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# Carbon dioxide fluxes and vegetation structure in rewetted and pristine peatlands in Finland and Estonia

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Vast areas of peatlands have been drained for forestry endangering their carbon sink function. Peatland rewetting aims at mitigating the situation through restoring the hydrology and vegetation of these areas. We compared the carbon dioxide ($CO_2$) fluxes and phytomass on four pairs of rewetted and pristine peatland sites in Finland and Estonia, and described correlations between phytomass and $CO_2$ fluxes. We measured the net ecosystem exchange of $CO_2$ (NEE), respiration and photosynthesis over one growing season using manual chambers, and biomass of plant functional types (PFT) on rewetted sites and their pristine counterparts. Although pair-wise differences in the vegetation were small, pristine sites were on average stronger $CO_2$ sinks than rewetted sites. Respiration was higher in hummocks while no differences were found in photosynthesis between hummocks and hollows. No clear relationship between the biomasses of PFTs and NEE was found. Generally, however, $CO_2$ uptake decreased with increase in *Sphagnum* biomass.

## Introduction

Northern peatlands cover an area of about 4 million km$^2$ (Yu 2012). Although carbon (C) exchange between the ecosystem and the atmosphere varies annually (Lafleur *et al*. 2003; Limpens *et al*. 2008; Lund *et al*. 2012; Yu 2012; Korrensalo 2017), long-term carbon dioxide ($CO_2$) sink function is prevailing in pristine peatlands (Yu 2012; Helfter *et al*. 2014; Korrensalo 2017). Thus, more carbon is assimilated by plants and deposited as litter to form soil organic matter (SOM) than is being released through respiration and SOM mineralisation. The carbon stock of peatlands in the northern hemisphere is estimated at 500 Gt C (Yu 2012), about 0.7 Gt C of which is in Estonia (Ilomets 1996) and about 5.5 Gt C in Finland (Minkkinen *et al*. 2002).

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In Finland, about 50 000 km$^2$ (Päivänen and Hånell 2012) and in Estonia about 5600 km$^2$ (Pikk 1997; Ilomets 2017) of peatlands have been drained for forestry, which makes up about 56% and 61% of total peatland area in Finland and Estonia, respectively. Drainage increases SOM decomposition and often turns peatlands from soil C sinks to C sources (Minkkinen and Laine 1998; Lohila *et al*. 2011; Simola *et al*. 2012, Meyer *et al*. 2013; Ojanen *et al*. 2013; Uri *et al*. 2017). Rewetting of especially low-productive forestry-drained peatlands, such as nutrient poor bogs and initially wet and very sparsely treed patterned fens, could provide a way to restore the C sink function of these peatlands (Komulainen *et al*. 1999). Although the knowledge base on carbon sequestration in pristine peatlands and its relationships with vegetation is increasing, only few studies (e.g., Komulainen *et al*. 1999; Urbanová *et al*. 2012; Laine *et al*. 2016) have tackled those questions on rewetted formerly forestry-drained peatlands.

Rewetting aims at recreating suitable conditions for the development of mire plant communities and ecosystem functions that are similar to pristine peatlands, especially the carbon accumulation function. Wilson *et al*. (2016a) report significant reduction of $CO_2$ emissions in case of rewetting of peatlands drained for forestry. About 30 000 ha of forestry-drained peatlands have been rewetted in Finland (Parks & Wildlife Finland, unpublished) and about 1800 ha in Estonia (Purre A.-H., unpublished). Knowledge of the restoration success of forestry-drained peatlands is, however, still relatively scarce, while more research has been done on rewetted milled peatlands (e.g., Waddington *et al*. 2001; Waddington and Warner 2001; Strack *et al*. 2016). More insight is needed about $CO_2$ fluxes and vegetation of forestry drained peatlands that have been rewetted at least five years ago, as earlier studies (e.g., Komulainen *et al*. 1999; Urbanová *et al*. 2012) analyse $CO_2$ fluxes only one to two years after rewetting. There are indications that the recovery of C accumulation may be relatively fast (less than decade) and it may occur before the recovery of mire plant communities has taken place (Komulainen *et al*. 1999; Urbanová *et al*. 2012; Kareksela *et al*. 2015; Wilson *et al*. 2016b).

Above-ground plant biomass has been found to correlate with the $CO_2$ exchange between ecosystem and the atmosphere. Several authors relate differences in photosynthesis and respiration rates with differences in vegetation structure in terms of species composition, plant functional types (PFT), and microtopography (Riutta *et al*. 2007a; Wilson *et al*. 2007; Korrensalo *et al*. 2016). Different PFTs have different photosynthetic capacities, e.g., vascular plants are more efficient assimilators in high light than mosses (Laine, A.M. *et al*. 2012; Strack *et al*. 2016) and the rate of photosynthesis and respiration of a given PFT can vary depending on the peatland's eco-hydrological state as affected by management (drained, rewetted, pristine; Laine *et al*. 2016). Higher photosynthesis rates have measured among vascular plant PFTs such as sedges and shrubs in comparison with mosses in pristine peatlands (Riutta *et al*. 2007b; Korrensalo *et al*. 2016), while higher bryophyte abundance is connected with lower ecosystem respiration (Laine *et al*. 2016). In restored milled peatlands, higher photosynthesis and growing season net $CO_2$ exchange has been reported from plots with higher sedge and *Sphagnum* abundance, while higher shrub and true moss abundance led to lower $CO_2$ sink or $CO_2$ source through increased respiration (Purre *et al*. 2019). Such studies are needed also on rewetted forestry drained peatlands.

After rewetting, vegetation tends to recover more rapidly in hollows than in higher microtopographic zones (Hancock *et al*. 2018). In addition, Komulainen *et al*. (1999) reported higher $CO_2$ net uptake in hollows than in hummocks of forestry drained peatlands two years after rewetting. Still, there's a lack of knowledge and discrepancy about $CO_2$ exchange on different microtopographic zones in rewetted forestry-drained peatlands that have been rewetted a longer time ago. Korrensalo (2017) detected high spatial variation in the carbon dioxide exchange of plant communities and found higher rates of photosynthesis and respiration in hummocks than in lower microforms of a pristine bog. Munir *et al*. (2013) also reported higher net primary production but lower respiration in hummocks than in hollows of a wooded peatland. This is probably the result of variations in hydrology and vegetation between hummocks and hollows.

The main aim of this study was to compare growing season $CO_2$ exchange and vegetation structure between four rewetted, previously forestry-drained boreal peatland sites and their pristine counterparts. Specifically, we focused on the vegetation structure by PFT's and the net ecosystem exchange (NEE) and its components between hummocks and hollows in rewetted and pristine peatlands. Based on earlier research, we hypothesize that rewetting results in: 1) restoration of the vegetation in terms of PFT biomasses' similarity with respective pristine peatlands within a decade; and 2) similar carbon dioxide balances (NEE) in pristine and rewetted sites.

**Fig. 1**. Location of the paired sites (▲ – only chamber measurements, ■ – EC measurements in pristine sites in addition to chamber measurements). A) Sodankylä, B) Tammela, C) Sipoo, D) Viljandi.

## Material and methods

### Site

The study was carried out on four paired sites, three of them located in Finland (Tammela, Sipoo and Sodankylä) and one in Estonia (Viljandi). Each pair consisted of a pristine (undrained) site and a formerly forestry-drained and then rewetted site. Three pairs represented southern ombrotrophic raised bogs and one pair northern minerotrophic aapa mire (Fig. 1, Table 1). The pristine and rewetted sites of all the raised bog pairs were located within the same mire basin (Tammela, Sipoo, Viljandi), whereas the aapa mire sites (Sodankylä) were in two separate but adjacent mire-basins. All pairs of sites were considered to represent initially similar eco-hydrological conditions based on microtopography, trophic level (species composition), and chemical and physical properties of peat (bulk density, C and N concentrations).

Tammela, Sipoo and Viljandi sites are *Sphagnum*-dominated peatlands with low cover of trees (*Pinus sylvestris*) and dominant vascular plant species are *Eriophorum vaginatum* and *Calluna vulgaris*. The rewetted site in Viljandi has also high cover of forest mosses (mainly *Pleurozium schreberi* and *Dicranum polysetum*) and *Vaccinium* species. Sodankylä sites have low cover of *Betula pubescens*, and are dominated by brown mosses, *Sphagnum*, *Carex* spp. and *Eriophorum* species. The drained site in Tammela was rewetted by Parks and Wildlife Finland (Metsähallitus) and in Viljandi by State Forest Management Centre (Riigimetsa Majandamise Keskus). The drained sites in Tammela and Sipoo sites were rewetted by filling the ditches with peat. In the Viljandi drained site, ditches were dammed with wooden and peat dams. The Sodankylä rewetted site has been self-restored due to blocking of ditches by army vehicles that have frequently crossed the downstream part of the peatland. In the Sodankylä and Tammela pristine sites, eddy covariance (EC) measurement stations were also present.

### Vegetation measurements

Biomass samples were collected at the end of July 2015 from each site in order to get the peak biomass of the growing season (Korrensalo *et al*. 2017). Based on visual evaluation of microtopography and vegetation measurements, plots were divided into hummocks and hollows. The

**Table 1**. Location and description of the study sites.

| Site | Sodankylä | | Tammela | | Sipoo | | Viljandi | |
|---|---|---|---|---|---|---|---|---|
| Site name | Halssiaapa (pristine)/ Välisuvannonjänkä (rewetted) | | Tervalamminsuo | | Stormossen | | Kuresoo | |
| Status | Rewetted | Pristine | Rewetted | Pristine | Rewetted | Pristine | Rewetted | Pristine |
| Coordinates | 67°22´N, 26°39´E | 67°25´N, 26°30´E | 60°38´N, 23°58´E | | 60°19´N, 25°20´E | | 58°28´N, 25°12´E | |
| Year of first-time drainage | before 1979 | n.a. | ca. 1969 | n.a. | before 1969 | n.a. | 1950–1960 | n.a. |
| Year of restoration | ca. 2006 | n.a. | 2005 | n.a. | 2006–2012 | n.a. | 2013 | n.a. |
| Site type[a] | n.d. | Tall-sedge flark fen, herb-rich flark fen, eutrophic flark fen | n.d. | Ridge-hollow pine bog | n.d. | Ridge-hollow pine bog | n.d. | Ridge-hollow pine bog |
| Water table (cm) | 0–8 | 2–5 | –5–23 | 4–22 | 6–28 | –3–28 | –7–35 | 5–26 |
| No. measurement plots[b] | HUM 2, HOL 2 | HUM 2, HOL 2 | HUM 5, HOL 3 | HUM 2, HOL 2 | HUM 2, HOL 2 | HUM 3, HOL 1 | HUM 2, HOL 2 | HUM 2, HOL 2 |
| Distance between rewetted and pristine site (m) | 9300 | | 986 | | 58 | | 430 | |
| Vegetation zone | Northern boreal | | Southern boreal | | Boreo-nemoral | | Boreo-nemoral | |
| Continuous PAR and $T_{\mathrm{AIR}}$ measurements | Sodankylä pristine site[c] | | Tammela pristine site[c] | | Kumpula WS[c] | | Pärnu-Sauga WS (PAR) and Riisa WS ($T_{\mathrm{AIR}}$)[d] | |

[a] site type according to Laine, J. et al. (2012)

[b] HUM–number of vascular plant biomass and CO2 flux measurement plots on hummocks; HOL–number of vascular plant biomass and CO2 flux measurement plots on hollows; WS–weather station

[c] data from Finnish Meteorological Institute

[d] data from Estonian Weather Service; n.a. – not applicable; n.d.- not determined.

average water table difference between hummocks and hollows was about 20–30 cm. We used different plot sizes for above-ground biomass measurements of vascular plants (circular plots with a 15 cm radius) and bryophytes (circular plots with a 2.5 cm radius). We clipped only the capitula from *Sphagnum* mosses and the uppermost 2 cm from other mosses. For vascular plants, all above-ground parts of plants (including stems of woody species) were collected for determination of above-ground biomass. We collected one vascular plant sample and three bryophyte samples per each $CO_2$ flux measurement plot. From Sipoo, Viljandi and Sodankylä we collected 24 bryophyte and 8 vascular plant samples from each paired site and from Tammela 36 bryophyte and 12 vascular plant samples. The sampling points were chosen from near the $CO_2$ flux measurement plots with similar vegetation. Plants were cleaned and dried for 48 h at 65°C. After drying, plants were weighed on the species level.

The leaf-area index of vascular plants (LAI, $m^2$ $m^{-2}$) were recorded during the $CO_2$ measurement campaigns. For the determination of LAI, four 10 cm × 10 cm subplots were marked with wooden sticks inside each NEE measurement plot and the number of leaves of vascular plants, leaf heights and widths were recorded by species as described by Wilson *et al*. (2007). To obtain the NEE measurement plots LAI, we summed the species specific LAI of each measurement plot as described in Badorek *et al*. (2011) and averaged the LAI of four subplots.

## $CO_2$ exchange measurements

NEE measurements were carried out during the growing season of 2015 (May–October in the southern sites, June–August in the north) at least once a month (twice in July). The growing season was defined based on degree-days. At least seven measurement campaigns were done in all sites resulting in total of 654 flux measurements, which fulfilled our quality requirements for data. The NEE measurement plots within each site (rewetted or pristine) were positioned into hummocks and hollows and were located within about 100 m distance of each other (Table 1). In preparation for the measurements, 60 cm × 60 cm square aluminium collars were permanently inserted to the selected measurement plots in spring 2015 at the latest, so that the sleeves of the collars extended to the depth of 20–30 cm into the soil. The collar sleeves prevented the roots of external vegetation from growing into the measurement plots. In Tammela and Sodankylä, vegetation analysis was made for the pristine sites when positioning the EC tower, and collars for chamber measurements were placed so that the locations of the collars should be representative for the whole site and also for EC footprint.

For $CO_2$ exchange measurements, we used a transparent 60 cm × 60 cm chamber (height 30 cm) equipped with a cooling system, ventilator and an infrared gas analyser (EGM-4, PP System (USA) in Sodankylä, Sipoo, Tammela, and Li-6400, Li-Cor (USA) in Viljandi). $CO_2$ concentration in the chamber was recorded every 15 s for two minutes. The chamber was ventilated between flux measurements. After measuring the $CO_2$ flux in full light, shading mesh nets were used to measure NEE in two irradiation levels, to develop light-response curves following the procedure described by Riutta *et al*. (2007b). One shading net reduced the penetration of photosynthetically active radiation (PAR, $\mu$mol $m^{-2}$ $s^{-1}$) on average by 65% and double netting by 88%, in comparison with ambient conditions. Finally, the chamber was covered with an opaque hood to measure ecosystem respiration ($R_{ECO}$). $CO_2$ flux rates were calculated based on a linear change in $CO_2$ concentration in time. Gross photosynthesis ($P_g$) was calculated by adding $R_{ECO}$ to NEE. We use sign convention so that $P_g$ and $R_{ECO}$ are always positive and thus positive NEE values indicate $CO_2$ net uptake to the ecosystem.

In addition to recording $CO_2$ fluxes, PAR inside the chamber was monitored and recorded (PAR-1, PP Systems (USA) in Finnish sites, and LI-190R, Li-Cor (USA) in Estonian site) during the $CO_2$ flux measurements. Also the temperature inside and outside the chamber, peat temperatures at 5 cm and 15 cm depths, water table depth and LAI of vascular plants were recorded during the measurement campaigns. PAR was not allowed to vary more than ±15% and inside temperature not to deviate for more than 5°C from the outside temperature. Water table (WT, cm) was measured manually from perforated plastic wells in each site. Continuously-measured PAR and air temperature ($T_{\mathrm{AIR}}$) hourly data for the reconstruction of $CO_2$ fluxes was granted from Finnish Meteorological Institute and Estonian Weather Service (Table 1). In Sodankylä and Tammela, continuous PAR and $T_{\mathrm{AIR}}$ measurements were from the respective pristine sites. In Sipoo, continuous measurements were done about 18 km from the study site in Kumpula and in Viljandi up to 29 km from the site (Pärnu-Sauga weather station).

In the Tammela pristine plot, eddy covariance (EC) measurements were carried out with infrared gas analyser LI-7200 (Li-Cor, USA) and in the Sodankylä pristine plot with LI-7000 (Li-Cor, USA). The ultrasonic anemometer USA-1 (Metek, USA) was used on both EC measurement sites. The measurement height was 6.5 m in Sodankylä and 7.0 m in Tammela. For data analysis, measurements from May–September 2015 were used in both sites. The EC fluxes were calculated as half-hourly block averages, taking into account the appropriate corrections following Aubinet *et al.* (2012). Data were screened for weak turbulence with a friction velocity threshold of 0.1 m $s^{-1}$. Gap-filling and partitioning of NEE data to $P_{\mathrm{g}}$ and $R_{\mathrm{ECO}}$ were done following the Reichstein *et al.* (2005). The measurement systems and the post-processing procedures are described in more detail in Aurela *et al.* (2009) and Lohila *et al.* (2011).

## Model description

### Vegetation

To model the change in the LAI of vascular plants ($\mathrm{LAI}_{\mathrm{vasc}}$) during the growing season, a Gaussian curve (Eq. 1; Wilson *et al.* 2007) was fitted for each plot using R-program (ver. 3.2.2.; R Core Team 2013) function *nls* from the *nlme* package (ver. 3.1 – 121; Pinheiro *et al.* 2015) for the estimation of parameters:

$$\mathrm{LAI}_{\mathrm{vasc}} = \mathrm{LAI}_{\mathrm{max}} \exp(-0.5(\frac{\mathrm{DOY} - x_{\mathrm{max}}}{b})^2), \qquad 1)$$

where $\mathrm{LAI}_{\mathrm{max}}$ is the maximum LAI of the vascular plants in the measurement plot during the growing season, DOY is the day of the year, $x_{\mathrm{max}}$ is the DOY when the maximum $\mathrm{LAI}_{\mathrm{vasc}}$ occurs and $b$ is a shape parameter.

### Carbon dioxide fluxes

Separate $P_{\mathrm{g}}$ and $R_{\mathrm{ECO}}$ models were parameterised for each measurement plot in order to reconstruct hourly $CO_2$ fluxes for the growing season (May–September 2015). To create $CO_2$ flux models, we only used measured fluxes that fulfilled requirements described by Järveoja *et al.* (2016). The $CO_2$ flux models were adapted from Wilson *et al.* (2007) and Kivimäki *et al.* (2008). The gross photosynthesis ($P_{\mathrm{g}}$; mg $CO_2$ $m^{-2}$ $h^{-1}$) model is a nonlinear model that uses the saturating response to PAR (Eq. 2), which also takes into account the $\mathrm{LAI}_{\mathrm{vasc}}$ during the growing season:

$$P_{\mathrm{g}} = \frac{P_{\mathrm{max}} \times \mathrm{PAR}}{(k + \mathrm{PAR})} \times \frac{\mathrm{LAI}_{\mathrm{vasc}}}{(\mathrm{LAI}_{\mathrm{vasc}} + s)}, \qquad (2)$$

where $P_{\mathrm{max}}$ is the maximum photosynthesis at light saturation (mg $CO_2$ $m^{-2}$ $h^{-1}$), $k$ is the PAR, when $P_{\mathrm{g}}$ reaches half its maximum (µmol $m^{-2}$ $s^{-1}$), $s$ is the value of $\mathrm{LAI}_{\mathrm{vasc}}$ ($m^2$ $m^{-2}$) where $P_{\mathrm{g}}$ reaches half its maximum. The parameters for $P_{\mathrm{g}}$ and $R_{\mathrm{ECO}}$ models are given in Appendix, Table A1.

The respiration model (Eq. 3) consists of an exponential response of ecosystem respiration ($R_{\mathrm{ECO}}$; mg $CO_2$ $m^{-2}$ $h^{-1}$) to the temperature inside the chamber ($T_{\mathrm{AIR}}$):

$$R_{\mathrm{ECO}} = r_0 \times \exp(b \times T_{\mathrm{AIR}}), \qquad (3)$$

where $r_0$ is the respiration rate at the temperature 0°C (mg $CO_2$ $m^{-2}$ $h^{-1}$), $b$ is the sensitivity of respiration to air temperature (1/°C) and $T_{\mathrm{AIR}}$ is the air temperature. Adding additional parameters (WT and LAI, as in Tuittila *et al.* (2004)) did not improve the $P_{\mathrm{g}}$ and $R_{\mathrm{ECO}}$ model performance. R-program (ver. 3.2.2.; R Core Team 2013) function *nls* from the *nlme* package (ver. 3.1 – 121; Pinheiro *et al.* 2015) was used for the estimation of parameters for

Eqs. 2 and 3. NEE was calculated by extracting $R_{ECO}$ from $P_g$. To evaluate model fit, we plotted observed vs. reconstructed values for each plot in addition to plotting measured vs. reconstructed $P_g$ values against PAR and respective $R_{ECO}$ values against $T_{AIR}$.

### Statistical analysis

Vegetation analysis was conducted at the PFT level on all sites. Laine A.M. *et al.* (2012) suggest the use of PFTs because species-level analyses are too complex for exploring feedbacks between the vegetation and ecosystem carbon dynamics. We divided above-ground plant biomass into five PFTs: (1) *Sphagna* (mainly *Sphagnum fuscum*, *Sphagnum rubellum*, *Sphagnum balticum*), (2) Bryopsida (*Polytrichum strictum*, *Aulacomnium palustre*, *Pleurozium schreberi*, *Warnstorfia* spp.), (3) shrubs (*Calluna vulgaris*, *Empetrum nigrum, Vaccinium* spp., *Rhododenron tomentosum*, *Andromeda polifolia*), (4) forbs and graminoids (*Eriophorum* spp., *Carex* spp., *Menyanthes trifoliata*, *Rubus chamaemorus*) and (5) tree seedlings (*Pinus sylvestris, Betula* spp.).

Descriptive and multivariate analyses of PFTs biomass and $CO_2$ fluxes were conducted with IBM SPSS Statistics ver. 21. As the data did not fulfil the normality requirements for parametric data analysis according to the Shapiro-Wilks test, a non-parametric data analysis method (Mann–Whitney test) was chosen for describing differences in average PFTs biomass (*Sphagna*, *Bryopsida*, shrubs, forbs and graminoids, and tree seedlings) and $CO_2$ fluxes (NEE, $P_g$, $R_{ECO}$) between hummocks and hollows of rewetted and pristine sites. The Spearman correlation coefficient was used to correlate *Sphagnum* biomass with NEE. Average values were brought out with standard error. Redundancy analysis (RDA) was conducted in PC-ORD ver. 7 (McCune and Mefford 2016) to relate PFTs biomass and $CO_2$ fluxes and model parameters. Response variables were standardized (centred and with unit variance), randomization test was applied to test if there is no relationship between matrices (PFT biomass matrix and $CO_2$ fluxes and model parameter's matrix).

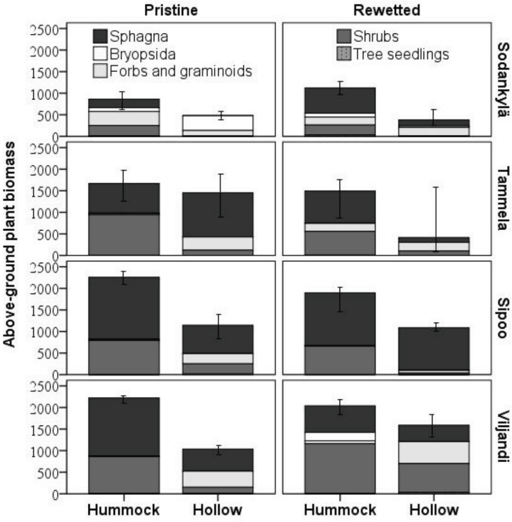

**Fig. 2**. Average above-ground plant biomass (g $m^{-2}$) in the study sites, measured during the peak (end of July) of the growing season. ± 95% confidence intervals are given for total above-ground plant biomass.

## Results

### Above-ground plant biomass

We found no differences in the PFT biomass in hummocks or hollows between the pristine and rewetted sites in any of the sites according to Mann-Whitney test (Fig. 2). The average biomass of bryophytes was about 800 g $m^{-2}$ in the pristine and 700 g $m^{-2}$ in rewetted sites ($n = 36$, $Z = -0.7$, $p = 0.484$), and the vascular plant biomass about 700 g $m^{-2}$ in the pristine and rewetted sites ($n = 36$, $Z = -0.1$, $p = 0.949$). In the most recently rewetted site of the study, Viljandi, Bryopsida were absent from the pristine plot, but were present in the rewetted site ($n = 8$, $Z = -2.0$, $p = 0.047$), also vascular plant biomass was somewhat higher in the rewetted site ($n = 8$, $Z = -2.0$, $p = 0.043$). In other paired sites, there were no differences in PFT abundance between rewetted and pristine sites according to Mann-Whitney test ($n = 4$–$8$, $Z > -1.9$, $p > 0.064$).

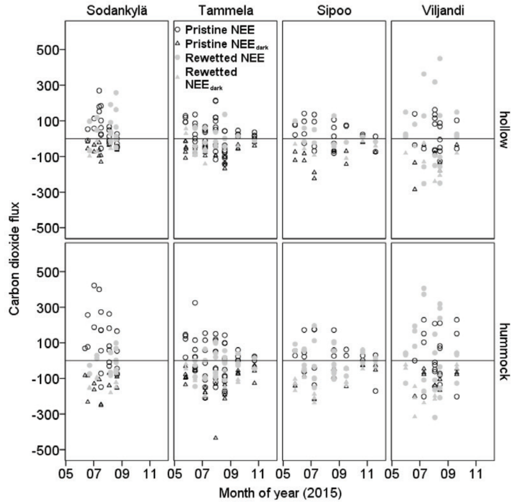

**Fig. 3**. Measured NEE (mg $CO_2$ $m^{-2}$ $h^{-1}$) and NEE$_{dark}$ (mg $CO_2$ $m^{-2}$ $h^{-1}$) based on chamber measurements during growing season of 2015 in hummocks and hollows of pristine and rewetted sites in each location. Positive values indicate net $CO_2$ uptake.

In all sites, plant biomass was higher in hummocks (1630 ± 140 g $m^{-2}$) than in hollows (1070 ± 130 g $m^{-2}$) ($n = 36$, $Z = -2.77$, $p = 0.001$). Shrub ($n = 36$, $Z = -3.98$, $p = 0.001$) and Sphagna ($n = 36$, $Z = -2.33$, $p = 0.002$) biomass was significantly higher in hummocks than in hollows. On the contrary, forbs and graminoids had higher biomass in hollows than in hummocks ($n = 36$, $Z = -3.3$, $p = 0.001$). In site-wise comparison of PFT distribution between the hummocks and hollows, Tammela pristine site hummocks had significantly higher biomass of tree seedlings ($n = 8$, $Z = -2.25$, $p = 0.024$) and shrubs ($n = 8$, $Z = -2.24$, $p = 0.025$), but lower biomass of forbs and graminoids ($n = 8$, $Z = -2.25$, $p = 0.024$). In other sites, none of the PFTs biomass differed significantly between hummocks and hollows ($n = 4$–$8$, $Z \leq -1.94$, $p \geq 0.053$).

## Carbon dioxide fluxes

The NEE and $R_{ECO}$ in hummocks and hollows of rewetted and pristine site pairs in Tammela, Sodankylä, and Sipoo, measured by chambers, varied in similar ranges, mainly between –300 mg $CO_2$ $m^{-2}$ $h^{-1}$ and 300 mg $CO_2$ $m^{-2}$ $h^{-1}$, whereas in Viljandi the measured fluxes varied more in the rewetted site than in the pristine site (Fig. 3). The maximum measured $CO_2$ net uptake was more pronounced in Sodankylä paired sites and in rewetted site in Viljandi than in other sites.

The average maximum level of photosynthesis in light saturation ($P_{max}$ in Eq. 2) was higher in the pristine sites, 357.9 ± 36.6 mg $CO_2$ $m^{-2}$ $h^{-1}$, and lower in the rewetted sites, 288.5 ± 46.0 mg $CO_2$ $m^{-2}$ $h^{-1}$ (Appendix, Table A2). When hummocks and hollows were analysed separately, pristine sites had a higher average $P_{max}$ and $k$ than rewetted sites. The level of PAR, where $P_g$ reaches half its maximum (parameter $k$ in Eq. 2) was similar on the pristine sites (477.2 ± 81.2 µmol $m^{-2}$ $s^{-1}$) as in the rewetted sites (313.0 ± 47.0 µmol $m^{-2}$ $s^{-1}$).

The temperature sensitivity of $R_{ECO}$ (parameter $b$ in Eq. 3) was on average higher in the pristine (296.6 ± 34.4 1/°C) than in the rewetted sites (239.0 ± 48.4 1/°C). This value deviated significantly in Tammela and Viljandi between the rewetted and pristine sites, but in opposite directions: while in Viljandi, the parameter $b$ was higher in the rewetted site than in the pristine site; in Tammela it was lower in the rewetted site. The $r_0$ parameter was similar in the pristine (46.1 ± 5.3 mg $CO_2$ $m^{-2}$ $h^{-1}$) and rewetted (64.0 ± 10.4 mg $CO_2$ $m^{-2}$ $h^{-1}$) sites. In Sipoo, none of the parameters in $P_g$ and $R_{ECO}$ models differed between the pristine and the rewetted sites.

### Reconstructed chamber fluxes and eddy covariance fluxes

Reconstructed NEE differed significantly between the pristine and rewetted sites in Tammela, Sodankylä and Sipoo (Fig. 4; Appendix, Table A2). The hourly-averaged reconstructed NEE was –5.4 ± 17.1 mg $CO_2$ $m^{-2}$ $h^{-1}$ (source) in the rewetted sites and 37.9 ± 9.9 mg $CO_2$ $m^{-2}$ $h^{-1}$ (sink) in the pristine sites. In addition to NEE, $P_g$ differed between the pristine and rewetted sites in Sodankylä. When rewetted and pristine sites

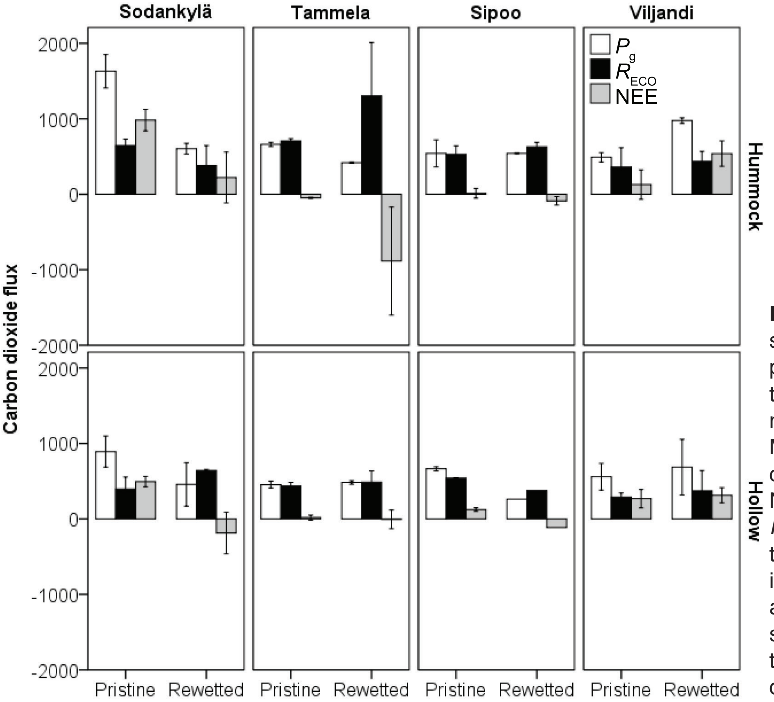

**Fig. 4**. Modelled gross photosynthesis ($P_g$), ecosystem respiration ($R_{ECO}$), and net ecosystem exchange (NEE) (g CO$_2$ m$^{-2}$ ) (± SE) for the period from May–September 2015 based on chamber measurements. NEE = $P_g$ – $R_{ECO}$ $R_{ECO}$. Note that $P_g$ and $R_{ECO}$ are always positive for clarity. Therefore, NEE is positive if the ecosystem is a CO$_2$ sink during the growing season while NEE is negative if the ecosystem is a CO$_2$ source during the growing season.

were pooled, photosynthesis was higher in the pristine (127.6 ± 16.1 mg CO$_2$ m$^{-2}$ h$^{-1}$), than in the rewetted sites (80.3 ± 9.1 mg CO$_2$ m$^{-2}$ h$^{-1}$). There was no statistically significant difference in respiration between the rewetted (83.6 ± 14.9 mg CO$_2$ m$^{-2}$ h$^{-1}$) and pristine sites (86.9 ± 11.4 mg CO$_2$ m$^{-2}$ h$^{-1}$).

Hummocks had significantly higher $R_{ECO}$ ($n_{hum}$ = 20, $n_{hol}$ = 16, $Z$ = –2.45, $p$ = 0.014) (Fig. 4) and $r_0$ ($Z$ = –2.34, $p$ = 0.019) than hollows. $P_g$ and NEE did not differ statistically significantly between hummocks and hollows (Fig. 4). Hummocks (Appendix, Table A3) and hollows (Appendix, Table A4) had no significant differences in their $P_g$, $R_{ECO}$, NEE or $P_g$ and $R_{ECO}$ model parameters between the pristine and rewetted sites within any of the site pairs.

According to EC measurements, average $P_g$ was 319.6 mg CO$_2$ m$^{-2}$ h$^{-1}$, average $R_{ECO}$ was 290.7 mg CO$_2$ m$^{-2}$ h$^{-1}$ and average NEE was 28.9 mg CO$_2$ m$^{-2}$ h$^{-1}$ in the Tammela pristine site from May–September 2015. In the Sodankylä pristine site, average $P_g$ (292.9 mg CO$_2$m$^{-2}$ h$^{-1}$) and average $R_{ECO}$ (217.4 mg CO$_2$m$^{-2}$ h$^{-1}$) were smaller, but due to greater difference between $P_g$ and $R_{ECO}$ as compared to Tammela, average NEE was higher (75.5 mg CO$_2$m–2 h$^{-1}$) in the Sodankylä pristine site, indicating higher net CO$_2$ uptake there.

## Relationship between CO$_2$ fluxes and PFT biomass

When all plots were combined, plots with higher *Sphagnum* biomass had lower CO$_2$-binding abilities (NEE) ($\rho$ = –0.36; $p$ = 0.032; $n$ = 36) (Fig. 5). According to RDA, two axes explained about 66 % in rewetted and 80 % in pristine plots of the variation in PFT biomass, CO$_2$ fluxes and model parameters (Fig. 5). In pristine plots, differences in biomass of forbs and graminoids, and shrubs described the first axis correlating with $P_g$ and NEE, while the second axis is described by differences in tree and bryopsida biomass correlating mainly with $b$ parameter of $R_{ECO}$ models. The third axis (not shown in the figures) explained about 14% of variance and was

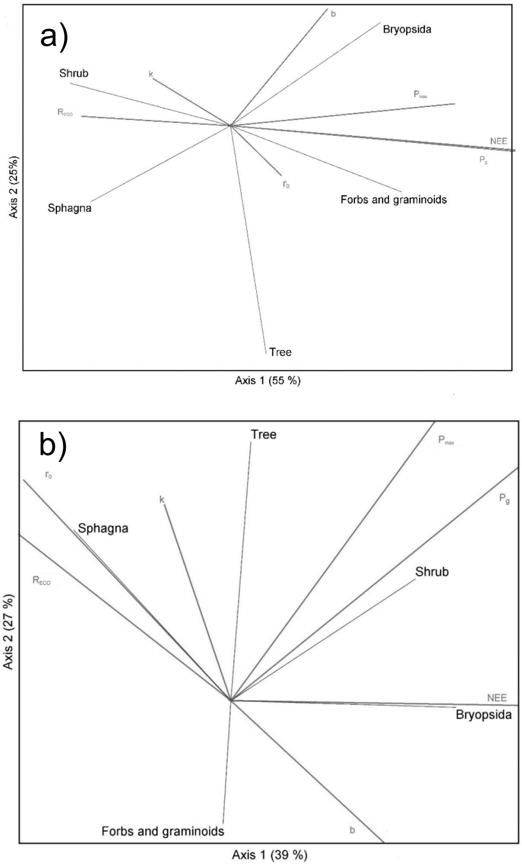

**Fig. 5**. Redundancy analysis of PFTs, $CO_2$ flux components (based on chamber measurements) and $CO_2$ model parameters in the (**a**) pristine and (**b**) rewetted sites.

defined by shrub biomass and *Sphagnum* biomass and correlated mainly with $R_{ECO}$. In rewetted plots, the third axis explained about 19% of total variance and was mainly described by forbs and graminoids and correlated with b parameter. In rewetted plots, first axis was described by variations in Bryopsida and shrub biomass and the second axis by tree and *Sphagnum* biomass. First axis correlated most strongly with NEE and $P_g$ and the second axis with $r_0$ and $P_{max}$.

## Discussion

### Above-ground biomass

Biomasses of plant functional types did not differ significantly in hummocks or hollows between the rewetted and pristine sites, thus supporting our first hypothesis stating that rewetting has restored the vegetation to similar PFT biomasses as in corresponding pristine sites. Still, lack of differences could be the result of the small number of samples in the study and relatively large variability in the PFT biomasses among measurement plots. On the species level, Kareksela *et al*. (2015) detected significant differences in vegetation composition between drained, pristine and rewetted sites. Also in our study, there were some differences in species abundances between rewetted and pristine sites. Especially in the most recently rewetted site in Viljandi, plant species typical to forests (e.g., *Pleurozium schreberi*, *Dicranum polysetum*, *Vaccinium vitis-idaea*) were present in the rewetted site but absent from the pristine site.

Peatland drainage sets vegetation community succession from peatland to forest trajectory (Pellerin *et al*. 2008; Urbanová *et al*. 2012). After drainage, shrub abundance increases (Laiho *et al*. 2003; Urbanová *et al*. 2012; Potvin *et al*. 2015; Paal *et al*. 2016; Mäkiranta *et al*. 2017) and peatland shrubs are replaced by forest shrubs (Laiho *et al*. 2003; Laine *et al*. 2011), also graminoid abundance decreases (Laiho *et al*. 2003; Straková *et al*. 2010). After water-level drawdown, also tree abundance increases significantly (Pellerin *et al*. 2008; Straková *et al*. 2010; Paal *et al*. 2016; Mäkiranta *et al*. 2017). In the bryophyte layer, *Sphagnum* and mire mosses are replaced by true mosses typical to forests (Straková *et al*. 2010; Laine *et al*. 2011; Potvin *et al*. 2015; Paal *et al*. 2016).

Similarly to parts of peatlands that have been rewetted about ten years before the measurements in the current study (Sipoo, Tammela, Sodankylä) and which have similar vegetation as their respective pristine parts, the recently rewetted Viljandi site is expected to develop similar vegetation composition over time as in the pristine part of the peatland. Typically after the rewetting, the abundance of *Sphagnum* increases, while other mosses and lichens decrease; also the abundances of different shrub species should approach the values characteristic of pristine bogs (Komulainen *et al*. 1999; Haapalehto *et al*. 2011; Laine *et al*. 2016). This is probably the reason for similarity of pristine and older rewetted sites in current studies. Still, vegetation composition in drained and rewetted sites is spatially more heterogeneous than in undrained sites (Laine *et al*. 2016; Haapalehto *et al*. 2017).

Vegetation in the older rewetted sites was similar to the respective pristine sites, while some significant differences were observed in the most recently rewetted site in Viljandi. This is in accordance with earlier results (Kareksela *et al*. 2015; Laine *et al*. 2016; Haapalehto *et al*. 2017) suggesting that vegetation composition and the amount and distribution of phytomass between the PFTs change over time after the rewetting — communities more similar to pristine sites evolve within ten years after rewetting, while more recently rewetted sites still resemble drained sites. The short period between the vegetation analysis and rewetting is probably the rationale behind the higher abundance of brown mosses (that were absent from the pristine site) and vascular plants in the rewetted site in Viljandi.

## Carbon dioxide fluxes

According to our results, ecosystem respiration was similar in the pristine and rewetted sites within all pairs of sites and photosynthesis differed significantly between the pristine and rewetted sites only in Sodankylä. Contrary to that, Urbanová *et al*. (2012) and Laine *et al*. (2016) measured higher respiration in rewetted than in pristine sites. In our measurements, variation between the sites in $CO_2$ fluxes was greater in the rewetted than in pristine sites (Fig. 4). Similar results were also reported by Soini *et al*. (2010) and Strack *et al*. (2016). Such a situation is explained by a larger variation in vegetation in rewetted sites due to large spatial variation in environmental conditions and varying development stages within the ecosystem.

Reconstructed average $R_{ECO}$ (Fig. 4) and respiration rates were about 40% higher in hummocks than in hollows. Similarly, Laine, A.M. *et al*. (2012), Maanavilja *et al*. (2011) and Korrensalo (2017) measured higher $R_{ECO}$ in hummocks. However, while several papers (Moore *et al*. 2002; Maanavilja *et al*. 2011; Laine, A.M. *et al*. 2012; Munir *et al*. 2013; Korrensalo 2017) measured also higher $P_g$ in hummock communities than in hollows, no significant difference in $P_g$ between hummocks and hollows was found in the current study. No significant differences in $R_{ECO}$ and $P_g$ between hollows and hummocks was found in Bubier *et al*. (2003) in a bog. These differences in results could be explained by various heights of the hummocks in different studies, as hummocks in the study by Bubier *et al*. (2003) were lower than those in the study by Maanavilja *et al*. (2011). Also different weather conditions could play a part in different results in various studies, as hollow species are more affected by drought than hummock species (Kuiper *et al*. 2014; Nijp *et al*. 2014) and also the presence of different plant functional types plays a role in drought resilience of hummock and hollow communities (Kuiper *et al*. 2014).

Our results indicated $CO_2$ net uptake during the growing season in pristine plots but net loss from rewetted plots in three of the four paired sites (Fig. 4) due to differences in vegetation (discussed thoroughly in subsequent sub-chapter). Only in our most recently rewetted site, Viljandi, both hummocks and hollows showed net uptake of $CO_2$. This contradicts our second hypothesis stating that $CO_2$ balance would not differ between the rewetted and pristine plots of the same site. Also Komulainen *et al*. (1999) measured $CO_2$ uptake during the growing season already one year after rewetting. The large carbon dioxide uptake in recently rewetted sites in our site in Viljandi and also those studied by Komulainen *et al*. (1999) could be induced by relatively high vascular plant biomass (Fig. 2), which has higher photosynthetic capabilities than bryophytes (Laine A.M. *et al*. 2012). In addition, we must emphasize that large annual variations in peatland NEE have been recorded previously (Lafleur *et al*. 2003; Riutta *et al*. 2007b; Lund *et al*. 2010; Munir *et al*. 2015), especially in the case of rewetted peatlands where $CO_2$ fluxes are more affected by weather conditions (Wilson *et al*. 2016b). As our study only covered one growing season, the average NEE of the growing season reported here for various peatlands likely differs between years with different environmental conditions.

The average growing season NEE in the pristine sites of Tammela and Sodankylä by the

EC showed somewhat smaller $CO_2$ sink function during the growing season than measurements by the chamber method, while the estimated photosynthesis and respiration were larger in EC measurements than in chamber measurements. Similar results have also been obtained by other authors (Moore *et al.* 2002; Aurela *et al.* 2007; Riutta *et al.* 2007a; Maanavilja *et al.* 2011). Chamber measurements are mainly used for fine-scale community $CO_2$ flux estimations and EC method for ecosystem fluxes and so these methods complement each other. NEE obtained with both methods should be comparable at least in open peatland ecosystems provided that the chamber measurement points have been distributed taking into account the spatial variation in the vegetation composition of the site. However, EC measurements cover continuously the whole growing season, while the manual chamber method uses several instantaneous measurements to reconstruct growing season fluxes. In our two study sites, the EC-based estimates of NEE seemed to corroborate those obtained from the chamber-based measurements.

## Relationships between phytomass and carbon dioxide fluxes

Several positive relationships were found between $CO_2$ flux components and PFT biomass, which varied between the pristine and rewetted sites. In the pristine sites, higher $CO_2$ uptake and maximum $P_g$ rates were connected to higher forb and graminoid biomass dominated by sedges (*Eriophorum* and *Carex* species). In the rewetted sites, higher $P_g$ was measured in plots with higher shrub biomass. Similarly, other authors have detected higher photosynthesis maximum rates with higher shrub (Riutta *et al.* 2007b; Badorek *et al.* 2011; Korrensalo *et al.* 2016) and sedge (Riutta *et al.* 2007b; Korrensalo *et al.* 2016; Laine *et al.* 2016) abundances. This indicates that in rewetted sites, shrubs have a higher photosynthetic efficiency, while sedges are the main photosynthesising plants in pristine peatlands — although there were no significant differences in shrub and sedge biomass between the pristine and the rewetted plots in our study. It could be expected that eventually sedges will replace shrubs as the main photosynthesising plants in rewetted sites due to their better adaptation to wet conditions.

The parameters of respiration and photosynthesis models have been reported to vary among plant communities (Riutta *et al.* 2007a; Badorek *et al.* 2011; Maanavilja *et al.* 2011) and are affected by the interaction between PFTs and peatland management type (drained, undrained, and rewetted; Laine *et al.* 2016). This concords with the results of our study as there were significant differences in $P_g$ and $R_{ECO}$ model parameters between pristine and rewetted sites. We found higher $k$ values with increased shrub biomass in the rewetted sites but no connections to *Sphagnum* biomass in the rewetted nor pristine sites. Low $k$ values in photosynthesis models indicate that the community could photosynthesize more effectively at lower PAR levels (Badorek *et al.* 2011), for example in cloudier weather. Higher photosynthetic efficiency at lower PAR levels in plots with higher shrub abundance has been reported by Riutta *et al.* (2007b) and Korrensalo *et al.* (2016). Some studies have provided contradictory results about the relationship between *Sphagnum* abundance and $k$ values. For example, according to Korrensalo *et al.* (2016) $k$ values are higher in *Sphagnum* than in vascular plants, while Riutta *et al.* (2007b) recorded lower $k$ values in plots with *Sphagnum*.

In the pristine sites, $R_{ECO}$ was higher in plots with higher biomass of tree seedlings, while in the rewetted sites it was higher in the case of higher *Sphagnum* biomass. Contrary to results from rewetted sites in the current study, Laine *et al.* (2016) measured lower respiration on mosses than vascular plants. These inconsistent results could be caused by different environmental conditions on rewetted and pristine sites. In pristine sites, tree seedlings mainly grow on aerated hummocks. In rewetted sites, the microtopography is often less pronounced and as *Sphagnum* is sensitive to water table fluctuations (Tuittila *et al.* 2004; Brown *et al.* 2016), it could show higher respiration. In addition, a higher heterotrophic respiration with a relatively low water table in some sites could have played a role in high $R_{ECO}$, especially during the drier summer period. The temperature sensitivity of respiration was negatively correlated with *Sphagnum* and shrub biomasses in the pristine sites and only with *Sphagnum* biomass in the rewetted sites. So respiration in plots with higher *Sphagnum* biomass is less sensitive to changes in air temperature than in plots with low *Sphagnum* biomass. This could be connected with reduced response of peat respiration in case of higher *Sphagnum* biomass insulating peat from fluctuations in air temperature.

NEE in the rewetted and pristine sites was lower in measurement plots with higher *Sphagnum* biomass. Lower $CO_2$ balance in the case of high *Sphagnum* biomass was connected mainly with lower photosynthetic capacities of *Sphagnum* in the pristine plots, but with higher respiration in the rewetted sites. Lower photosynthetic capacities and $CO_2$ balance of *Sphagnum* in comparison with vascular plants have also been reported in earlier studies (Riutta *et al*. 2007b; Korrensalo *et al*. 2016; Laine *et al*. 2016; Korrensalo 2017). In the current study, greater $CO_2$ net uptake occurred mainly in the case of higher photosynthesis in the pristine sites but was rather connected with lower respiration in the rewetted sites.

## Conclusions

Our study suggests that despite insignificant differences in PFT biomass, photosynthesis, respiration and net ecosystem exchange can vary significantly between rewetted and pristine peatlands. Plots, rewetted about ten years before measurements, still were smaller carbon dioxide sinks than pristine peatlands. This emphasizes the importance of long-term monitoring of restored sites as opposed to typical projects lasting up to five years. This lets us evaluate the time needed for the drained and rewetted sites to reach the similar $CO_2$ sink function as their pristine counterparts. For that, $CO_2$ measurements should be continued or repeated also on older rewetted sites in the future.

High $CO_2$ uptake soon after rewetting as in the most recently rewetted site in the current study, could be deceptive as it is the result of still highly abundant vascular plants that have higher photosynthetic capacities than mosses. More knowledge is needed on the relationship between $CO_2$ fluxes and PFTs biomass on differently managed peatlands, as these correlations could vary on sites with different management regimes.

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# Appendix

**Table A1**. Model parameters and their standard errors for $P_g$ ($P_{max}$ and $k$) and $R_{ECO}$ ($r_0$ and $b$) models. SOD = Sodankylä, TAM = Tammela, SIP = Sipoo, VIL = Viljandi, P = pristine, R = rewetted. $P_g$ model $s$ parameter values are given here for SOD (0.0002 ± 0.0000, df = 99), TAM (0.0004 ± 0.0001, df = 134), SIP (0.0164 ± 0.0205, df = 66), and VIL (0.0070 ± 0.0015, df = 38).

| Plot | $P_{max}$ | $k$ | df | $r_0$ | $b$ | df |
|---|---|---|---|---|---|---|
| SOD_P_1 | 559.8 ± 151.6 | 534.6 ± 285.5 | 11 | 70.4 ± 11.1 | 302.8 ± 49.6 | 4 |
| SOD_P_2 | 338.8 ± 175.8 | 472.0 ± 455.8 | 10 | 43.5 ± 8.2 | 265.8 ± 62.9 | 4 |
| SOD_P_3 | 805.5 ± 73.2 | 271.0 ± 56.0 | 9 | 98.5 ± 24.7 | 355.2 ± 128.1 | 4 |
| SOD_P_4 | 644.6 ± 206.3 | 1619.2 ± 732 | 9 | 14.7 ± 7.4 | 660.3 ± 218.1 | 4 |
| SOD_R_1 | 349.8 ± 140.4 | 77.4 ± 56.7 | 6 | 90.5 ± 20.9 | 117.5 ± 77.6 | 2 |
| SOD_R_2 | 199.5 ± 50.2 | 119.1 ± 114.3 | 6 | 85.6 ± 46.7 | 170.8 ± 166.8 | 2 |
| SOD_R_3 | 68.8 ± 21.1 | 202.3 ± 191.0 | 6 | 90.5 ± 20.9 | 117.5 ± 77.6 | 2 |
| SOD_R_4 | 268.4 ± 30.9 | 472.9 ± 115.6 | 3 | 89.4 ± 78.2 | 108.9 ± 258.5 | 1 |
| TAM_P_1 | 212.6 ± 101.8 | 530.8 ± 197.8 | 11 | 25.7 ± 15.7 | 376.7 ± 199.3 | 5 |
| TAM_P_2 | 252.2 ± 49.4 | 144.9 ± 105.5 | 11 | 50.3 ± 13.7 | 265.4 ± 91.5 | 5 |
| TAM_P_3 | 172.8 ± 17.7 | 235.0 ± 72.9 | 11 | 20.5 ± 9.9 | 398.5 ± 157.9 | 5 |
| TAM_P_4 | 465.6 ± 144.1 | 1106.3 ± 595.7 | 10 | 43.4 ± 17.2 | 241.2 ± 111.2 | 5 |
| TAM_P_5 | 247.0 ± 102.6 | 234.3 ± 299.2 | 10 | 21.1 ± 31.1 | 634.2 ± 383.1 | 5 |
| TAM_P_6 | 292.3 ± 105.9 | 392.8 ± 346.9 | 11 | 32.2 ± 18.7 | 462.8 ± 182.2 | 5 |
| TAM_P_7 | 464.8 ± 154.2 | 688.4 ± 515.2 | 11 | 54.6 ± 33.9 | 317.0 ± 202.2 | 5 |
| TAM_P_8 | 323.7 ± 78.8 | 281.8 ± 164.8 | 10 | 79.7 ± 28.0 | 146.4 ± 121.4 | 5 |
| TAM_R_1 | 172.6 ± 110.2 | 231.8 ± 381.9 | 9 | 81.3 ± 71.2 | 201.2 ± 159.4 | 5 |
| TAM_R_2 | 295.4 ± 149.5 | 768.6 ± 646.6 | 11 | 36.6 ± 13.1 | 127.8 ± 122.6 | 5 |
| TAM_R_3 | 154.7 ± 25.0 | 171.3 ± 69.0 | 10 | 59.2 ± 20.6 | 161.8 ± 105.5 | 5 |
| TAM_R_4 | 268.4 ± 123.3 | 516.5 ± 463.1 | 9 | 64.3 ± 28.0 | 154.8 ± 158.3 | 5 |
| SIP_P_1 | 282.3 ± 84.5 | 373.6 ± 301.1 | 10 | 56.7 ± 35.7 | 191.9 ± 189.7 | 5 |
| SIP_P_2 | 254.5 ± 39.8 | 180.0 ± 95.9 | 9 | 54.3 ± 25.4 | 227.1 ± 118.5 | 5 |
| SIP_P_3 | 368.7 ± 74.2 | 491.3 ± 261.4 | 9 | 71.1 ± 32.0 | 162.3 ± 123 | 5 |
| SIP_P_4 | 199.6 ± 142.2 | 521.1 ± 813.9 | 8 | 37.4 ± 29.3 | 287.6 ± 194.3 | 5 |
| SIP_R_1 | 179.0 ± 47.1 | 256.7 ± 175.8 | 9 | 46.9 ± 19.1 | 83.6 ± 129.9 | 5 |
| SIP_R_2 | 198.4 ± 24.7 | 179.2 ± 70.2 | 6 | 48.3 ± 27.0 | 265.1 ± 148.7 | 5 |
| SIP_R_3 | 241.2 ± 42.1 | 299.3 ± 116.4 | 7 | 82.3 ± 46.3 | 79.9 ± 187.0 | 4 |
| SIP_R_4 | 297.3 ± 79.2 | 479.2 ± 286.9 | 9 | 76.6 ± 41.0 | 183.5 ± 148.4 | 4 |
| VIL_P_1 | 452.0 ± 562.4 | 799.5 ± 1721.6 | 4 | 28.8 ± 69.4 | 112.2 ± 544.0 | 2 |
| VIL_P_2 | 326.7 ± 215.5 | 345.2 ± 499.7 | 4 | 12.8 ± 26.3 | 112.3 ± 288.5 | 2 |
| VIL_P_3 | 274.7 ± 126.9 | 247.8 ± 273.2 | 3 | 72.6 ± 78.6 | 143.1 ± 248.7 | 2 |
| VIL_P_4 | 258.6 ± 37.9 | 74.7 ± 39.6 | 5 | 33.5 ± 82.5 | 268.4 ± 525.0 | 1 |
| VIL_R_1 | 528.2 ± 375.9 | 267.5 ± 419.3 | 7 | 22.5 ± 43.2 | 430.9 ± 411.4 | 2 |
| VIL_R_2 | 683.5 ± 341.3 | 308.2 ± 337.1 | 6 | 59.7 ± 96.1 | 220.2 ± 356.0 | 2 |
| VIL_R_3 | 127.7 ± 135.1 | 137.7 ± 492.8 | 3 | 3.1 ± 6.7 | 861.6 ± 472.2 | 1 |
| VIL_R_4 | 682.4 ± 197.8 | 519.6 ± 319.6 | 6 | 61.6 ± 9.6 | 275.5 ± 35.8 | 2 |

**Table A2**. Statistical significance of differences in $CO_2$ flux components and their model parameters between the rewetted and pristine plots of the study sites based on the Mann-Whitney test. Asterisk indicates statistically significant differences in $CO_2$ fluxes and their model parameters between rewetted and pristine sites.

| | | Sodankylä | Tammela | Sipoo | Viljandi | All study sites |
|---|---|---|---|---|---|---|
| *n* (pristine) | | 4 | 8 | 4 | 4 | 20 |
| *n* (rewetted) | | 4 | 4 | 4 | 4 | 16 |
| Photosynthesis | | | | | | |
| | *Z* | –2.16 | –1.85 | –1.44 | –1.16 | –1.80 |
| | *p* | 0.031* | 0.064 | 0.149 | 0.248 | 0.073 |
| $P_{max}$ | | | | | | |
| | *Z* | –2.72 | –1.19 | –1.16 | –1.16 | –2.37 |
| | *p* | 0.007* | 0.234 | 0.248 | 0.248 | 0.018* |
| *k* | | | | | | |
| | *Z* | –1.87 | –0.34 | –1.16 | –0.00 | –1.91 |
| | *p* | 0.062 | 0.734 | 0.248 | 1.000 | 0.057 |
| Respiration | | | | | | |
| | *Z* | –0.46 | –0.62 | –0.29 | –0.58 | –0.08 |
| | *p* | 0.643 | 0.537 | 0.773 | 0.564 | 0.934 |
| $r_0$ | | | | | | |
| | *Z* | –0.17 | –1.70 | –0.58 | –0.29 | –1.10 |
| | *p* | 0.865 | 0.089 | 0.564 | 0.773 | 0.269 |
| *b* | | | | | | |
| | *Z* | –1.70 | –2.21 | –1.16 | –2.02 | –2.04 |
| | *p* | 0.089 | 0.027* | 0.248 | 0.043* | 0.041* |
| NEE | | | | | | |
| | *Z* | –2.78 | –2.78 | –2.02 | –1.44 | –2.04 |
| | *p* | 0.005* | 0.005* | 0.043* | 0.200 | 0.041* |

**Table A3**. Model parameters, modelled photosynthesis, respiration and net ecosystem exchange on hummocks of the study sites. The statistical significance of differences in the average levels of variables ($P_g$, $R_{ECO}$, NEE, $P_{max}$, $k$, $r_0$, $b$) between the pristine and rewetted states was found with the Mann-Whitney test.

| | $n$ | $P_g$ | $P_{max}$ | $k$ | $R_{ECO}$ | $r_0$ | $b$ | NEE |
|---|---|---|---|---|---|---|---|---|
| Sodankylä | | | | | | | | |
| Pristine | 2 | 250.9 ± 40.7 | 682.6 ± 122.8 | 402.8 ± 131.8 | 94.6 ± 17.2 | 84.4 ± 14.0 | 329.0 ± 26.2 | 156.3 ± 23.5 |
| Rewetted | 2 | 84.9 ± 10.0 | 234.0 ± 34.4 | 296.0 ± 176.9 | 53.5 ± 37.3 | 87.5 ± 1.9 | 139.9 ± 31.0 | –4.8 ± 11.1 |
| Statistical significance | | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ |
| Tammela | | | | | | | | |
| Pristine | 5 | 92.8 ± 4.0 | 308.6 ± 43.3 | 348.4 ± 93.9 | 99.5 ± 4.2 | 47.6 ± 10.1 | 365.2 ± 84.3 | –6.6 ± 1.0 |
| Rewetted | 2 | 58.9 ± 1.2 | 163.7 ± 8.9 | 201.6 ± 30.3 | 183.1 ± 99.5 | 121.1 ± 61.9 | 181.5 ± 19.7 | –124.2 ± 100.6 |
| Statistical significance | | $Z = -1.94$;<br>$p = 0.053$ | $Z = -1.94$;<br>$p = 0.053$ | $Z = -1.55$;<br>$p = 0.245$ | $Z = 0.0$;<br>$p = 1.000$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.16$;<br>$p = 0.245$ | $Z = -1.94$;<br>$p = 0.053$ |
| Sipoo | | | | | | | | |
| Pristine | 2 | 76.2 ± 25.1 | 284.2 ± 84.6 | 506.2 ± 14.9 | 74.3 ± 16.5 | 54.3 ± 16.9 | 225.0 ± 62. | 6 1.9 ± 9.0 |
| Rewetted | 3 | 76.2 ± 0.9 | 245.7 ± 28.5 | 319.2 ± 87.2 | 88.4 ± 8.3 | 69.1 ± 10.5 | 176.2 ± 53.6 | –12.2 ± 7.8 |
| Statistical significance | | $Z = 0.0$;<br>$p = 1.000$ | $Z = -0.58$;<br>$p = 0.564$ | $Z = -1.73$;<br>$p = 0.083$ | $Z = -1.16$;<br>$p = 0.248$ | $Z = -1.16$;<br>$p = 0.248$ | $Z = -0.58$;<br>$p = 0.564$ | $Z = -1.16$;<br>$p = 0.248$ |
| Viljandi | | | | | | | | |
| Pristine | 2 | 68.9 ± 8.7 | 300.7 ± 26.0 | 296.5 ± 48.7 | 50.8 ± 36.1 | 42.7 ± 29.9 | 127.7 ± 15.4 | 18.1 ± 27.4 |
| Rewetted | 2 | 137.2 ± 5.1 | 605.9 ± 77.7 | 287.9 ± 20.4 | 61.4 ± 18.5 | 41.1 ± 18.6 | 325.5 ± 105.4 | 75.7 ± 23.6 |
| Statistical significance | | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = 0.0$;<br>$p = 1.000$ | $Z = 0.0$;<br>$p = 1.0001$ | $Z = 0.0$;<br>$p = 1.000$ | $Z = -1.55$;<br>$p = 0.121$ | $Z = -1.55$;<br>$p = 0.121$ |

**Table A4**. Model parameters, modelled photosynthesis, respiration and net ecosystem exchange on hollows of the study sites. The statistical significance of differences in the average levels of variables ($P_g$, $R_{ECO}$, NEE, $P_{max}$, $k$, $r_0$, $b$) between the pristine and rewetted states was found with the Mann-Whitney test.

|  | $n$ | $P_g$ | $P_{max}$ | $k$ | $R_{ECO}$ | $r_0$ | $b$ | NEE |
|---|---|---|---|---|---|---|---|---|
| Sodankylä |  |  |  |  |  |  |  |  |
| Pristine | 2 | 250.9 ± 40.7 | 682.6 ± 122.8 | 402.8 ± 131.8 | 94.6 ± 17.2 | 84.4 ± 14.0 | 329.0 ± 26.2 | 156.3 ± 23.5 |
| Rewetted | 2 | 84.9 ± 10.0 | 234.0 ± 34.4 | 296.0 ± 176.9 | 53.5 ± 37.3 | 87.5 ± 1.9 | 139.9 ± 31.0 | –4.8 ± 11.1 |
| Statistical |  | $Z = 0.0$; | $Z = –1.55$; | $Z = –1.55$; | $Z = –0.55$; | $Z = 0.0$; | $Z = –0.78$; | $Z = –1.55$; |
| significance |  | $p = 1.000$ | $p = 0.121$ | $p = 0.121$ | $p = 0.121$ | $p = 1.000$ | $p = 0.439$ | $p = 0.121$ |
| Tammela |  |  |  |  |  |  |  |  |
| Pristine | 3 | 92.8 ± 4.0 | 308.6 ± 43.3 | 348.4 ± 93.9 | 99.5 ± 4.2 | 47.6 ± 10.1 | 365.2 ± 84.3 | –6.6 ± 1.0 |
| Rewetted | 2 | 58.9 ± 1.2 | 163.7 ± 8.9 | 201.6 ± 30.3 | 183.1 ± 99.5 | 121.1 ± 61.9 | 181.5 ± 19.7 | –124.2 ± 100.6 |
| Statistical |  | $Z = –1.55$; | $Z = –1.55$; | $Z = 0.0$; | $Z = 0.0$; | $Z = 0.0$; | $Z = –1.55$; | $Z = –1.55$; |
| significance |  | $p = 0.121$ | $p = 0.121$ | $p = 1.000$ | $p = 1.000$ | $p = 1.000$ | $p = 0.121$ | $p = 0.121$ |
| Sipoo |  |  |  |  |  |  |  |  |
| Pristine | 2 | 76.2 ± 25.1 | 284.2 ± 84.6 | 506.2 ± 14.9 | 74.3 ± 16.5 | 54.3 ± 16.9 | 225.0 ± 62. | 6 1.9 ± 9.0 |
| Rewetted | 1 | 76.2 ± 0.9 | 245.7 ± 28.5 | 319.2 ± 87.2 | 88.4 ± 8.3 | 69.1 ± 10.5 | 176.2 ± 53.6 | –12.2 ± 7.8 |
| Statistical |  | $Z = –1.23$; | $Z = –1.23$; | $Z = 0.0$; | $Z = –1.23$; | $Z = –1.23$; | $Z = –1.23$; | $Z = –1.23$; |
| significance |  | $p = 0.221$ | $p = 0.221$ | $p = 1.000$ | $p = 0.221$ | $p = 0.221$ | $p = 0.221$ | $p = 0.221$ |
| Viljandi |  |  |  |  |  |  |  |  |
| Pristine | 2 | 68.9 ± 8.7 | 300.7 ± 26.0 | 296.5 ± 48.7 | 50.8 ± 36.1 | 42.7 ± 29.9 | 127.7 ± 15.4 | 18.1 ± 27.4 |
| Rewetted | 2 | 137.2 ± 5.1 | 605.9 ± 77.7 | 287.9 ± 20.4 | 61.4 ± 18.5 | 41.1 ± 18.6 | 325.5 ± 105.4 | 75.7 ± 23.6 |
| Statistical |  | $Z = 0.0$; | $Z = 0.0$; | $Z = 0.0$; | $Z = 0.0$; | $Z = 0.0$; | $Z = –1.55$; | $Z = –0.78$; |
| significance |  | $p = 1.000$ | $p = 1.000$ | $p = 1.000$ | $p = 1.0001$ | $p = 1.000$ | $p = 0.132$ | $p = 0.439$ |