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PEATLANDS

Vegetation Composition and Carbon Dioxide Fluxes on Rewetted Milled Peatlands — Comparison with Undisturbed Bogs

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Abstract
Rewetting is the most common restoration approach for milled peatlands in Europe, with the aim of creating suitable conditions for the development of peatland specific plant cover and carbon accumulation. Therefore, it is important to determine if milled peatlands become functionally and structurally similar to their undisturbed counterparts. We measured plant functional type (PFT) cover and biomass, bryophyte production and CO_2 fluxes on three rewetted peatlands in Estonia restored 4, 15, and 35 years before the measurements and compared observations at rewetted sites to two nearby reference bogs. We hoped to better understand whether structure and function return at rewetted sites over time. Differences in vegetation composition and CO_2 fluxes between the sites were greater for rewetted than undisturbed sites. The most recently rewetted site was mainly covered in bare peat and *Eriophorum vaginatum* and was a CO_2 source. On the rewetted site of 15 years, *Sphagnum* was present in addition to ombrotrophic sedges, and in the rewetted site of 35 years, lawn-hollow microtopography is starting to develop with various PFTs. Both of these sites were CO_2 sinks. Lawn *Sphagnum* was abundant on the two older rewetted sites, and was connected with CO_2 sink functioning in the rewetted sites. Still, hummock *Sphagnum* species, which were present in undisturbed bogs, were absent from all of the rewetted sites. With time, CO_2 fluxes, microtopography and vegetation develop after rewetting in the direction of undisturbed bogs, while vegetation composition still differs from the reference sites even 35 years after rewetting.

Keywords Milled peatlands · Above-ground biomass · Rewetting · CO_2 exchange · Reference ecosystem · Peatland restoration

Introduction

Undisturbed peatlands are important carbon sinks in the long term (Yu 2012) as well as a suitable habitat for plant species that have adapted to survive in acidic and waterlogged conditions (Minayeva 2008). Northern peatlands have been widely affected by peat mining for horticulture or energy production (Leifeld et al. 2019), particularly since the 1950 s when peat milling became the main technique for peat extraction. This method involves drainage and the removal of vegetation in large areas, so thin layers of peat can be extracted every summer season.

Excavated peatlands have several negative environmental effects, such as peat loss through mineralisation, high CO_2 emissions, fire hazard, no plant diversity and low aesthetic value. The natural revegetation of those site takes a long time, depends on the environmental conditions of the site and usually does not lead to mire-specific plant communities (Lavoie et al. 2003; Graf et al. 2008; Orru et al. 2016). Unrestored milled peatlands are important CO_2 sources to the atmosphere due to the low water tables allowing peat mineralisation and sparse or absent vegetation (Strack et al. 2016; Rankin et al. 2018). In Estonian conditions, Salm et al. (2012) have measured the median annual emissions of active peat excavation sites to be 1 741 kg CO_2-C ha^{-1}. The main mitigation possibility for those negative impacts is peatland rewetting, which through higher water tables creates suitable conditions for revegetation and thus reduces CO_2 emissions (Wilson et al. 2016) and the flammability of these sites

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(Granath et al. 2016). Although rewetting increases CH_4 emissions on restored peatlands, CH_4 is a short-lived gas in the atmosphere, rewetting of peatlands has potential to mitigate climate change in the long-term (Günther et al. 2020). Various criteria have been taken into account throughout the history of restoration ecology to assess restoration success. First, biodiversity measures and hydrology were used to indicate the success of restoring the ecosystem, which in recent decades have been integrated with greenhouse gas balances showing recovery of ecosystem functioning (Kløve et al. 2017; Renou-Wilson et al. 2018).

The initial response of the plant community and its diversity to rewetting is complex and depends also on the pre-rewetting state of the peatland (Tuittila et al. 2000). After peatland rewetting or self-recovery, plant cover increases over the time-scale of several decades (Orru et al. 2016; Priede et al. 2016). Furthermore, CO_2 fluxes change in time after rewetting (Beyer and Höper 2015; Kløve et al. 2017) estimate based on their experience of greenhouse gas measurements in temperate peatland that rewetted peat extraction sites may become peat accumulating ecosystems after about 30 years. Even after 30 years post rewetting, milled peatlands can remain CO_2 sources, but those emissions from rewetted sites tend to be smaller than from active peat extraction sites, especially if *Sphagnum* is dominating (Samaritani et al. 2011; Vanselow-Algan et al. 2015).

Milled peatlands have been ombrotrophic bogs and in some cases bog remnants border the peat extraction areas. Usually during peat extraction, layers of *Sphagnum* peat are removed, so more nutrient-rich peat deposits at the bottom of the former mire with varying thickness are left on the site. This leads to the development of wet minerotrophic vegetation (Tuittila et al. 2000; Renou-Wilson et al. 2018), which is different from typical raised bog vegetation (Renou-Wilson et al. 2018). With vegetation succession and distancing peatland surface from the water table minerotrophic vegetation will be replaced by bog species in time (Samaritani et al. 2011).

The rate of vegetation recovery likely depends on successfully raising the water table (Konvalinková and Prach 2014; Strack et al. 2014; Priede et al. 2016), the presence of plant propagules (Campbell and Rochefort 2003; Konvalinková and Prach 2014) and the nutrient status of the site (Komulainen et al. 1999; Konvalinková and Prach 2014; Kozlov et al. 2016; Priede et al. 2016). However, even after decades, rewetted boreal peatlands mostly differ from their reference ecosystem regarding carbon accumulation and vegetation structure (Moreno-Mateos et al. 2012). The quicker return of CO_2 sink function has been reported on milled peatlands restored using the moss-layer-transfer technique (Strack et al. 2016; Nugent et al. 2018).

Due to the challenges related to raising and keeping the stable water table close to the peat surface throughout the year (Price et al. 2003; Brown et al. 2017), functional dryness of the residual peat layer (Price and Whitehead 2001; Price et al. 2003), the smaller water holding capacity of developed moss layer (Waddington et al. 2011; McCarter and Price 2015) and the moisture conditions being closely related with the microtopography of the site (Bugnon et al. 1997; Price et al. 1998; Price and Whitehead 2001; Purre and Ilomets 2018) environmental conditions in restored sites may be drier than in undisturbed sites. Restoration sites have generally lower bryophyte and shrub but higher graminoid cover than in undisturbed peatlands (Soini et al. 2010; González et al. 2013; Strack et al. 2016). Some studies report that vegetation in rewetted sites is more heterogeneous than in pristine peatlands due to the patchiness and incompleteness of the plant cover on restoration sites as vegetation cover starts to develop near the drainage ditches and close to existing vegetation (Soini et al. 2010; Laine et al. 2016).

Undisturbed peatlands are CO_2 sinks at least over longer time-scales, but CO_2 exchange of the peatland can vary annually (Wilson et al. 2016; Kløve et al. 2017; Nugent et al. 2018) stress the lack of knowledge about the greenhouse gas fluxes in rewetted peatlands, especially on sites that have been rewetted for decades. Restored milled peatlands can have larger (Soini et al. 2010; Strack et al. 2016; Wilson et al. 2016; Nugent et al. 2018, 2019) or smaller (Renou-Wilson et al. 2018; Nugent et al. 2019) CO_2 uptake than similar eco-hydrologically undisturbed sites. Similar carbon sequestration as in undisturbed peatlands is reported to return sooner to rewetted milled peatlands than the development of typical raised bog species composition (Soini et al. 2010; Renou-Wilson et al. 2018). Although photosynthesis on restored milled peatlands develops akin to undisturbed peatland, ecosystem respiration stays lower (Strack et al. 2016). Therefore, on rewetted sites, Net Ecosystem Exchange (NEE) is reported to be driven by respiration rather than by photosynthesis (Samaritani et al. 2011; Wilson et al. 2016). Due to their transitional stages, rewetted sites have large interannual and within-site variations in CO_2 fluxes (Wilson et al. 2016; Nugent et al. 2019), whereas undisturbed peatlands have reached a mature development stage regarding their vegetation, water retention capacity and CO_2 balance (Wilson et al. 2016).

Plant communities vary by their photosynthesis and respiration rates. The highest photosynthesis on nutrient-poor peatlands is reported from *Eriophorum* communities (Beyer and Höper 2015; Wilson et al. 2016), but this is accompanied by higher respiration (Beyer and Höper 2015). Higher CO_2 net sink function (Kivimäki et al. 2008) and soil organic matter accumulation (Andersen et al. 2013) have been recorded on plots with mixed graminoid and *Sphagnum* patches compared to pure graminoid patches. *Sphagnum* species have lower photosynthetic capacities (Korrensalo et al. 2016) and lower respiration, therefore plots with *Sphagnum* are larger

CO_2 sinks than plots with only graminoids (Beyer and Höper 2015). Vascular plants are also important in peatland CO_2 exchange, especially by mitigating the effect of drought on CO_2 sink functioning (Kuiper et al. 2014). In similar climatic conditions, correlating vegetation cover and CO_2 fluxes differs between land-use types (Laine et al. 2016; Strack et al. 2016) — in restored sites, CO_2 net uptake increases with vascular plant cover (Strack et al. 2014, 2016), while in undisturbed sites plots with higher moss cover are greater CO_2 sinks (Strack et al. 2016).

In this case study, we analyse the success of rewetting by comparing CO_2 fluxes and vegetation on relatively similar rewetted milled peatlands and initially eco-hydrologically similar undisturbed bogs located near the disturbed sites. This is done to assess if rewetting or ecosystem recovery leads to ecosystems that functionally converge to the state of reference bogs. For that, we established the following postulates:

1) CO_2 fluxes and vegetation structure on rewetted milled peatlands develop in the direction of undisturbed reference bogs;
2) Higher amount of plant above-ground biomass, especially *Sphagnum* biomass, is related to higher CO_2 sink function on rewetted milled peatlands.

Methods

Study Sites

Two paired study sites (Kõrsa and Hara) were selected (Table 1), both of which include rewetted abandoned milled peatlands and remnant open raised bog areas (Fig. 1). The Kõrsa site is located in southwestern Estonia next to an active peat extraction site. The Kõrsa rewetted (Kõrsa$_R$) site has self-recovered after the end of peat extraction due to the water level being raised up to the peat surface in 1980 following a damming to create a firewater reservoir (Ramst et al. 2007). Revegetation began at Kõrsa$_R$ two years later with the self-establishment of *E. vaginatum* tussocks in 1982. The Hara site is located in Northern Estonia, in Lahemaa National Park. The Hara rewetted site divides into a self-recovered northern part (Hara$_{RN}$) and an actively rewetted southern part (Hara$_{RS}$). The water table in Hara$_{RN}$ rose in 2000-2002 due to closing of the bordering ditch, and vegetation started to develop earlier in that area. Hara$_{RS}$ was rewetted in 2012 by the State Forestry Centre of Estonia. No additional restoration measures were applied in addition to rewetting.

The rewetted and undisturbed sites of both paired sites initially had a similar ecohydrological status (raised bog), which is still present in the undisturbed parts of Kõrsa (Kõrsa$_P$) and Hara (Hara$_P$). Previously, the vegetation of the rewetted sites was described by Ramst et al. (2007), as the following:

- Hara$_{RS}$: *Eriophorum vaginatum* and bare peat;
- Hara$_{RN}$: *E. vaginatum, Warnstorfia fluitans, Sphagnum riparium* and *Sphagnum cuspidatum*;
- Kõrsa$_R$: *E. vaginatum, Chiloscyphus pallescens, Pleurozium schreberi, Polytrichum strictum, W. fluitans, Brachythecium mildeanum, S. cuspidatum* and *Sphagnum balticum*.

The respective paired sites are located in the same mire-basin, and the distances between the rewetted and undisturbed sites range from 140 m in Hara to 500 m in Kõrsa.

Among the five research sites, in total, 18 plots were fluxed. Four measurement plots per site were established during the previous year (2015). As two of the plots in Hara$_{RN}$ became flooded during the measurement period, they were omitted from the study, and data from two measurement plots in Hara$_{RN}$ were used. The locations of the

Table 1 Locations and descriptions of the study site

	Hara	Kõrsa
Coordinates	N 59°33’, E 25°36’	N 58°24’, E 24°41’
End of extraction	1994	1980
Water table depth below surface (cm)[a]	Hara$_{RS}$: -10 Hara$_{RN}$: 0 Hara$_P$: -5 – -30	Kõrsa$_R$: 0 – -15 Kõrsa$_P$: -10 – -35
Long-term (1981-2010) average annual/growing season temperature (°C)[b,c]	5.7/12.4	6.3/13.4
Long-term (1981-2010) average annual/growing season precipitation (mm annually/growing season)[b,c]	587/381	746/418
Average annual/growing season temperature (°C) 2016[b,c]	6.6/13.4	6.7/13.5
Average annual/growing season precipitation (mm annually) 2016[b,c]	849/430	757/398

[a]- Average growing season water table according to manual measurements during the CO_2 measurement sessions; [b]- data from Estonian Weather Service; [c]- Growing season data for May-October

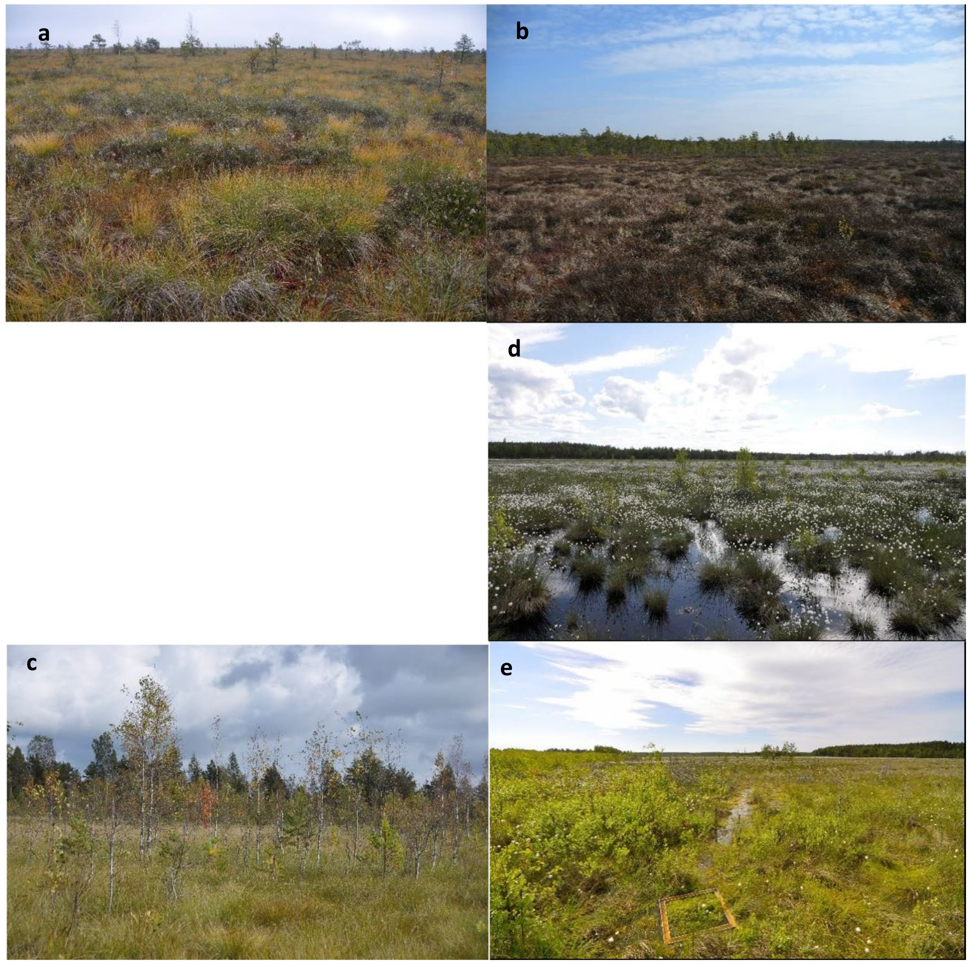


Fig. 1 Undisturbed reference sites (Kõrsa$_P$ (**a**) and Hara$_P$ (**b**), Kõrsa 35 years before rewetted (Kõrsa$_R$ (**c**)) site, and Hara rewetted fields 4 (Hara$_{RS}$ (**d**)) and 15 (Hara$_{RN}$ (**e**)) years after rewetting, respectively

permanent measurement plots were chosen based on the dominant vegetation and by taking into account its variability between micro-topographic levels. In undisturbed sites and Kõrsa$_R$, where microtopography has already developed, two measurement plots were situated on the hummocks and two plots on the lawns of each site. In other sites, two replicates for each vegetation type were established.

Vegetation Analysis

Vegetation analyses were conducted on the plant functional type (PFT) level, and we used the PFT division described in Laine et al. (2012). In our study sites, the following PFTs were present from the larger number of PFTs described by Laine et al. (2012):

- Hummock *Sphagnum*: *S. rubellum*, *S. fuscum* and *S. capillifolium*;
- Lawn *Sphagnum*: *S. angustifolium*, *S. balticum*, *S. medium*, *S. fallax*, *S. papillosum*, *S. squarrosum, S. riparium* and *S. cuspidatum*;
- True mosses: *Polytrichum strictum, Warnstorfia fluitans, Chiloscyphus pallescens, Pleurozium schreberi* and *Brachythecium mildeanum*;
- Evergreen shrubs: *Calluna vulgaris*, *Vaccinium oxycoccus* and *Andromeda polifolia*;
- Ombrotrophic forbs: *Drosera rotundifolia* and *Rubus chamaemorus*;
- Minerotrophic forbs: *Melampyrum* spp., *Menyanthes trifoliata* and *Thelypteris palustris*;
- Ombrotrophic sedges: *Eriophorum vaginatum*;
- Trees: *Pinus sylvestris*, *Betula pubescens*, and *Salix* spp.

The nomenclature followed Ingerpuu and Vellak (1998) for bryophytes and Leht (2010) for vascular plants.

We measured the plant species coverage (%), vascular plant leaf area index (LAI_{vasc}; m^2 m^{-2}), above-ground biomass of PFTs (AGB; g dm^{-2}) and moss production (AGP; g dm^{-2} year^{-1}) as well as the length increment of mosses (LI; mm year^{-1}). The plant cover of measurement plots was determined visually at the peak of the 2016 growing season (end of July) from inside the CO_2 flux measurement collars (four plots per each site/management type combination, but two plots in $Hara_{RN}$). LAI_{vasc} was determined according to Wilson et al. (2007a) during the CO_2 flux measurement campaigns.

Biomass samples were collected from near the measurement plots with vegetation as similar as possible to those in the collars. Vascular plant biomass samples were collected at the end of July 2016 and bryophyte samples at the beginning of October 2016 to capture the maximum biomass of each plant group. We used two plot sizes for the AGB measurements of vascular plants (15 cm radius circular plot) and bryophytes (2.5 cm circular round plot) and collected one vascular plant sample and three bryophyte samples per measurement point (a total of four vascular plant and 12 bryophyte samples from $Hara_{RS}$, $Hara_P$, $Kõrsa_R$ and $Kõrsa_P$ each, and two vascular plant and six bryophyte samples in $Hara_{RN}$). Only the capitula for *Sphagnum* species was used as there is no clear distinction between the live and dead material of *Sphagnum* (Clymo 1970), and the upper 2 cm layer for other bryophytes to obtain biomass samples up to the similar depth of biomass as *Sphagnum* were collected to determine bryophyte biomass similar to Moore et al. (2002); Laine et al. (2012); Purre et al. (2019b). The collected samples were divided into species level. The sampling and laboratory analysis of biomass is described in Purre et al. (2019b). During the data analysis, the biomass of different species was compiled into PFTs. From the air-dried (65ºC) bryophyte samples, the border of AGP and LI was determined using the innate markers method (Clymo 1970; Pouliot et al. 2010), then separated from the rest of the biomass and weighed (AGP). The LI of ten individuals from the dominant species of each sample were measured with a digital caliper. In $Hara_{RS}$, bryophytes were absent and thus biomass AGP and LI were considered to be zero.

CO_2 Flux Measurements and Data Processing

CO_2 measurements were carried out at least once a month during the growing season (May-October 2016). NEE and ecosystem respiration (R_{ECO}) was measured on 60×60 cm square aluminium collars inserted to about a 20 cm depth, with the rim filled with water to ensure an air-tight fit during flux measurements. We measured CO_2 concentrations with the infrared gas analyser Li-6400 (Li-Cor (USA)) from transparent Plexiglas chamber ($60 \times 60 \times 30$ cm) with a cooling system. The measurements period was two minutes, and the CO_2 content in the chamber was recorded with an interval of 15 s. After measuring the CO_2 concentrations in full-light, NEE was measured on two lower irradiation levels by using one or two shades that reduced the photosynthetically active radiation (PAR (µmol m^{-2} s^{-1})) reaching the vegetation in the chamber at an average of 65% and 88%, respectively. Lastly, R_{ECO} was measured by covering the chamber with an opaque hood. Between each measurement period, the measurement chamber was ventilated. During the measurement campaigns, plant parameters for determining LAI_{vasc} inside the measurement collars were measured according to Wilson et al. (2007a) in addition to recording PAR, the temperature inside the chamber, peat temperatures at 5 and 15 cm depths and the water table (cm).

Input data (PAR, T_{AIR}) for CO_2 flux reconstruction were measured with hourly intervals in stations belonging to the Estonian Weather Service. For Hara, the temperature data was obtained from the nearest station in Vanaküla (about 10 km from the site) and radiation data from Harku meteorological station (about 70 km from Hara). For Kõrsa, all meteorological data was obtained from Pärnu-Sauga meteorological station located about 15 km from the site. Those stations were the closest to the study sites where PAR and T_{AIR} were continuously measured, and they were located within a 10 km distance from the sea similarly to the study sites.

The flux rates were estimated based on linear change in CO_2 concentrations in time. The linear method was chosen, as this method was considered suitable by Kandel et al. (2016) for CO_2 flux calculations in the case of short (few minutes) chamber closure periods (2 min in current study). The measured NEE and R_{ECO} fluxes were considered suitable according to the following quality criteria: variation of PAR during the flux measurement not exceeding ±15%, variation of inside temperature of the chamber not varying more than ±5 °C and the determination coefficient (R^2) of the measured flux of at least 0.9. Very small fluxes (±0.2 ppm s^{-1}) were accepted regardless of their R^2 value. Similar quality criteria in respect of R^2 values were used by Järveoja et al. (2016). A total of 215 CO_2 flux measurements fulfilled the set criteria and were used for CO_2 flux reconstructions. Photosynthesis (P_g) was calculated by adding R_{ECO} to NEE.

CO_2 fluxes were reconstructed for the period from the beginning of May until the end of September 2016 at each site. With these reconstructions, based on measured and calculated CO_2 fluxes and other parameters (PAR, LAI_{vasc} and air temperature (T_{AIR})), models were created for relating differences in measured CO_2 fluxes with differences in input parameters for reconstructing the whole growing season CO_2 fluxes. CO_2 flux and LAI_{vasc} reconstruction was carried out in program R version 3.2.2 package nlme (Linear and Nonlinear Mixed Effects Models, ver. 3.1 – 121; Pinheiro et al. (2015)). Gaussian curves were fitted to LAI_{vasc} values, which were calculated according to the vegetation parameters measured during the CO_2 measurement campaigns for reconstructing the change in LAI_{vasc} during the vegetation season as described by Wilson et al. (2007a) in each measurement collar.

The gross photosynthesis (P_g (mg CO_2 m^{-2} h^{-1})) model uses the saturating response to PAR (Eq. 1) and records the change in LAI_{vasc} during the vegetation season:

$$P_g = \frac{P_{max} \times PAR}{(k + PAR)} * \frac{LAI_{vasc}}{(LAI_{vasc} + s)} \quad (1)$$

where P_{max} is the maximum photosynthesis at light saturation, k and s are respectively the PAR and LAI_{vasc} values when P_g reaches half of its maximum level.

The respiration model (Eq. 2) expresses an exponential response of ecosystem respiration (R_{ECO} (mg CO_2 m^{-2} h^{-1})) to the temperature inside the chamber (T_{AIR}).

$$R_{ECO} = r0 \times \exp(b \times T_{AIR}) \quad (2)$$

Where parameters r0 and b are respectively the respiration at the 0 °C temperature and the sensitivity of respiration to air temperature, and T_{AIR} is the air temperature (°C). CO_2 measurements and reconstructions are described in more detail in Purre et al. (2019a, b).

Data Analysis

Data analyses were conducted with IBM SPSS ver. 23. As the data did not fulfil the requirements for parametric data analysis according to the Shapiro-Wilk test, non-parametric data analysis methods were chosen. The Kruskal-Wallis and Mann-Whitney tests with Bonferroni correction for the pairwise comparison of vegetation parameters and CO_2 fluxes between the sites were applied. Spearman correlations were used to relate separate plant group abundances with different parameters of CO_2 fluxes (NEE, P_g, R_{ECO}) in rewetted and undisturbed peatlands. Generalized linear mixed models (GLMMs) were applied on data from rewetted milled peatlands to determine the effect of site, microtopography and time since rewetting (fixed factors) on CO_2 fluxes (growing season NEE, P_g or R_{ECO} as target variables), biomass of studied plant functional types (PFTs) were incorporated in the models as random factors. For information criterion of the GLMMs log-likelihood was used, lower log-likelihood values showing better model fit. The results were considered statistically significant if $p < 0.05$. Average values are reported with standard errors.

The multivariate analysis methods Redundancy Analysis (RDA) and Detrended Correspondence Analysis (DCA) were applied in PC-ORD ver. 7 to relate the abundances of PFTs and CO_2 fluxes on rewetted and undisturbed sites. In RDA, the response variables were standardised and a randomisation test was applied to test for any significant relationship between the PFT and CO_2 flux matrices. DCA was used to find the main gradients in PFT and CO_2 flux data using time since rewetting and the site as supplementary variables.

Results

Vegetation

Vegetation varied between rewetted and undisturbed sites and between all rewetted sites, while small differences also occurred between both undisturbed sites (Fig. 2). More PFTs were present on undisturbed and older rewetted sites, while many PFTs such as *Sphagnum* and evergreen shrubs

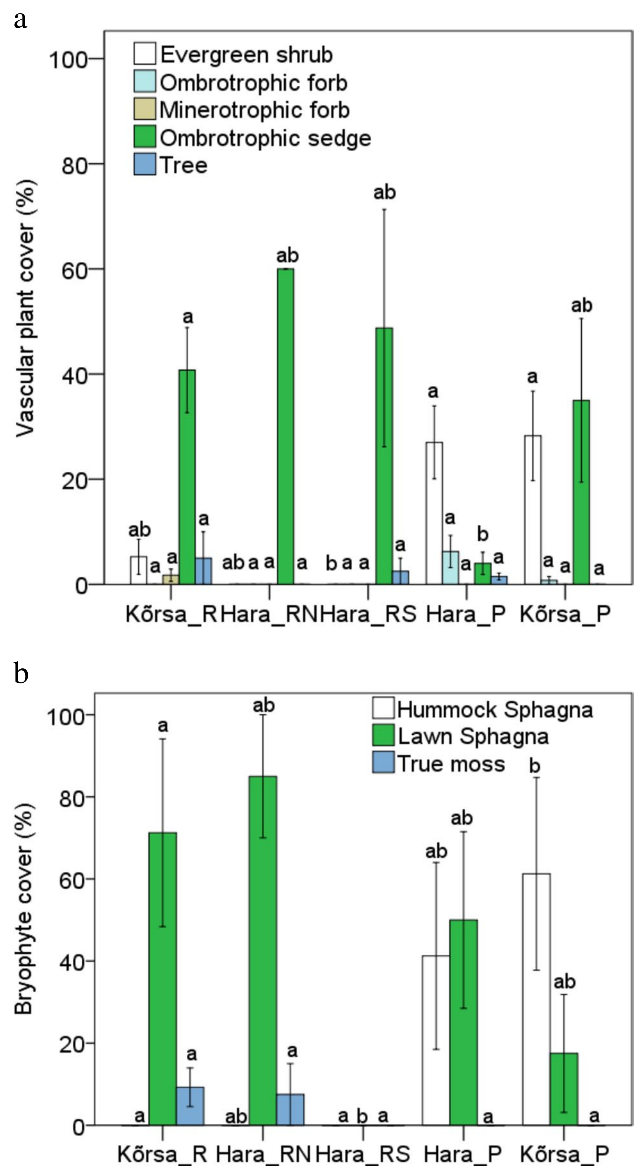


Fig. 2 Average cover (in %) of vascular plant (**a**) and bryophyte (**b**) plant functional types of the study sites (±SE). Different small case letters indicate statistically significant differences between the sites (p < 0.05). Statistical significance was tested using the Kruskal-Wallis test, and pairwise comparison was concluded using the Mann-Whitney test with Bonferroni correction

were absent from the recently rewetted Hara$_{RS}$. Evergreen shrubs such as *C. vulgaris* and *A. polifolia* had higher cover in undisturbed sites, while *V. oxycoccus* was present with low cover only in Kõrsa$_R$. Evergreen shrub biomass was absent or lower in rewetted sites compared to undisturbed sites (Appendix S1). Ombrotrophic forbs *R. chamaemorus* and *D. rotundifolia* were only present in undisturbed plots, but with relatively low cover (0.5-3%). Only in Kõrsa$_R$ minerotrophic forbs like *Melampyrum* species and *T. palustris* were present. Tree seedling of *Salix* spp., *Betula* spp. and *P. sylvestris* had about 1% cover on all sites, or were absent.

In undisturbed sites, hummock (*S. fuscum*, *S. rubellum*, *S. angustifolium*) and lawn (*S. medium*, *S. balticum*, *S. papillosum*) *Sphagnum* species were present in relatively similar cover (ranging from 5% (*S. balticum* in Kõrsa) to 45% (*S. rubellum* in Kõrsa)). Only lawn species (*S. medium*, *S. fallax*, and *S. squarrosum*) were present in Kõrsa$_R$ and Hara$_{RN}$ site. True mosses (*P. strictum* and *P. schreberi*) had low cover (1-3%) on Kõrsa$_R$ and Hara$_{RN}$ but were absent from all of the other study sites.

Small differences in plant cover and AGB occurred between the measurement plots in hummocks and lawns. Hummocks had higher AGB (15.3 ± 1.3 g dm^{-2}), AGP of *Sphagnum* (3.4 ± 0.5 g dm^{-2} year^{-1}) and mosses (3.5 ± 0.5 g dm^{-2} year^{-1}) than lawns (AGB 9.9 ± 0.8 g dm^{-2}. AGP of *Sphagnum* 1.5 ± 0.5 g dm^{-2} year^{-1} and mosses 1.5 ± 0.4 g dm^{-2} year^{-1}) ($p < 0.05$). In contrast, the cover of lawn *Sphagna* was higher in lawns (72 ± 14%) than in hummocks (21 ± 15%) ($p < 0.05$).

Carbon Dioxide Fluxes

Measured NEE and R_{ECO} varied spatially to a larger extent in rewetted rather than in undisturbed sites (Appendix S2). CO_2 net uptake and P_g increased with higher PAR on rewetted and undisturbed sites.

Reconstructed P_g and NEE did not differ ($p > 0.05$) between the rewetted and the undisturbed sites, whereas R_{ECO} was higher in the rewetted than in the undisturbed sites ($p < 0.05$; Fig. 3). The respiration model's parameter r0 was higher in the rewetted (41.8 ± 11.4 mg CO_2 m^{-2} h^{-1}; $p < 0.05$) than in the undisturbed sites (9.4 ± 3.1 mg CO_2 m^{-2} h^{-1}; Appendix S3). In Kõrsa$_R$ the reconstructed P_g was higher than in the undisturbed sites and at Hara$_{RS}$ ($p < 0.05$). Also, Kõrsa$_R$ had higher R_{ECO} than Kõrsa$_P$, whereas all of the other sites had a similar R_{ECO}. Although there were no differences in the model parameters between Hara$_{RN,}$ Hara$_{RS}$ and Hara$_P$ ($p > 0.05$), P_{max} and r0 were higher in Kõrsa$_R$ than in Kõrsa$_P$ ($p < 0.05$) indicating a higher maximum CO_2 uptake in case of light saturation and also a higher minimum respiration rate in rewetted sites. Undisturbed sites did not differ according to their CO_2 fluxes ($p > 0.05$). There were

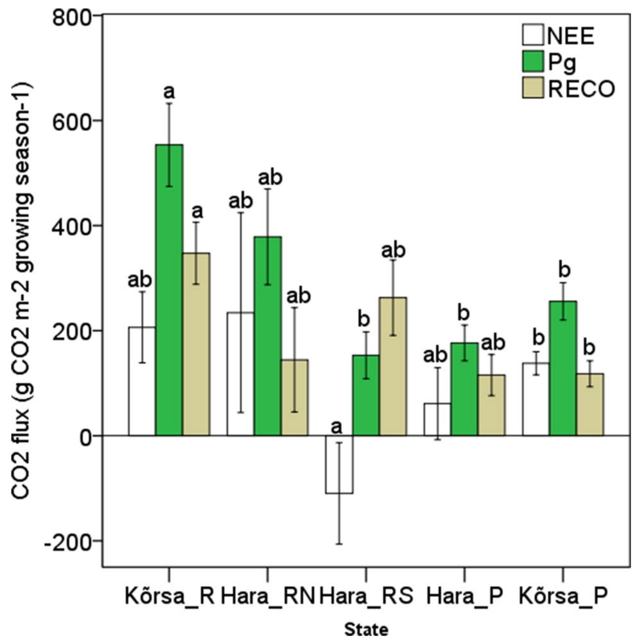


Fig. 3 Cumulative reconstructed growing season CO_2 fluxes in study sites ±SE. Different lower-case letters indicate a statistically significant ($p < 0.05$) difference in certain CO_2 flux component between the sites. The statistical significance was tested using the Kruskal-Wallis test, and pairwise comparison was concluded with the Mann-Whitney test and Bonferroni correction. NEE = P_g – R_{ECO}, note that Pg and R_{ECO} are always positive for clarity

no differences in CO_2 fluxes between the hummocks and the lawns in the undisturbed sites and Kõrsa$_R$ ($p < 0.05$).

GLMMs were used specify the effect of site, microtopography and time since rewetting on growing season CO_2 flux components (R_{ECO}, P_g, NEE) on rewetted peatlands. Although none of the fixed effects and GLMMs were statistically significant, time since rewetting had strongest effect on all of the CO_2 flux components (Table 2). In addition to time since rewetting, microtopography and combination of microtopography and site had also relatively strong, but still statistically non-significant effect on R_{ECO}.

CO_2 Fluxes and Vegetation

CO_2 fluxes correlate with every PFT differently between the undisturbed and rewetted plots (Fig. 4, Appendix. S4). In the undisturbed sites, P_g was higher in measurement plots with higher ombrotrophic sedge (*E. vaginatum*) cover and biomass but lower with higher tree cover, which was related with the higher values of the parameter k indicating the PAR value when P_g reaches half of its maximum value. In the rewetted sites, NEE was higher in the case of higher *Sphagnum* abundance, and higher photosynthesis rates were connected with the cover of minerotrophic forbs.

Table 2 Statistical results of general linear mixed models (GLMM) determining effect of site conditions (site, microtopography, time since rewetting) on CO_2 flux components (NEE, P_g, R_{ECO}) in rewetted milled peatlands

CO_2 flux component	Effect	F	p
NEE	Site	$F_{1,10}$=0.03	0.87
	Microtopography	$F_{1,3}$=0.00	0.95
	Time since rewetting	$F_{1,1}$=2.93	0.40
	Site*Microtopography	$F_{1,8}$=0.59	0.47
P_g	Site	$F_{1,0}$=0.03	1.00
	Microtopography	$F_{1,2}$=0.12	0.76
	Time since rewetting	$F_{1,6}$=1.87	0.22
	Site*Microtopography	$F_{1,10}$=0.40	0.54
R_{ECO}	Site	$F_{1,0}$=0.00	1.00
	Microtopography	$F_{1,10}$=3.50	0.09
	Time since rewetting	$F_{1,8}$=3.74	0.09
	Site*Microtopography	$F_{1,9}$=1.09	0.32

P_g increases with higher bryophyte and vascular biomass in rewetted sites, whereas this correlation was non-significant in the undisturbed sites (Fig. 5). In the undisturbed sites, higher R_{ECO} was measured on plots with higher vascular plant biomass, whereas this correlation was insignificant in the rewetted sites. There were no other statistically significant correlations between vascular plant, bryophyte and plant biomass, and P_g, R_{ECO} and NEE in the rewetted nor in the undisturbed plots.

With time since rewetting, communities evolve in the direction of undisturbed mires, where several PFTs are present, including *Sphagnum* and evergreen trees (Fig. 6). $Hara_{RS}$ is characterised by high R_{ECO} and biomass of ombrotrophic sedges, $Hara_{RN}$ and $Kõrsa_R$ contain lawn *Sphagnum* and P_g, while undisturbed sites ($Hara_P$ and $Kõrsa_P$) have higher NEE along with the presence of hummock *Sphagnum*, ombrotrophic forbs and evergreen shrubs. With this transition, high R_{ECO} is replaced with higher P_g, and eventually with higher NEE, indicating CO_2 sink function during the growing season.

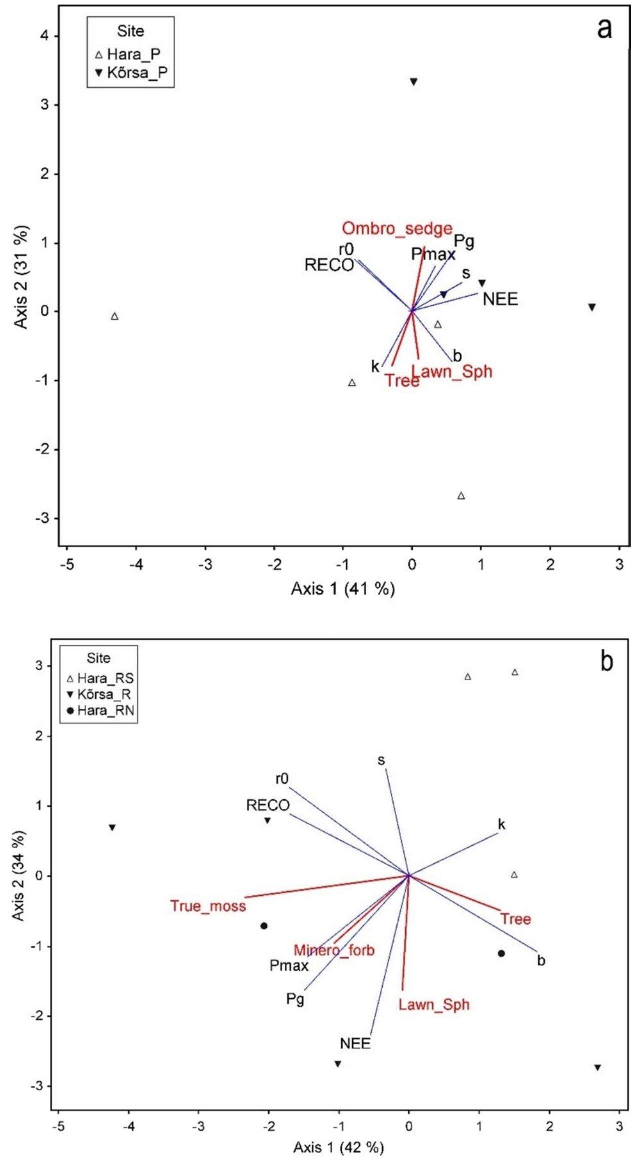


Fig. 4 Redundancy analysis of plant functional type cover, CO_2 fluxes (NEE, P_g, R_{ECO}) and CO_2 model parameters (P_{max}, k, s, r_0, b) in the undisturbed (**a**) and rewetted (**b**) sites. Only plant functional types, which are significant predictors explaining CO_2 fluxes and model parameters, are shown. Minerotrophic forbs and true mosses in the case of undisturbed sites, and ombrotrophic forbs and hummock *Sphagnum* in the case of rewetted sites, were omitted from the analysis due to their absence from the respective sites. NEE – net ecosystem exchange, Pg – gross photosynthesis, RECO – ecosystem respiration, ombro_sedge – ombrotrophic sedges, Minero_forb – minerotrophic forbs, True_moss – true mosses, Lawn_Sph – lawn *Sphagnum*

Discussion

Vegetation

Vegetation differed between the undisturbed and rewetted sites. The undisturbed sites had oligotrophic raised-bog vegetation, whereas rewetted sites contained vegetation assemblages more characteristic of mesotrophic environments with higher water tables, an observation previously reported also by others (Tuittila et al. 2000; Samaritani et al. 2011; Renou-Wilson et al. 2018). Commonly, the less humified *Sphagnum* peat has been removed from abandoned milled peatlands, as the mineral-rich substrate supports the establishment and development of more nutrient demanding plant species. Contrary, oligotrophic vegetation is prevailing in bogs where the peat layer is more nutrient-poor and the water level deeper. After rewetting,

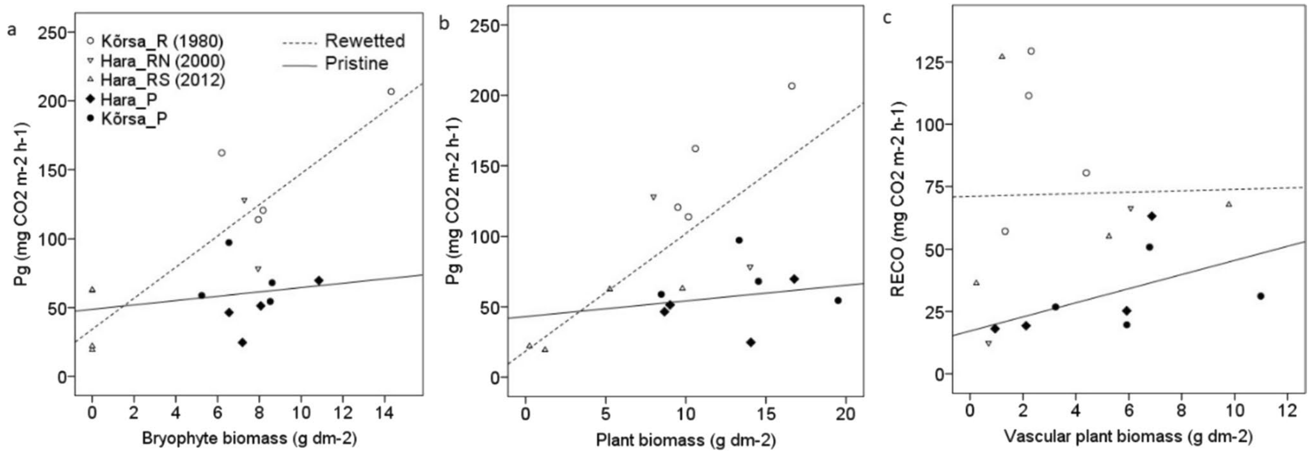
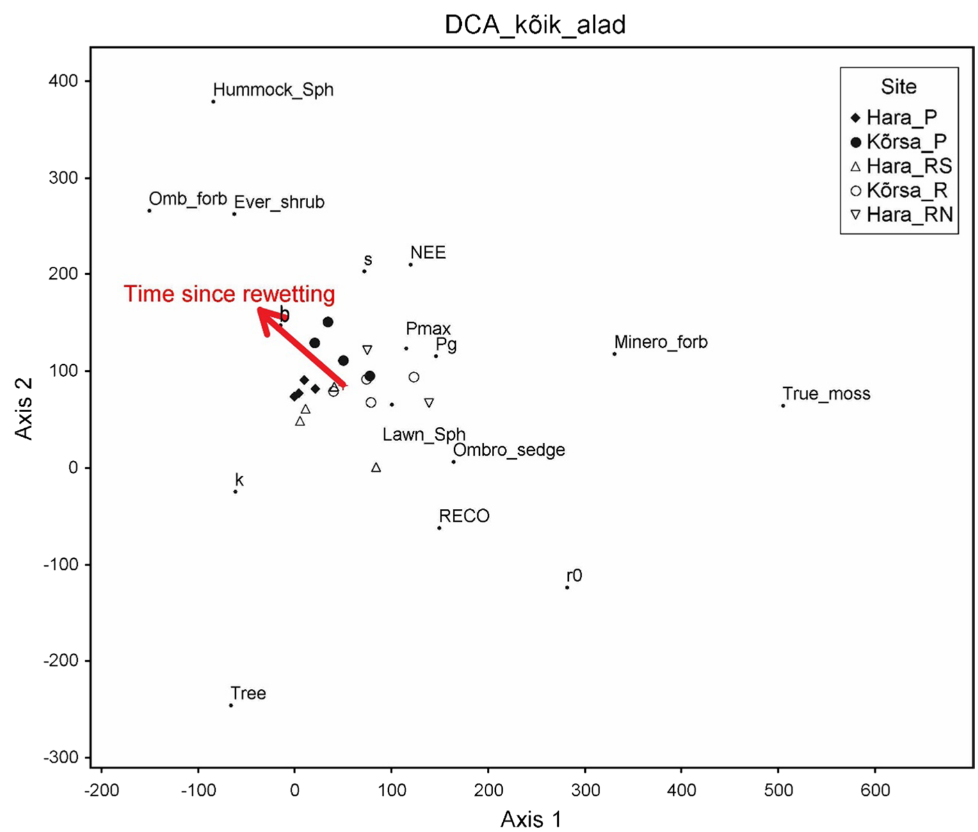


Fig. 5 Bryophyte (**a**), plant (**b**) and vascular plant (**c**) biomass related with average growing season photosynthesis (**a**, **b**), and ecosystem respiration (**c**) in rewetted and undisturbed plots

Fig. 6 Detrended correspondence analysis (DCA) of plant functional types and CO_2 fluxes (NEE, P_g, R_{ECO}) and its model parameters (P_{max}, k, s, r_0, b) in the study sites. The eigenvalues for the first and second axes are 0.181 and 0.067, respectively. NEE – net ecosystem exchange, Pg – gross photosynthesis, RECO – ecosystem respiration, Ombro_sedge – ombrotrophic sedges, Omb_forb – ombrotrophic forbs, Minero_forb – minerotrophic forbs, Ever_shrub – evergreen shrubs, True_moss – true mosses, Lawn_Sph – lawn *Sphagnum*, Hummock_Sph – hummock *Sphagnum*



vegetation establishment is more rapid and species rich in sites with more nutrients (Komulainen et al. 1999; Kozlov et al. 2016). This could have caused the relatively rapid vegetation succession on Kõrsa$_R$ where peat ash content is reported to be about twofold higher (2-3%) than in Hara rewetted sites (about 1-2%; Orru 1995). In Kõrsa$_R$, a rather diverse peatland community with a thick *Sphagnum* mat had developed in about 35 years.

Of note, in Kõrsa$_R$ a thin layer of new peat – an acrotelm – has formed, which suggests that the site is functionally (but not structurally) quite similar to a pristine bog. According to results reported by Lucchese et al. (2010), about a 19 cm thick bryophyte layer would be needed in the Bois-des-Bel restored milled peatland in Canada to mitigate summer water level drawdown; this could be reached about 17 years after restoration. Throughout the study period in Kõrsa$_R$

and $Hara_{RS}$, the water level stayed inside the moss layer, mainly near the moss surface, therefore not inhibiting the moss growth during the summer period. In the rewetted sites with thick moss layer in the current study, the moss layer was looser than in the undisturbed reference sites. This was probably due to the higher water table along with the high abundance of hollow *Sphagna* in the rewetted sites. Hollow *Sphagnum* could be affected by extreme droughts to a larger degree due to their larger pore size and less connectivity with the residual peat layer (McCarter and Price 2015) than the denser *Sphagnum* cover of undisturbed bogs, therefore making CO_2 exchange on rewetted sites more susceptible to drought impacts.

Some PFTs were lacking or had very low abundances in the rewetted sites but were present in the reference sites. We found significantly lower biomass and cover of evergreen shrubs on the rewetted than in the undisturbed sites, similar to results by Soini et al. (2010) and González et al. (2013), and they were absent from the most recently rewetted sites. Hummock *Sphagna*, which was present in both undisturbed bog sites was completely absent from the rewetted sites. The low occurrence and dying-off of hummock *Sphagnum* due to high water tables has been reported previously by Soini et al. (2010) and González et al. (2013). In contrast, Karofeld et al. (2015) recorded relatively high cover of hummock *Sphagna* and the presence of shrubs on restored milled peatland site where those species were dispersed using the moss-layer-transfer technique (Rochefort et al. 2003). Therefore, the application of this technique could lead to a more diverse vegetation composition of restoration sites.

While vegetation differs between the rewetted sites, being more diverse in the older sites, the vegetation in both undisturbed sites was similar with hummock and hollow vegetation pattern. Hummocks on the two undisturbed sites are typical *Calluna vulgaris-Sphagnum fuscum* communities, the most common plant associations in Estonian bogs (Masing 1982), and are comparable to the high hummock communities described by Korrensalo et al. (2018). Lawns in the undisturbed sites belong to the tussocky *Eriophorum* community or the *Sphagnum balticum-Sphagnum rubellum* community (Masing 1982), described also by Korrensalo et al. (2018) in an undisturbed bog in central Finland as lawn and high lawn communities. A large variation in vegetation between the measurement plots occurred in rewetted sites, especially in the most recently rewetted $Hara_{RS}$. However, this could also be caused by the relatively low number of measurement plots in each study site and their positioning on the site. In recovering milled peatlands, vegetation is developing in patterns due to large variations in suitable substrate conditions for plant growth (Tuittila et al. 2000; Purre and Ilomets 2018) and the presence of nurse-plant species (Tuittila et al. 2000; Groeneveld et al. 2007), whereas in undisturbed bogs microtopography explains the largest portion of variation in vegetation composition (Korrensalo et al. 2018; Mežaka et al. 2018).

Sphagnum has been considered a keystone genus of peatland restoration (Rochefort 2000). In the newly rewetted $Hara_{RS}$ site, *Sphagnum* was not yet present in the measurement plots, although some patches of lawn *Sphagnum* (mainly *Sphagnum cuspidatum*) were present in depressions with high water level. After rewetting, the height of the water table should remain a few centimetres below the peat surface, which leads to optimal conditions for *Sphagnum* growth and peat accumulation (Beyer and Höper 2015). *Sphagnum* has relatively high immigration potential (Campbell et al. 2003) and is abundant on the undisturbed plots bordering the rewetted ones, so further colonisation of *Sphagna* in recently rewetted sites is expected. In both older rewetting sites, *Sphagnum* had almost total cover. In addition, in the oldest $Kõrsa_R$ site, lawn *Sphagnum* species have created some relatively high hummocks and overgrow *E. vaginatum* tussocks. The AGP and IL of *Sphagnum* in the rewetted sites was similar to those reported by Ilomets (1982) in Estonian undisturbed peatlands, while we measured about double the production and somewhat higher IL of *Sphagna* on the undisturbed sites. This probably results from different methods used for growth measurements (Pouliot et al. 2010), variations in weather conditions (Vitt 1990; Bengtsson et al. 2020) and species composition (Lindholm and Vasander 1990; Bengtsson et al. 2020).

Carbon Dioxide Fluxes

Both the undisturbed sites ($Kõrsa_P$ and $Hara_P$) and the older rewetted sites ($Kõrsa_R$ and $Hara_{RN}$) were CO_2 net sinks during the growing season, while the more recently rewetted site ($Hara_{RS}$) was still a CO_2 source. Variations in CO_2 fluxes between the rewetted sites are largely due to differences in vegetation, weather and water levels — while some sites are important CO_2 sinks (Tuittila et al. 1999; Beyer and Höper 2015; Wilson et al. 2016; Lee et al. 2017; Purre et al. 2019a), others could be small CO_2 sources (Tuittila et al. 1999; Waddington and Warner 2001; Beyer and Höper 2015; Purre et al. 2019a). Although rewetted sites could be CO_2 sources in the first decades after rewetting, they should become a CO_2 net sink with time (Samaritani et al. 2011). Similar (Komulainen et al. 1999) or higher (Soini et al. 2010; Strack et al. 2016) CO_2 net uptake on rewetted sites as in reference sites has been reported about ten years after rewetting, which is consistent with our results.

NEE in the rewetted sites is likely connected with differences in R_{ECO} rather than P_g (Samaritani et al. 2011; Wilson et al. 2016). Similar to our results from the Hara rewetted site, lower CO_2 net uptake due to higher R_{ECO} has been reported from newly rewetted sites than from undisturbed bogs (Urbanová et al. 2012). In contrast, in the studies by

Soini et al. (2010), Christen et al. (2016) and Strack et al. (2016), higher P_g compensated for high R_{ECO}, therefore leading to a higher CO_2 net uptake on a rewetted site, which is consistent with our results from the Kõrsa$_R$.

CO_2 fluxes and model parameters varied more strongly between the measurement plots of the rewetted sites compared to undisturbed sites, as also reported by Soini et al. (2010), Laine et al. (2016) and Strack et al. (2016). Observations may be driven by larger variations in PFT cover in the rewetted sites. Unvegetated plots on rewetted sites remain CO_2 sources (Wilson et al. 2016; Purre et al. 2019a) but measurement plots turn from a CO_2 source to a sink with increasing plant cover (Strack et al. 2016; Purre et al. 2019a). Respiration on younger sites still containing fragmented vegetation cover and lower diversity of plant species is largely influenced by peat temperature and water table depth, whereas those factors have a smaller effect on sites where vegetation has recovered well (Waddington and Warner 2001; Samaritani et al. 2011; Vanselow-Algan et al. 2015). Therefore, it could be expected that the CO_2 sink function will increase and be more stable with secondary succession after rewetting, especially as the actual acrotelm is formed with time.

We detected some effect of site status on plant aboveground biomass, which on rewetted sites had a strong positive correlation with P_g, whereas in undisturbed plots the correlation between plant biomass and P_g was insignificant. Similarly to our rewetted sites, Marinier et al. (2004) reported higher photosynthesis in plots with higher AGB, but plots with high AGB have also been reported to have higher R_{ECO} (Marinier et al. 2004; Strack et al. 2016; Brown et al. 2017). This was not the case in our rewetted sites, although in the undisturbed sites, R_{ECO} and vascular plant biomass had a strong positive correlation. The lack of correlations between the R_{ECO} and vascular plant biomass on rewetted milled peatlands is probably due to the domination of heterotrophic respiration on such sites (Wilson et al. 2007b; Järveoja et al. 2016; Purre et al. 2019a, b; Laine et al. 2016; Strack et al. 2016) also reported interaction between peatland management (undisturbed, rewetted), PFTs and carbon sequestration. According to Järveoja et al. (2016), those correlations depend on water level depth — if the water level is high in restored milled peatlands, bryophyte cover correlates with NEE, P_g and autotrophic respiration, whereas with deeper water table CO_2 fluxes correlate with vascular plant cover. Therefore, the different correlations on rewetted and undisturbed sites are consistent with previous studies (Strack et al. 2016) and could be related to differences in water table height and fluctuations on sites with different management.

There are large differences in photosynthetic capacities between PFTs. In the undisturbed sites, we measured higher photosynthesis and maximum photosynthesis rates (P_{max}) in plots exhibiting higher *E. vaginatum* cover. Vascular plant, especially graminoid biomass, has a relatively large impact on NEE in comparison with their abundance (Laine et al. 2012; Hassanpour Fard et al. 2020), due to their high photosynthetic capacity (Komulainen et al. 1999; Kivimäki et al. 2008; Urbanová et al. 2012; Strack et al. 2014; Laine et al. 2016). As *E. vaginatum* was present or abundant on most of the rewetted plots, the lack of correlation between the sedge cover and photosynthesis on the rewetted sites was unexpected. In addition to having high P_{max}, this sedge species also has high light use efficiency (parameter k in the photosynthesis model) (Kivimäki et al. 2008) and high respiration rate (Jordan et al. 2016). Still, in the case of a high water table, rewetted sites with high *E. vaginatum* cover have a CO_2 net sink function, even in unfavourable habitat conditions such as the occasionally lower water table during drought periods (Tuittila et al. 1999).

In the rewetted sites, higher P_g and P_{max} were measured with higher evergreen shrub cover. Evergreen shrubs stand out from other vascular plants with low photosynthesis and respiration rates (Laine et al. 2016), while in contrast Korrensalo et al. (2016) reported high P_{max} on evergreen shrubs like *A. polifolia*, *C. vulgaris* and *V. oxycoccus*, which are also present in the undisturbed sites and Kõrsa$_R$ in our study. According to Korrensalo et al. (2016), the P_{max} of evergreen shrubs varies between species belonging to the same PFT. Still, the cause of controversies between different studies remains unclear and could be result of a rather low number of measurements that do not cover the whole ecosystem variation.

High photosynthesis in the case of higher evergreen shrub cover in this study could also be connected with higher plant cover and the number of PFTs on the measurement plots in Kõrsa$_R$ where evergreen shrubs were present. According to Kivimäki et al. (2008), the presence of different PFTs lowers the R_{ECO}/P_g ratio, so creating conditions for higher CO_2 net uptake as in Kõrsa, while in monostands of *E. vaginatum* this ratio is higher, which also explains a lower CO_2 net uptake, as well as CO_2 net emissions from the younger site in this study. According to Hassanpour Fard et al. (2020), the presence of some key species or PFTs either in monostand or in mixed community support the larger carbon accumulation during the growing season than the mixed communities with a different number of PFTs lacking such certain species. Whereas most vascular plants, especially sedges, have high P_g during summer when their LAI is highest, the importance of *Sphagnum* in CO_2 sequestration expresses itself during spring and autumn, when LAI_{vasc} is low (Korrensalo et al. 2017).

In the rewetted sites, CO_2 net sink function was larger in plots with higher *Sphagnum* cover. *Sphagnum* has lower photosynthetic capacities than vascular plants (Laine et al. 2012; Christen et al. 2016; Korrensalo et al. 2016) and also low respiration rates (Waddington and Warner 2001; Laine et al. 2016), and by increasing soil moisture content, a *Sphagnum* carpet could reduce soil respiration (Waddington and Warner 2001). However, restoring the *Sphagnum* carpet may not be enough for CO_2 sequestering (Samaritani et al. 2011), especially as a newly formed *Sphagnum* carpet is sensitive to drier conditions (Tuittila et al. 2004). Therefore, constant high water tables are necessary, which support CO_2 accumulation of those sites early on after restoration activities (Günther et al. 2017).

Conclusion

Although vegetation structure on rewetted milled peatlands approached the reference condition with time, some plant functional types present in the undisturbed reference sites such as late succession shrubs and hummock *Sphagnum* could be absent even decades after rewetting. Vegetation composition developing with time affects the carbon accumulation of rewetted sites. During the studied growing season, milled peatlands rewetted more than 10-years prior were carbon sinks similar to the reference sites, whereas the most recently rewetted site was still a carbon source to the atmosphere. Although graminoids play an important role in the photosynthesis of rewetted sites, as they do in undisturbed reference bogs, the carbon accumulation of rewetted peatlands is related with development of the *Sphagnum* mat, which is present in the reference sites. A well-developed *Sphagnum* mat also reflects the development of other environmental variables, of a functioning acrotelm and the development of a C sink function. Thus, a well-developed *Sphagnum* lawn could be used as an indicator of successful restoration. However, general plant functional type composition can still differ from reference sites in some accounts even several decades after rewetting.

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Author Contributions Both authors contributed to the study conception and design. Anna-Helena Purre conducted the material preparation, fieldwork, laboratory and data analysis, and she wrote the first draft of the manuscript. Mati Ilomets commented on previous versions of the manuscript. Both authors read and approved the final manuscript.

Animal Research (Ethics): Not applicable.

Data Availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Code Availability The codes used for data modelling and analysis are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Consent to Participate Not applicable.

Consent to Publish Not applicable.

Plant Reproducibility Not applicable.

Clinical Trials Registration Not applicable.

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