was found in surface peat of forestry drained peatlands (Pitkänen *et al.*, 2012). The growth of the surface peat layer is a prerequisite for subsequent deposition of biomass to lower anaerobic peat layers and long-term C accumulation in peatlands. Therefore, the re-establishment of the surface peat accumulation rate to the targeted level only a few years after restoration suggests a surprisingly rapid recovery of an important peatland ecosystem function. On the other hand, a small difference was still observed between the C accumulation rates of restored and pristine sites (see also Tolonen & Turunen, 1996 for pristine RERCA over 35 years). C sequestration is a combination of growth and decomposition of vegetation, both affected by the hydrological conditions. Thus, the relatively small difference in the annual C sequestration rate between pristine and restored sites is probably partly due to a time-lag in the response of the plant community to new selection pressures set by the restoration actions. Indeed, relatively large annual variation in C sequestration is likely during the first years of post-restoration vegetation succession. This time period is characterized by initial reduction of forest vegetation and increasing domination of opportunistic rapidly growing early colonists like *Eriophorum vaginatum* followed by a state of *Sphagnum* mosses domination (e.g. Haapalehto *et al.*, 2011). On the other hand, if the conditions for slow decomposition are effectively restored, any vegetation that is able to endure the physical conditions, should contribute to the C sequestration and peat accumulation with some variation caused by differences in the specific traits of plant species (e.g. De Deyn *et al.*, 2008).

Our analysis of plant community composition suggests only limited recovery 10 years after restoration. Despite the communities still being distinct from the pristine communities, some post-restoration recovery was already taking place: the communities of the sites restored 10 years ago had evolved towards the pristine communities, while the communities of the sites restored 5 years ago were still indistinguishable from the drained communities. Our findings of partial recovery of plant community composition after peatland restoration are in line with earlier case-studies (Hedberg *et al.*, 2012; Haapalehto *et al.*, 2011). The dissimilarity in the plant community composition of pristine and restored sites is mainly due to some forest species still remaining in greater abundance than in pristine sites, ii) some pristine peatland species occurring in greater abundance than at pristine sites due to their ability to survive through the drainage period and to exploit the post restoration enhanced conditions, and iii) some pristine peatland species being absent from the restored sites due to local extinctions during drainage period and dispersal and/or re-establishment limitations (see e.g. Hedberg *et al.*, 2012; Haapalehto *et al.*, 2011). It should be noted, however, that the plant community dissimilarity occurring 10 years after restoration does not mean failure of restoration but only that it quite expectedly takes longer than 10 years for the structure of this ecosystem to fully recover (Hedberg *et al.*, 2012; Moreno-Mateos *et al.*, 2012; Jones & Schmitz, 2009).

Potential ecosystem level consequences of biodiversity loss are gaining increasing attention (Cardinale *et al.*, 2012; Hooper *et al.*, 2012; Reich *et al.*, 2012; Convention on Biological Diversity, 2010; Hector & Bachi, 2007). In ecological restoration the question is most tangible: how much of the original structure or community composition needs to be recovered in order to regain the original ecosystem functions (Cortina *et al.*, 2006; Bradshaw, 1984)? Plasticity in the relationship of biodiversity and ecosystem functioning is likely although not yet well understood (Cardinale *et al.*, 2012; Hooper *et al.*, 2012; Naeem *et al.*, 2012; Reich *et al.*, 2012). From the practical restoration perspective the magnitude of plasticity in this relationship is important to understand because it directly relates to the net costs of restoration actions. Indeed, it is likely that the stronger and more causative the relationship of ecosystem functions and certain community composition or biodiversity *per se*, the more complicated and costly are the actions needed to reach the ecosystem level restoration targets. Our results suggest considerable plasticity in the studied structure-function relationship of peatland ecosystems as a valuable ecosystem function of surface peat accumulation was recovered already with minor recovery of the original composition of the plant community (for restored cut-away peatlands and C accumulation see Soini *et al.*, 2010; Waddington *et al.*, 2010). It appears also that while this kind of a plastic ecosystem function could, indeed, be re-established with minor recovery of ecosystem structure, this did not result in similar recovery of C accumulation in surface peat layer. Not surprisingly, this suggests that evolution of the relationship between one ecosystem structural component (plant community composition) and two ecosystem functions may differ even between closely linked functions (peat growth rate and C accumulation rate). Nevertheless, there is still work to be done to fully understand the magnitude of the recovery of the original structure needed for the full recovery of ecosystem multifunctionality (McCarter & Price, 2013; Montoya *et al.* 2012; Lucchese et al., 2010; Hector & Bachi, 2007).

Being aware of recent large scale international targets for restoration (Aichi targets of Convention on Biological Diversity, 2010, Maron *et al.* 2012), it is interesting and necessary to consider also the economic value of restored ecosystems (Menz *et al.*, 2013; Bullock *et al.*, 2011). Estimating the economic value of C sequestration at restored peatlands is a relatively new idea (Russi *et al.*, 2013; Alexander & McInness, 2012; Kettunen *et al.*, 2012; Nelson *et al.*, 2009) and still far from straightforward (see e.g. Tanneberger & Wichtmann, 2012). Nevertheless, the results like ours including the calculation of C fixed by the studied peat layer can be used to evaluate the economic value related to the accumulated C in the recovering ecosystem. The average and the highest prices in the voluntary C market for comparable terrestrial C projects in 2010 were 6 and 136 USD per credit (t CO_2e (carbon dioxide equivalents)), respectively (Peters-Stanley, 2011; for future price assessments see also ten Brink *et al.*, 2011; European Commission, 2008). We estimated that on average 116.3 g C $m^{-2}yr^{-1}$ accumulated into the surface peat during the 3-12 years' post-restoration time period corresponding to 426.4 g $m^{-2}yr^{-1}$ of CO_2e. Although our estimates cover only the surface layer and a relatively short time span, we can estimate the market value for the C sequestered into the accumulated layer of surface peat. Thus, with the 2010 prices, the surface peat of the restored sites sequesters C at a rate corresponding to 26 – 580 USD ha^{-1} $year^{-1}$ for the 3-12 years' post-restoration time period (note that the accumulation of peat and input of C into long-term storage is not linear in time due to decomposition (e.g. Clymo, 1984)). These are not trivial numbers. For example, in Finland alone there are *ca*. 1 million hectares of peatlands drained for forestry where the drainage has not been economically profitable in terms of increasing the timber growth as intended. According to our results and the 2010 C market prizes, the market value of surface-peat C of 1 million hectares of restored boreal *Sphagnum* peatlands would amount between 26 to 580 million USD annually over the first decade after restoration.

While considering the potential market values offers impressive figures, it should be noted that these figures show only the potential of the economic value of these restored ecosystems as they are and the true market value or the net C accumulation effect of restoration action could only be estimated by comparing net ecosystem C balance before and after restoration (see e.g. Kimmel & Mander 2010). For example, with these data we cannot tell how restoration influences the lower peat layers. We find that long-term experiments e.g. on the changes in greenhouse gases (for restoration of cut-away peatlands see e.g. Strack & Zuback, 2013; Waddington & Day, 2007) and fluvial DOC fluxes (e.g. Moore *et al.*, 2013) as well as the development of tree stands (e.g. Ojanen *et al.*, 2013) are also needed to reliably estimate if peatland restoration may really produce tradable C-related ecosystem services. Our rough and unrealistic calculation above, hopefully, attracts scientific and societal interest to establish such studies.

Here we studied peatlands 3-12 years after restoration. This can be regarded as a relatively long time scale in ecosystem ecology studies (e.g. Reich *et al.*, 2012). However, from the perspective of peatland ecology it is only a moment considering that it has taken several millennia for the boreal peatlands to accumulate their remarkable C storages. With this in mind, achieving recovery of this function with such rough and straightforward ecological restoration methods already within a decade post restoration certainly serves as a jump-start for the ecosystem functioning. Although it may well take several decades before original species communities are achieved (if they ever will be) it is very promising that it is not an insurmountable task to restore the needed amount of the original community composition to restart at least some of the essential ecosystem functions.

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Figures

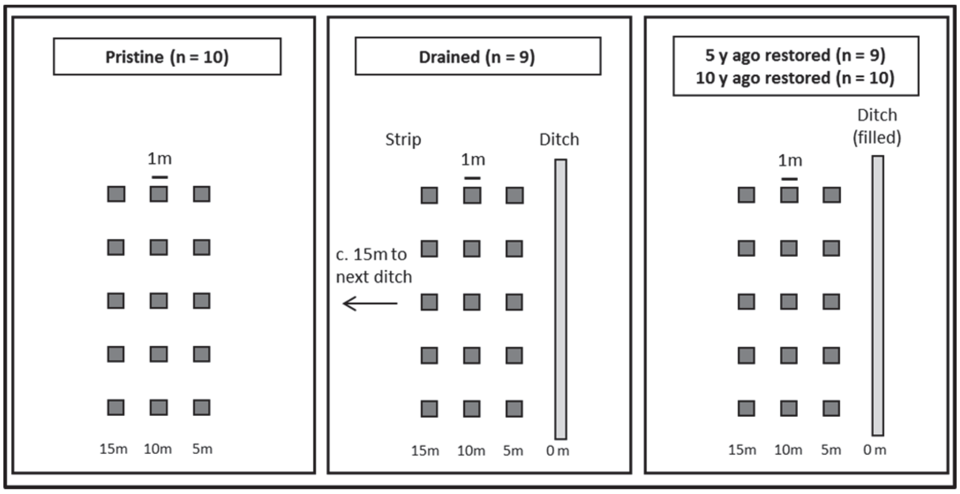

Fig. 1 Experimental set-up at pristine, drained and restored sites. Each grey square represents a 1-m^2 vegetation plot. At each site 2 peat core samples were taken at each distance to ditch (5, 10, and 15 m) close to the vegetation plots at both ends of each distance transect (i.e. altogether 6 peat core samples per site).

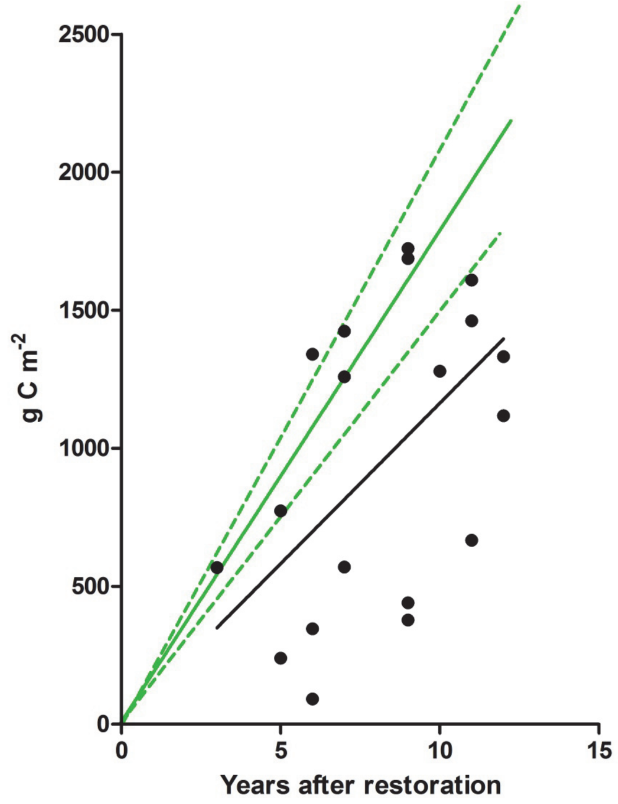

Fig. 2. The mass of C (g m^{-2}) in the surface peat accumulated after restoration with the site-specific post-restoration years (black circles). Black line depicts the linear regression (cumulative C mass over time since restoration) fitted to the restored site's data (y = 116.3x). The green linear line from origo goes through the 10-year recent apparent rate of C accumulation (RERCA) of pristine sites (y = 178.2x, hatched lines 95% CI).

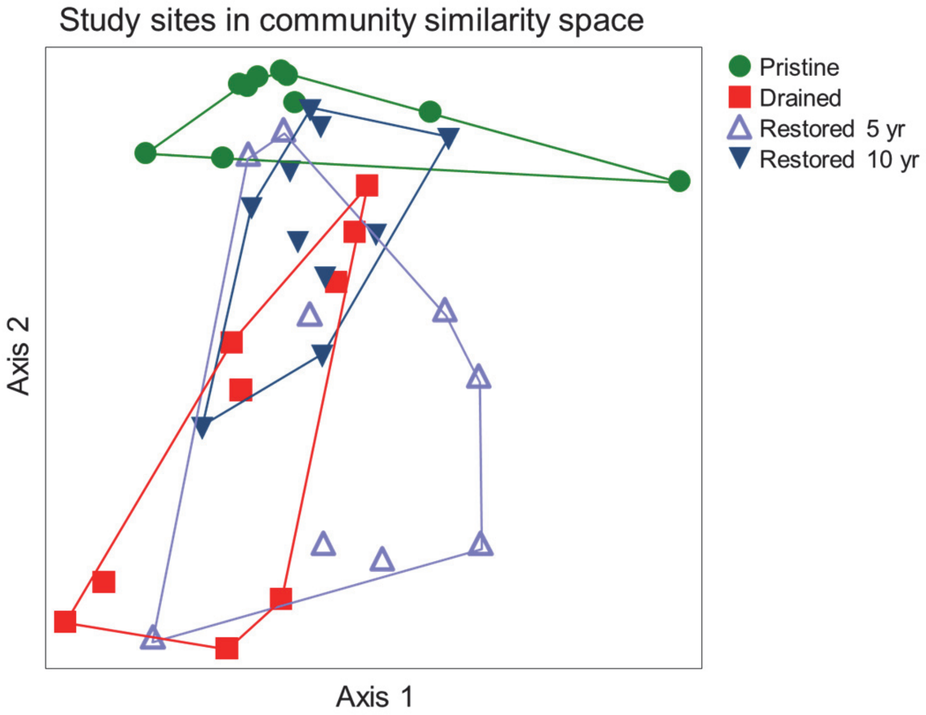

Fig. 3 Vegetation community similarity between the pristine (filled circles), drained (filled square), 5 years ago restored (hollow triangle) and 10 years ago restored (filled triangle) study sites presented in an ordination space (NMS ordination with Bray-Curtis distance measure, 2-dimensional solution, stress = 11.22). Most distinctive differences between treatments are shown on the Axis 2 where the distribution of drained and 5 years ago restored sites are nearly identical and 10 years ago restored sites show a trend of clustering closer to the pristine sites, which are strongly clustered on the upper part of the Axis 2.

Supporting information

Appendix 1. Example photographs of the study sites of different treatments.

Figure S1. Picture of the study sites with different treatments. Panels: a) pristine, b) drained, c) restored 5 years ago, and d) restored 10 years ago.

Appendix 2. Chemical analyses of the peat samples and mean element concentrations and proportions for surface peat samples for pristine and drained sites.

Experimental

Chemicals

Ultra pure water was obtained by passing distilled water through an ELGA Elgastat Maxima (Elga Ltd, UK) and it was shown to have a resistivity greater than 18,2 MΩ/cm. The 1000 mg L^{-1} ICP multi-element standard solution IV (CertiPur, Merck, Darmstad, Germany) was used for determination of Al, Ca, Fe, K, Mg and Mn. For the determination of phosphorous the 1000 mg L^{-1} of phosphorous stock solution was made by appropriate weighing of KH_2PO_4 (pro analysi) also supplied by Merck. Acetanilid (pro analysi, Merck) was used for performance check of CHN-analyzer. 65 % nitric acid (Sigma Aldrich, Steinheim, Germany) and 30 % hydrogen peroxide (Riedel-de Haën, Seelze, Germany) was used in digestion of samples.

Analysis of peat samples

About 60 g of peat samples were collected regularly from each layer of the peat clods and all foreign matter, such as sticks, roots and stones were removed and also soft lumps were crushed with spatula. The samples were dried at 105 °C for 18 h in a heating oven (Heraeus Thermo Scientific, Langenselbold, Germany). After the drying the samples were milled using Franz Morat A 70 (Eisenbach, Germany) milling apparatus. About 7 g of the milled sample was ashed in a programmable furnace (Naber Industrieofenbau, Lilienthal, Germany) at 400 °C for 1h and then at 550 °C for 4h. Both milled and ashed samples were sealed in plastic bags in exigator. Moisture content (%), ash content (%) and organic matter content (%) (100 – moisture-% - ash-%) of the peat samples were calculated.

About 200 mg of the ashed peat samples were digested in sealed Teflon vessels in a Milestone microwave oven (Milestone Ethos Touch, Sorisole, Italy) after addition of 4 ml HNO_3 (65%) and 1 ml H_2O_2 (30%). The digestion program consisted of two steps: room temperature to 205 °C in 10 min and then heating at 205 °C for 10 min. After the digestion samples were filtered through Whatman No. 42 filter paper (Maidstone, UK) and then made up to 50 ml with 2% (v/v) HNO_3. The sample solutions were transferred into plastic screw-top bottle for storage in a refrigerator.

The concentration measurements of the selected elements in peat samples were performed with a PerkinElmer (Norwalk, CT, USA) model Optima 4300 DV inductively coupled plasma optical emission spectrometer (ICP-OES). A Scot-type double-pass spray chamber and cross-flow nebulizer was used throughout.

The measurements were done using a nebulizer flow of 0.8 L min^{-1}, auxiliary gas flow of 0.2 L min^{-1}, plasma gas flow of 15 L min^{-1}, plasma power of 1300 W and sample flow of 1.5 L min^{-1}. The plasma was radially viewed. The concentrations of calibration standards for all the measured elements were 5, 15, 25, 35, 45 and 100 mg L^{-1} and they were made up with 2 % (v/v) HNO_3. The wavelengths used, linearity, limit of detection (LOD) and limit of quantification (LOQ) are shown in Table 1.

Table S1. The calibration parameters in ICP-OES measurements for each element analyzed.

Element	Wavelength (nm)	R^2	LOD (mg L^{-1})	LOQ (mg L^{-1})
Al	396.153	> 0.996	0.009	0.03
Ca	317.933	> 0.997	0.02	0.06
Fe	238.204	> 0.997	0.04	0.13
K	766.490	> 0.997	0.02	0.08
Mg	285.213	> 0.998	0.003	0.01
Mn	257.610	> 0.997	0.003	0.009
P	213.617	> 0.998	0.4	1.3

Carbon, hydrogen and nitrogen content of about 5 mg of dried and grinded peat samples were measured with a CHN analyzer (VARIO EL III Elementar Analysensystem, GmbH, Hanan, Germany).

Table S2. Mean element concentration (mg/g dry weight) and proportion (%) of N, C, H, and Ash for 0-10 cm and 10-20 cm surface peat samples for pristine and drained sites.

Pri		**Al**	**Ca**	**Fe**	**K**	**Mg**	**Mn**	**P**	**N**	**N (%)**	**C (%)**	**H (%)**	**Ash(%)**
0-10	Mean	0.378	2.934	1.871	1.590	0.843	0.159	0.470	6.671	0.667	46.987	5.905	2.764
	SD	0.197	1.237	1.200	0.430	0.255	0.059	0.118	1.305	0.130	0.375	0.044	0.806
10-20	Mean	0.716	3.026	2.256	0.294	0.694	0.031	0.423	9.442	0.944	47.591	5.892	3.292
	SD	0.319	1.429	1.113	0.086	0.272	0.024	0.051	2.565	0.256	0.417	0.097	0.993
Dra													
0-10	Mean	0.790	3.500	1.341	1.146	0.797	0.143	0.755	11.459	1.146	50.103	5.682	4.866
	SD	0.362	0.918	0.841	0.400	0.159	0.085	0.149	2.307	0.231	0.693	0.095	2.340
10-20	Mean	1.406	2.521	2.231	0.307	0.448	0.010	0.623	14.091	1.409	49.890	5.876	5.130
	SD	0.594	0.966	0.662	0.083	0.172	0.009	0.163	3.663	0.366	2.277	0.196	1.577

Appendix 3. Calculation of ΔC estimates and calculated ΔC estimates for surface peat with different minerals (or ash) as a comparison.

ΔC estimates (g m^{-2}) for surface peat (0-20 cm) of drained peatlands calculated as a difference between observed and expected carbon mass. The expected carbon mass is based on the observed mass of a mineral element in the drained peatland sample (Mi_d) multiplied by average ratio of carbon to mineral concentration observed in pristine peatlands (C_p/Mi_p). The observed carbon mass is the product of dry weight (DW_d, mass) and carbon concentration (C_d) of the sample. Value per m^2 for 0-20 cm peat depth is derived by multiplying the result per sample with 1/sampler area (A_s). Negative values in the table indicate relative loss of mineral element and positive values indicate relative loss of carbon.

$$\Delta \mathrm{C}_{0-20}(\mathrm{g\ m}^{-2}) = \left(\frac{\mathrm{C}_p}{\mathrm{Mi}_p} \times \mathrm{Mi}_d - \mathrm{DW}_d \times \mathrm{C}_d\right) \times \frac{1}{A_s}$$

Table S3. ΔC estimates (g m^{-2}) for surface peat (0-20 cm) with different minerals (or ash) as a comparison.

Mn		**Mg**		**Fe**		**Ca**	
Mean	-2467.7	Mean	-2301.4	Mean	-1442.3	Mean	-1043.9
SD	4322.0	SD	2554.3	SD	2404.9	SD	3124.3
SE	1440.7	SE	851.4	SE	801.6	SE	1041.4
Median	-3879.8	Median	-1945.4	Median	-1500.2	Median	-1150.4
N		**P**		**K**			
Mean	3915.7	Mean	4616.7	Mean	227.8		
SD	3953.1	SD	4041.2	SD	2463.3		
SE	1317.7	SE	1347.1	SE	821.1		
Median	3186.3	Median	3511.9	Median	1011.3		
Total ash		**Al**		**Residual ash**			
Mean	5172.4	Mean	6713.6	Mean	7293.2		
SD	7017.1	SD	8723.6	SD	9521.2		
SE	2339.0	SE	2907.9	SE	3173.7		
Median	2302.4	Median	4026.0	Median	3658.9		

Appendix 4. Age-depth data for peat accumulation.

Figure S2. Untransformed age-depth data used in peat accumulation estimation. Note that in the analyses we used log transformed data, regression through the origin and only the first 10 years of the data to compare the peat growth between the treatments (see Methods, Peat growth).