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

Short title: Jump-starting ecosystem functioning

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Author contribution: SK, TH, TT, and SJK designed the study, SK, TH, and RJ gathered the data, TH, RJ, and RM planned and performed the lab analyses. SK, TH, TT, and JSK analysed the data. SK, TH, RJ, RM, TT, and JSK wrote the article.

Abstract

Degradation of ecosystems is a great concern 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 peatland surface layer C storage, ii) can restoration recover ecosystem functioning (surface layer 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 layer of drained sites. Restoration was successful in regaining natural growth rate in the peatland surface layer already within 5 years after restoration. However, the regenerated surface layer sequestered C at a mean rate of 116.3 g $m^{-2}yr^{-1}$ (SE 12.7), when a comparable short-term rate was 178.2 g $m^{-2}yr^{-1}$ (SE 13.3) 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 of 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.

Keywords: carbon sequestration; plant community composition; ecosystem degradation; ecosystem recovery; ecosystem structure-function relationship; peat

1. 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 (Bradshaw 1996; Dobson 1997; Vanha-Majamaa et al. 2007). 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 (Hobbs and Cramer 2008; Benayas et al. 2009; Aerts and Honnay 2011; Bullock et al. 2011; Suding 2011). 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 (Zedler and Kercher 2005; Benayas et al. 2009). 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 (Bradshaw 1996; Cortina et al. 2006; Cardinale 2012).

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 depends on the degree of ecosystem complexity and on our understanding of ecologically effective restoration practices (Cortina et al. 2006; Pocock et al. 2012). 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 (Nelson et al. 2009; Alexander and McInnes 2012; Kettunen et al. 2012; Russi et al. 2013), 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 store C (Feng 2005; Davidson and Janssens 2006; Freeman et al. 2012). Compared to other ecosystems, peatlands are the largest reserves of organic C in the soil (e.g. Gorham 1991; Page et al. 2002; Zedler and Kercher 2005; Page et al. 2011): 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 layer of a peatland) 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 (Minkkinen et al. 2008; Oleszczuk et al. 2008; Hooijer et al. 2010; Simola et al. 2012; Moore et al. 2013; Pitkänen et al. 2013). 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 (Silvola et al. 1996; Hooijer et al. 2010; Fenner and Freeman 2011). 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 (Minkkinen and Laine 1998; Minkkinen et al. 2008; Ojanen et al. 2010, 2012, 2013; Lohila et al. 2011; Simola et al. 2012; Pitkänen et al. 2013). 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 (Parish et al. 2008; Erwin, 2009; Ramchunder et al. 2009; Thiele et al. 2009; Worrall 2009; European Commission 2011). 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 and 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. Still,

the efficiency of the current methods in re-establishing the C sequestration function has not been comprehensively studied. Large body of the current research concentrates on peat-mining areas (e.g. Cagampan and Waddington 2008; Soini et al. 2010; Waddington et al. 2010; Moreno-Mateos et al. 2012; Strack and Zuback 2013) that globally cover only a minor fraction of degraded peatlands (Strack et al. 2008) or fens (e.g. Lamers et al. 2015; Zak et al. 2015), both of which as systems and type of degradation (mostly agriculture with fens) greatly differ from the 15 000 000 hectares of forestry-drained boreal peatlands. 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). However, the relationship between the recovery of vegetation and C sequestration in e.g. restored boreal sphagnum peatland ecosystems is far from properly studied and understood and more research is needed for the often complicated ecosystem level effects to be systematically quantified.

In this study, we address three questions related to degradation and restoration of C sequestration function of boreal sphagnum peatlands. First, what is the long-term effect of drainage on surface layer 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 functions? To answer our questions, we examined the recovery of the peatland surface layer, 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 (Clymo 1984; Francez and Vasander 1995; Gunnarsson et al. 2008). We first quantify the change in the surface layer C storage due to drainage by using the C to ash and C to Al

ratios of the surface layer of pristine peatlands to determine the expected C mass for the surface layer of drained peatlands. We use the C to ash and C to Al ratios for the comparison, because drainage results in compaction of the surface layer, making the comparison of absolute C per volume values alone flawed for measuring the change in the C storage. Then, to determine whether ecosystems regain their original surface layer growth function after restoration, we compare the surface layer 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 the surface layer of the restored sites and compare it to the RERCA of the 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.

2. Materials and methods

2.1. 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

Supplementary material: Appendix A). Distances between the study sites ranged from 200 m to 150 km. The study sites were independent from one another 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 (1960-1970) with ditch interval of 30-50 meters.

Drainage had changed the peatlands' hydrology mainly by lowering the water table and altering the water chemistry (More detailed description of the hydrology of the studied peatlands can be found in Haapalehto et al. 2014). 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 Metsähallitus, Parks and Wildlife Finland (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.

2.2. Sampling of peatland surface layer 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.

Six vertical cores of the peatland surface layer were sampled at each site with a side-cutting box sampler (sampler area: 8.3 × 8.4 cm). We focused the sampling on the uppermost 20-25 cm thick peatland surface layer (hereafter simply surface layer) that cover the main range of water table level fluctuation in natural sites and most of the layer

exposed to increased aeration in drained sites. This layer consists of the continuum of growing, dying, and decomposing biomass, and the resulting new peat. 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 the core samples and avoiding this requires careful operation in the field (Pitkänen et al. 2011). In addition, we carefully examined the core 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.

2.3. Carbon loss

To answer our first question about the effect of drainage on the amount of C in the surface layer, we estimated the C loss from the 0-20 cm surface layer cores 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 layer samples of drained peatlands by

multiplying their observed ash content with the average C to ash ratio obtained from the pristine peatlands (see Appendix B 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 (i.e. pristine reference) and the observed mass of C of the samples from the drained sites (Grønlund et al. 2008; Leifeld et al. 2011). 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 C). 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 C). 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 layer. 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.

2.4. Surface layer growth rate

To study the surface layer growth rate we constructed empirical age-depth models of the surface layers of the study sites using the pine method (e.g. Borggreve 1889; Ohlson and Dahlberg 1991; Pitkänen et al. 2012) and estimated the annual growth rate of the surface layer 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 peatland 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 layer as a linear regression coefficient between the rooting depth and age of the pines for each site (i.e. coefficient for the depth of the layer accumulated above the root collar since the rooting) and used analysis of variance (ANOVA, IBM SPSS Statistics 20) and appropriate post-hoc test to compare the site level growth 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 layer depth corresponded to zero age.

2.5. Recent apparent rate of carbon accumulation in the surface layer

We determined the recent apparent rate of carbon accumulation (RERCA) in the surface layer after restoration and for comparable period for the pristine sites. By definition,

RERCA only includes C bound in the layer 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 layer 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 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 layer 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 origin (i.e. zero 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).

2.6. 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 layer 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 (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 and 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.

3. Results

3.1. Carbon loss

The comparison of expected and observed C masses in the surface layer of drained sites showed substantial loss of C due to drainage. The estimates for average C loss from the 0-20 cm surface layer 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 supplementary material for derived ΔC estimates for the other elements (Appendix C) and total mineral concentrations (Appendix B).

3.2. Surface layer growth rate

According to the age-depth models peatlands in all treatments accumulated some biomass (Appendix D), but there was a significant difference in the net growth rate (mm yr^{-1}) of the surface layer 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 D.

3.3. Recent apparent rate of C accumulation in the surface layer

We observed a roughly linear rate of C accumulation into surface layer of restored sites after restoration. According to the slope of the regression model the regenerated surface 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 C accumulation in the surface layer than predicted by the pristine reference estimate (Fig. 2).

3.4. Plant community composition

The ecosystem structure measured as plant community composition was significantly different between the treatments (PERMANOVA $F = 4.719$, $p < 0.001$, Fig. 3). 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 $p = 0.024$).

4. Discussion

Our analyses indicate that drainage-induced degradation of the peatland ecosystems results in significant net loss of carbon from the surface layer when compared to the undisturbed state of the ecosystem. However, we also learned that the straightforward

restoration by filling the ditches can jump-start the ecosystem function of surface layer 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 layer 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 layer 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 layer 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. Silvola et al. 1996; Minkkinen and Laine 1998; Minkkinen et al. 2008; Hooijer et al. 2010; Ojanen et al. 2010; Lohila et al. 2011; Simola et al. 2012; Pitkänen et al. 2013; Ojanen et al. 2012, 2013). Although environmental conditions undoubtedly add variation 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 layer 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. Minkkinen et al. 2008; Lohila et al. 2011; Ojanen et al. 2010, 2012, 2013). 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 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 (Simola et al. 2012; Pitkänen et al. 2013).

The reduced surface layer growth 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 the surface layer of

forestry drained peatlands (Pitkänen et al. 2012). The growth of the surface layer is a prerequisite for subsequent deposition of biomass to lower anaerobic peat layers and long-term C accumulation in peatlands. Therefore, the returning of the surface layer growth 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 and 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 biomass 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 (Haapalehto et al. 2011; Hedberg et al. 2012). The dissimilarity in the plant community composition of pristine and restored sites is mainly due to i) 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. Haapalehto et al. 2011; Hedberg et al. 2012). 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 (Jones and Schmitz 2009; Hedberg et al. 2012; Moreno-Mateos et al. 2012).

Potential ecosystem level consequences of biodiversity loss are gaining increasing attention (Hector and Bachi 2007; Convention on Biological Diversity 2010; Cardinale et al. 2012; Hooper et al. 2012; Reich *et al* 2012). 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 (Bradshaw 1984; Cortina et al. 2006)? 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, the peatland surface layer growth, 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 the surface 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 (surface layer 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 (Hector and Bachi 2007; Lucchese et al. 2010; Montoya et al. 2012; McCarter and Price 2013). Moreover, this study presents one ecosystem type and already different type of peatlands and the variability in forms and magnitude of degradation may well result in more or less different outcomes than presented here (see e.g. Cabezas et al. 2014; Zak et al. 2015 for fens).

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 (Bullock et al. 2011; Menz et al. 2013). Estimating the economic value of C sequestration at restored peatlands is a relatively new idea (Nelson et al. 2009; Alexander and McInness 2012; Kettunen et al. 2012; Russi et al. 2013) and still far from straightforward (see e.g. Fenner and Freeman 2011; Tanneberger and Wichtmann 2012). In addition to the perhaps more obvious concerns on economically evaluating ecological success (e.g. Palmer and Filoso 2009) there are also concerns on the societal equity when economics take part in guiding restoration actions (Pasqual et al. 2014). Nevertheless, the results like ours including the calculation of C fixed to the re-established peatland surface layer can be used to evaluate the economic value related to accumulated C in a 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 European Commission 2008; ten Brink et al. 2011). We estimated that on average 116.3 g C $m^{-2}yr^{-1}$ accumulated into the surface layer 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 layer 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 the surface layer 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 the figures above show only the potential of the economic value of one part of these restored ecosystems as they are. The true market value or the net C accumulation effect of restoration action can only be estimated by comparing net ecosystem C balance before and after restoration (see e.g. Kimmel and Mander 2010). For example, with these data we cannot tell how restoration influences the lower peat layers, with potentially unpredictable initial post-restoration effects on the ecosystem's total C balance (Fenner and Freeman 2011; Zak et al. 2015). We find that long-term experiments e.g. on the changes in greenhouse gases (for restoration of cut-away peatlands see e.g. Waddington and Day 2007; Strack and Zuback 2013) 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 truly produces tradable C-related ecosystem services. Our rough calculation above, hopefully, attracts scientific and societal interest to establish such studies.

Here we studied peatlands up to 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 the recovery of the surface layer growth 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

Figure 1

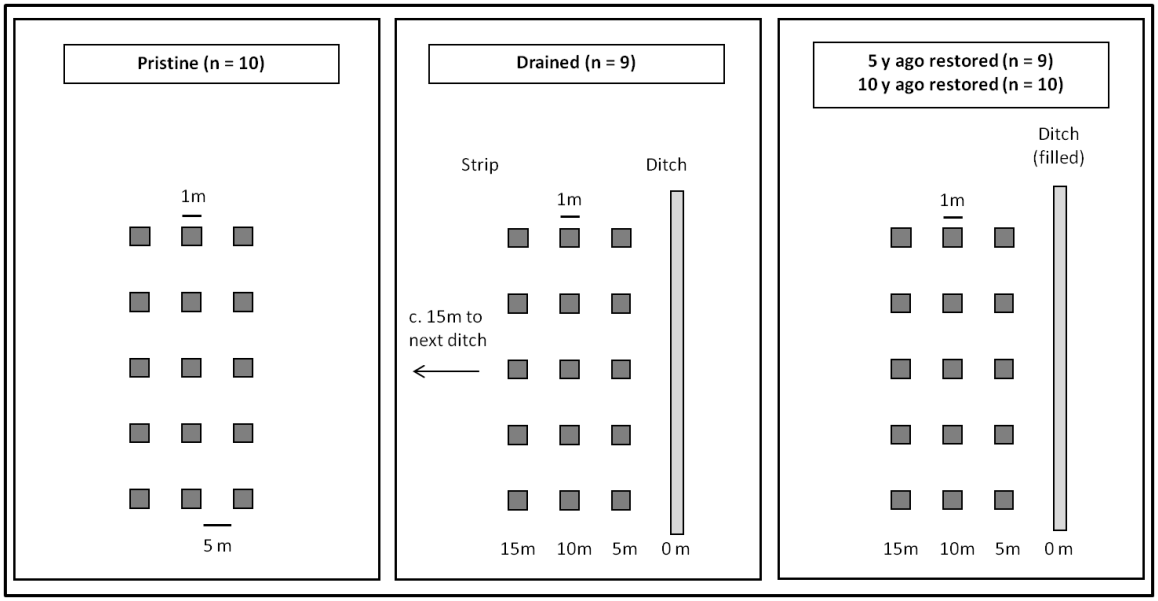
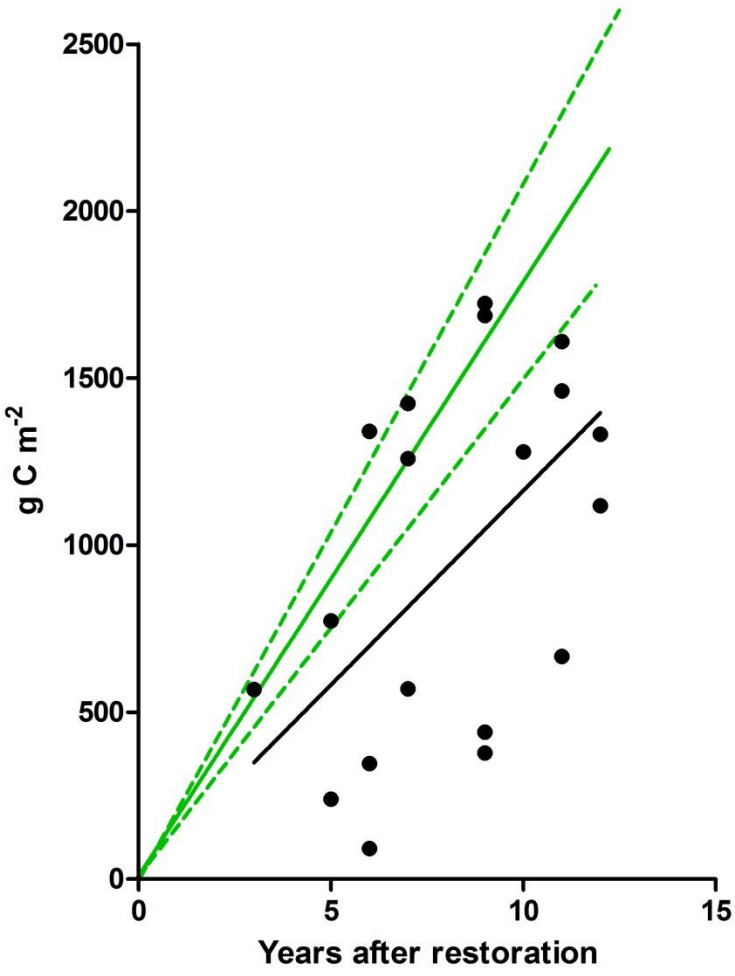


Figure 2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Years after restoration

Figure 3

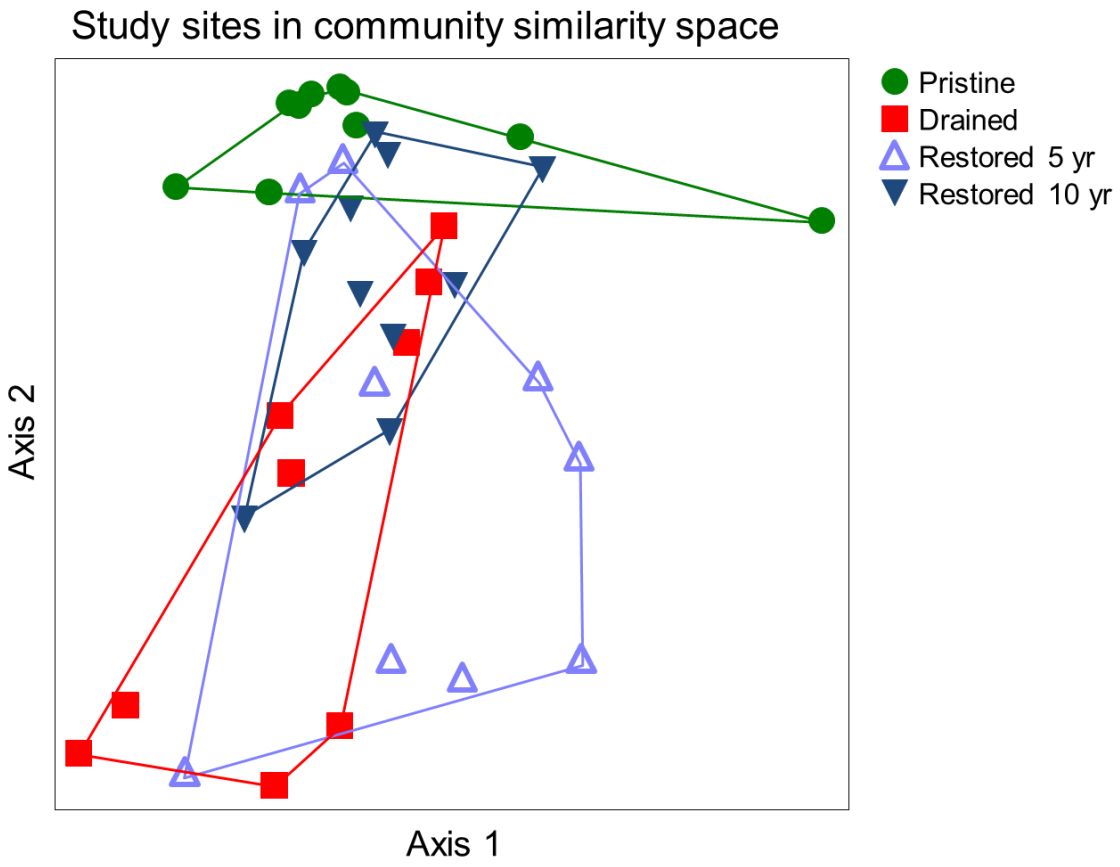
Study sites in community similarity space
Pristine
Drained
Restored 5 yr
Restored 10 yr
Axis 2
Axis 1

Figure legends

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 surface layer 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 surface layer core samples per site).

Fig. 2. The mass of C (g m^{-2}) in the surface layer 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 origin 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.