Back to the Future: Restoring Northern Drained Forested Peatlands for Climate Change Mitigation

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Draining peatlands for forestry in the northern hemisphere turns their soils from carbon sinks to substantial sources of greenhouse gases (GHGs). To reverse this trend, rewetting has been proposed as a climate change mitigation strategy. We performed a literature review to assess the empirical evidence supporting the hypothesis that rewetting drained forested peatlands can turn them back into carbon sinks. We also used causal loop diagrams (CLDs) to synthesize the current knowledge of how water table management affects GHG emissions in organic soils. We found an increasing number of studies from the last decade comparing GHG emissions from rewetted, previously forested peatlands, with forested or pristine peatlands. However, comparative field studies usually report relatively short time series following rewetting experiments (e.g., 3 years of measurements and around 10 years after rewetting). Empirical evidence shows that rewetting leads to lower GHG emissions from soils. However, reports of carbon sinks in rewetted systems are scarce in the reviewed literature. Moreover, CH4 emissions in rewetted peatlands are commonly reported to be higher than in pristine peatlands. Long-term water table changes associated with rewetting lead to a cascade of effects in different processes regulating GHG emissions. The water table level affects litterfall quantity and quality by altering the plant community; it also affects organic matter breakdown rates, carbon and nitrogen mineralization pathways and rates, as well as gas transport mechanisms. Finally, we conceptualized three phases of restoration following the rewetting of previously drained and forested peatlands, we described the time dependent responses of soil, vegetation and GHG emissions to rewetting, concluding that while short-term gains in the GHG balance can be minimal, the long-term potential of restoring drained peatlands through rewetting remains promising.

Keywords: peatland, restoration, rewetting, GHG balance, forest, land-use, management

1 INTRODUCTION

Organic soils, such as peatlands, cover 3% of the terrestrial land area, but store 30% of the total soil carbon (FAO, 2020). Northern peatlands cover 3.7 million km², including 1.7 million km² in permafrost, and store around 530 PgC, making them an important component in the global carbon cycle (Tanneberger et al., 2017; Hugelius et al., 2020).

Peatlands are characterized by organic matter accumulation when water saturation leads to anoxic conditions in the soil (Braganza et al., 2009; Leifeld et al., 2019; Conchedda and Tubiello, 2020).
However, these ecosystems have been systematically drained for agriculture, forestry and peat extraction for fuel (Laine et al., 2009; Montanarella et al., 2006). To date, 30% of the peatlands located in Nordic and Baltic countries have been drained and are being used for commercial forestry (Laine et al., 2009). Draining organic soils creates aerobic conditions that promote the decomposition of soil organic matter, leading to CO₂ (Kasimir et al., 2018) and, in nutrient rich sites, N₂O emissions (Klemetsson et al., 2005).

Forestry, commonly perceived as climate friendly thanks to its carbon storage potential, can become an important source of greenhouse gases (GHGs) when associated with peatland drainage (Arnold et al., 2005). The positive climate effect of lower CH₄ emissions and higher CO₂ uptake, due to better conditions for forest production (Korkiakoski et al., 2019) can be offset by CO₂ and N₂O emissions from the drained soil (Ojanen et al., 2010; Lohila et al., 2011; Kasimir et al., 2018).

Increasing water table through ditch blocking to restore anoxic conditions has been proposed as an alternative to reduce GHG emissions from forested and drained peatlands (Martens et al., 2021). Rewetting drained peatlands could have positive effects in countries with extensive areas in drained forested peatlands, such as United Kingdom, Ireland, Estonia, Sweden, Norway and Finland (Kløve et al., 2017; Tanneberger et al., 2017). However, the effect of rewetting on GHG emissions depends on the restoration of peat forming plant and microbial communities and stabilization of hydrological conditions, which might require several years. Moreover, the net effect of rewetting drained and forested peatlands on global warming is still a matter of debate (Tanneberger et al., 2017; Ojanen and Minkkinen, 2020).

Measuring GHG fluxes in the field is technically and logistically difficult, which limits the collection of empirical evidence (Jauhiainen et al., 2019). Additionally, GHG fluxes are highly dynamic due to several interacting controlling factors such as soil temperature, soil moisture, nutrient availability, soil physical properties, plant community, microbial community, soil organic matter quality, among others (Bragazza et al., 2009; Jauhiainen et al., 2019; Huang et al., 2021). Moreover, the definition of the system boundary determines which fluxes are considered, thereby affecting the estimated net GHG balance (Chapin et al., 2006).

These difficulties hinder our understanding of how peatland management can help climate change mitigation and motivate this contribution. In this paper, we aim to answer the following questions:

1. Is there empirical evidence that rewetting decreases net GHG emissions of drained and forested peatlands?
2. What processes control the response of GHG fluxes to rewetting on drained and forested peatlands?
3. Based on empirical evidence and process understanding, what is the expected effect of rewetting forested peatlands on GHG fluxes over time?

2 MATERIAL AND METHODS

We focused on GHG fluxes from forested and drained peatlands and wet peatlands. For wet peatlands we focused on rewetted previously drained and forested peatlands as well as pristine peatlands. We defined GHG fluxes as the vertical transport of N₂O, CH₄ and CO₂ between the atmosphere and the soil-vegetation continuum during a specific time interval in a specific area characterized by forested and drained or wet peat soils. We considered GHG fluxes from ditches and CO₂ fluxes from all the vegetation as part of the system GHG fluxes. Deviations of measured GHG fluxes from this definition are indicated.

To address the first question, we performed a systematic literature search focusing on GHG fluxes from rewetted peatlands that were previously drained and forested. The literature search was performed on Web of Science in October 2021, using the following string: ("organic soil" OR "peatland" OR "histosol") AND ("forest" OR "forestry" OR "forested" OR "afforested" OR "deciduous" OR "coniferous") AND ("drained" OR "drainage") AND ("restored" OR "restoration" OR "rewetting" OR "rewetted") AND ("greenhouse gases" OR "GHG" OR "fluxes" OR "emissions" OR "uptake" OR "removals" OR "soil emissions” OR “CO₂” OR "carbon dioxide" OR “CH₄” OR "methane" OR "N₂O" OR “nitrous oxide”). In addition, we considered relevant articles cited in those found from the systematic search.

The search returned 121 papers, of these we retained 18 articles based on the following criteria:

- Organic soils reported had more than 12% of organic content and more than 10 cm of peat.
- Drained peatlands under study were forested.
- Rewetted peatlands under study were previously drained and forested.
- Pristine peatlands under study were not managed ecosystems and had vegetation typical of water saturated peatlands.
- Soil GHG fluxes were compared between rewetted and pristine or drained peatlands
- Peatlands under study were located in boreal or temperate climate zones.
- GHG values were obtained through field measurements or meta-analysis of relevant literature (model results are excluded).

We reported statistically significant differences in GHG fluxes for studies empirically comparing the systems of interest (drained forested, pristine, and rewetted previously drained and forested). Emissions factors derived from meta-analysis in review papers are also reported.

The second question was addressed by a non-systematic literature review. Causal Loop Diagrams (CLDs) were constructed to describe how controlling factors identified affect GHG dynamics in peatlands. A CLD presents the causal relations between the state variables in a system, and how changes in the driving factors propagate throughout the system (Anderson and Johnson, 1997). In the CLD, an arrow with a plus sign indicates a change in the variable affected that is in the same direction of the change in the driving variable, and an arrow with a minus sign indicates a change in variable affected that is in the opposite direction of the change in the driving variable (Wallman et al., 2006). By following these arrows through the system, reinforcing
and balancing feedbacks can be revealed (Wallman et al., 2006). CLD’s are useful to differentiate direct and indirect causalities and explore complex systems such as peatlands.

For the third question, we hypothesized time dependent effects of rewetting on GHG fluxes by dividing the restoration process in three phases. We used empirical data collected for the first question, process understanding derived from the second question, and relevant scientific literature to characterize the three restoration phases.

3 RESULTS AND DISCUSSION

3.1 Evidence That Rewetting Drained Peatlands Reduces Greenhouse Gas Emissions

We identified 18 studies comparing empirical GHG emissions data from rewetted peatlands that were previously drained and forested with still forested and drained peatlands or pristine peatlands. The studies were published mostly after 2012. Of these, 12 studies performed GHG measurements using different variations of the chamber method (Komulainen et al., 1998, 1999; Juottonen et al., 2012; Bohdálková et al., 2013; Urbanová et al., 2013; Koskinen et al., 2016; Hambley et al., 2019; Laine et al., 2019; Purre et al., 2019; Creevy et al., 2020; Jurasinski et al., 2020; Minkkinen et al., 2020), three studies reported eddy covariance measurements (Petrone et al., 2001; Hambley et al., 2019; Purre et al., 2019), one study estimated emissions with chemical tracers and soil and water samples (Tauchnitz et al., 2015) and four studies conducted a meta-analysis of relevant empirical data (Wilson et al., 2016; Evans et al., 2017; Juutinen et al., 2020; Tiemeyer et al., 2020).

Only two of the field based studies reported data from a site before and after restoration (Komulainen et al., 1998, 1999). Instead, most field studies used space for time substitutions by contrasting drained, rewetted and pristine sites at the same time. Yet, reported observations remain short term, with usually less than 3 years of reported data and an average time of restoration before the first measurement of 10 years.

While the reviewed studies remain few, they show that rewetting of drained forested peatlands can reduce soil GHG emissions, and in certain cases even revert them to net carbon sinks. Below we summarize the reviewed findings according to the following categories:

1. GHG emissions comparison between drained and rewetted systems by GHG type
2. GHG emissions comparison between rewetted and pristine systems by GHG type
3. Net GHG emissions of drained, rewetted and pristine ecosystems.

3.1.1 Rewetted vs. Drained Systems

Rewetted peatlands often exhibited lower heterotrophic or ecosystem respiration compared to drained ones due to higher water table and lower soil oxygen (Komulainen et al., 1999; Laine et al., 2019). However some studies found no significant differences in ecosystem respiration after rewetting (Jurasinski et al., 2020; Komulainen et al., 1999). In Jurasinski et al. (2020) both wet and dry systems were older forest and the rewetted treatment had significantly higher nutrient content than the drained system. In Komulainen et al. (1999) there were water table and vegetation composition differences between the plots measured within the rewetted treatment. When interpreting these results, it should be kept in mind that definitions of respiration differ; e.g., ecosystem respiration in Komulainen et al. (1999) and Laine et al. (2019) did not account for aboveground tree respiration. However, comparisons across treatments should still hold because the same measurement approach is used in any given study.

Methane emissions were consistently higher in rewetted treatments compared to drained treatments, due to restored anoxic conditions in the soil caused by increased water table (Urbanová et al., 2013; Koskinen et al., 2016; Laine et al., 2019; Jurasinski et al., 2020). CH4 emissions from the ditches were not included in the comparative studies. However, Koskinen et al. (2016) and Urbanová et al. (2013) included measurements from soil near the ditches.

Nitrous oxide emissions were lower in rewetted treatments compared to drained treatments across studies (Tauchnitz et al., 2015; Laine et al., 2019; Minkkinen et al., 2020), highlighting the relevance of soil oxygen availability in N2O emissions. However, the difference was not significant in the nutrient poor sites reported in Minkkinen et al. (2020) due to already low emissions measured in drained nutrient poor sites.

Field based comparative studies show that rewetting previously forested and drained peatlands increases CH4 emissions and decreases N2O emissions in nutrient rich systems. Rewetting can potentially decrease CO2 emissions by decreasing ecosystem respiration from drained and forested peatlands but few comparative field-based studies have been published.

3.1.2 Rewetted vs. Pristine Systems

The difference in CO2 emissions between rewetted and pristine conditions is inconsistent (Table 1). Compared to pristine conditions, rewetting could result in lower CO2 emissions from ecosystem respiration (Creevy et al., 2020), higher emissions (Petrone et al., 2001; Hambley et al., 2019), or no difference (Purre et al., 2019). Both Hambley et al. (2019) and Purre et al. (2019) reported higher net ecosystem exchange and lower gross primary productivity in rewetted treatments. In contrast, Laine et al. (2019) and Creevy et al. (2020) found no significant differences. The oldest rewetted treatment in Creevy et al. (2020) had a lower net ecosystem exchange than the pristine counterpart, likely due to the higher water table in the rewetted system and sparse vegetation in the pristine system.

Most studies reported higher CH4 emissions in rewetted treatments compared to pristine conditions (Bohdálková et al., 2013; Koskinen et al., 2016; Creevy et al., 2020). This can be explained by time after restoration, differences in plant communities (Creevy et al., 2020) and higher water table in the rewetted sites reported in some studies (Koskinen et al., 2016).
In contrast, Juottonen et al. (2012) and Urbanová et al. (2013) found lower CH$_4$ emissions in rewetted treatments due to poor establishment of both microbial and plant communities. Laine et al. (2019) found similar levels of CH$_4$ emission between rewetted and pristine. CH$_4$ emissions in rewetted sites seem to depend on restoration of ecological communities typical of pristine peatlands.

Direct comparisons of N$_2$O emissions from rewetted and pristine sites were only reported in two studies. Often, there were no significant differences in N$_2$O emissions between rewetted and pristine sites (Laine et al., 2019; Minkkinen et al., 2020). However, some rewetted nutrient rich sites had lower N$_2$O emissions than their pristine counterparts (Minkkinen et al., 2020).

Field-based comparisons between pristine peatlands and rewetted previously forested and drained peatlands show similar negligible N$_2$O emissions. However, CO$_2$ and CH$_4$ emissions of rewetted sites can be higher, lower or the same as in pristine sites. Moreover, most rewetted sites were net sources of CO$_2$ (Petrone et al., 2001; Hambley et al., 2019; Purre et al., 2019; Crevey et al., 2020). Net CO$_2$ sinks in rewetted peatlands were scarcely reported. Two sites rewetted for at least 15 years were net CO$_2$ sinks, highlighting the necessity to restore peatland plant communities for long-term carbon storage (Hambley et al., 2019; Crevey et al., 2020). Laine et al. (2019) also reported a net sink in rewetted treatments, but CO$_2$ uptake was probably overestimated, because measurements were conducted in light saturated conditions.

Overall the number of comparative field-based studies on the subject remains limited, providing limited data suitable for performing quantitative meta-analysis. The results of the comparative studies are presented in Table 1.

### 3.1.3 Net Total Greenhouse Gas Fluxes From Rewetted, Pristine and Drained Systems

Here we focus on one field study and four reviews discussing the overall impact of rewetting by estimating all major GHGs.

Through a direct field based comparison, Laine et al. (2019) calculated net GHG emissions from drained, pristine and rewetted peatlands for six sites during 2 years. The restored and pristine sites had on average lower net GHG emissions than the drained sites and during a wet year had negative net GHG emissions. The study did not account for aboveground tree respiration.

The reviews generated emission factors (EFs) based on the IPCC guidelines and therefore did not account for vegetation related CO$_2$ fluxes (Evans et al., 2017; Juutinen et al., 2020; Tiemeyer et al., 2020; Wilson et al., 2016). Consequently, CO$_2$ emissions represent the carbon balance between litter inputs and heterotrophic respiration. The reported EFs (Table 2) did not include dissolved organic carbon (DOC) and particulate organic carbon (POC) exports, even though these fluxes can be significant.

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### TABLE 1 | Trends on GHG fluxes from field-based studies comparing rewetted peatlands with drained and pristine peatlands. D means drained, R means rewetted, and P means pristine. Higher (+) means significantly higher, lower (-) means significantly lower and equal (=) means no significant differences. Contrasting results between rewetted sites within studies are reported.

| Reference                  | Paired sites          | Comparison                  | Number of rewetted sites | Time after rewetted (years)* | CO$_2$* | CH$_4$ | N$_2$O | NEEa |
|----------------------------|-----------------------|-----------------------------|--------------------------|------------------------------|---------|--------|--------|------|
| Bohdáková et al. (2013)    | No Rewetted and Pristine | 1                          | 2                        | n/a                          | R > P   | n/a    | n/a    |      |
| Crevey et al. (2020)       | Yes Rewetted and Pristine | 1                          | 6                        | R < P                        | P = P   | +      |        |      |
| Hambley et al. (2019)      | No Rewetted and Pristine | 1                          | 10                       | R > P                        | n/a    | n/a    | +      |      |
| Juottonen et al. (2012)    | No Rewetted and Pristine | 3                          | 11                       | NA                           | R < P   | n/a    | n/a    |      |
| Juutinen et al. (2020)     | No Rewetted and Drained | 1                          | 17                       | R = D                        | R > D   | R = D   | n/a    |      |
| Komulainen et al. (1998)   | Yes Rewetted and Drained | 1                          | 2                        | R = D*                       | R > D   | n/a    | n/a    |      |

*When more than one rewetted site is reported, the average time after rewetted between the sites is reported.
*CO$_2$ refers to emissions due to ecosystem respiration ($R_{eco}$).
*NEE is negative (-)/positive (+) when the rewetted site acts as a net CO$_2$ sink/source on average for a year or a growing season.

*Drained sites $R_{eco}$ did not account for aboveground tree respiration.
from a full carbon balance perspective and had been accounted in some studies (Wilson et al., 2016; Evans et al., 2017). Net GHG emissions were higher at drained sites than in rewetted soils except for temperate nutrient rich soils in Wilson et al. (2016). Boreal organic soils had lower net GHG emissions than temperate ones at any nutrient level, whereas nutrient rich organic soils had higher emissions than nutrient poor soils in both climate zones.

Wilson et al. (2016) concluded that rewetting reduces net total soil GHG emissions of drained forested peatlands by 74, 27 and 74% in boreal nutrient rich, boreal nutrient poor and temperate nutrient poor systems respectively. Tiemeyer et al. (2020) estimated 72% reduction in net emissions from drained and forested peatlands in Germany when rewetted. Juutinen et al. (2020) developed reference emission levels for different types of boreal forested and drained soils, and for rewetted soils and concluded that rewetting reduces drained peatlands net GHG emissions only under some conditions. In contrast, Evans et al. (2017) established that converting forested drained organic soils into fens or bogs through rewetting can reduce net GHG emissions by 53 and 102%, respectively. The reviews estimated mostly net positive GHG emissions from rewetting drained and forested peatlands, contrary to observations of net carbon sinks in non-managed and waterlogged peatlands. Estimations were highly variable both for forested and rewetted system, which might be explained by both lack of empirical data and high dependence on local conditions. Furthermore, these reviews did not include time after restoration, therefore they give limited insight into the time dependent effects of rewetting.

In general, comparative studies did not always consider the same GHG fluxes. Studies accounted differently for tree related carbon fluxes. Some studies incorporated carbon exports (e.g., POC and DOC) within the GHG balance (Wilson et al., 2016; Evans et al., 2017) while others did not. Moreover, the implications of ditches on site emissions were often not accounted within the system balance. Differences in system boundaries limited the comparisons across studies and across systems. Furthermore, most studies compared GHG fluxes between systems through Global Warming Potential (GWP), which might overestimate initial climate benefits of rewetting due to the short term but strong warming effects of atmospheric CH4 (Ojanen and Minkkinen, 2020).

Combining existing empirical evidence, we conclude that rewetting generally reduces soil GHG emissions compared to drained conditions. Nevertheless, net emissions often remain positive for several years. Restoring GHG emissions to levels typical of pristine conditions can take more than 10 years. However, the lack of long-term rewetting experiments with consistent measurement leaves a gap in the observation of the effects of ecosystem functions that may require longer to recover after rewetting and may dominate the long-term regulation of GHG fluxes in rewetted sites such as vegetation succession and changes in soil properties (Creevy et al., 2020).

### 3.2 Processes Controlling the Response of Greenhouse Gas Fluxes to Rewetting

Several biological processes are affected by draining and rewetting, and therefore affect GHG production and consumption in peatlands.

Draining organic soils makes oxygen available in the soil. Changes in oxygen content generate a cascade of direct and indirect effects in processes producing and consuming GHGs. Furthermore, changes in water regimes affect gas transport by changing diffusion rates in soil and vegetation.

Under conditions of high nutrient and water availability, oxygen promotes both organic matter inputs to the soil and

| Source | Climate | System | CO₂ | CH₄ | N₂O | NET |
|--------|---------|--------|-----|-----|-----|-----|
| Wilson et al. (2016) | Boreal | Productive forest in nutrient poor drained organic soil | 0.92 | 0.42 | 0.1 | 1.44 |
| | Boreal | Productive forest in nutrient rich drained organic soil | 3.41 | 0.25 | 1.5 | 5.16 |
| | Boreal | Rewetted nutrient poor organic soil previously forested | −1.52 | 1.87 | 0.03 | 3.38 |
| | Boreal | Rewetted nutrient rich organic soil previously forested | −1.93 | 5.64 | 0.03 | 3.74 |
| | Temperate | Productive forest in drained organic soil | 9.53 | 0.27 | 1.31 | 11.11 |
| | Temperate | Rewetted nutrient poor organic soil previously forested | −1.22 | 4.09 | 0.03 | 2.9 |
| | Temperate | Rewetted nutrient rich organic soil previously forested | 0.96 | 10.07 | 0.03 | 11.69 |
| Tiemeyer et al. (2020) | Temperate | Productive forest in drained organic soil | 28.23 | 0.14 | 0.6 | 28.97 |
| | Temperate | Rewetted organic soil | −1.47 | 9.49 | 0.03 | 8.05 |
| Juutinen et al. (2020) | Boreal | Productive forest in drained organic soil with herb-rich layer | 1.83 | −0.03 | 0.54 | 2.34 |
| | Boreal | Productive forest in drained organic soil with Vaccinium myrtillus layer | 2.66 | −0.03 | 0.54 | 3.17 |
| | Boreal | Productive forest in drained organic soil with Vaccinium vitis-idaea layer | −1.09 | −0.03 | 0.54 | −0.58 |
| | Boreal | Productive forest in drained organic soil with dwarf shrub and Cladina spp. layer | 1.35 | −0.03 | 0.54 | 1.86 |
| | Boreal | Rewetted organic soil previously forested with herb-rich and Vaccinium myrtillus layer | −1.1 | 2.74 | 0.24 | 1.88 |
| | Boreal | Rewetted organic soil previously forested with Vaccinium vitis-idaea, dwarf shrub and Cladina spp. layer | −0.99 | 1.4 | 0.24 | 0.65 |
| Evans et al. (2017) | Temperate | Productive forest in drained organic soil | 7.39 | 0.12 | 0.65 | 8.16 |
| | Temperate | Rewetted organic soil (bog) | −2.23 | 2.02 | 0.04 | −0.17 |
| | Temperate | Rewetted organic soil (fen) | 0.66 | 4.24 | 0.24 | 5.34 |

GHG emissions represent only soil fluxes. Rewetted systems values are presented in bold.
mineralization rates. Under constant anoxic conditions, low biomass productivity—and thus low carbon input to soil—is compensated by even lower mineralization rates leading to peat accumulation. Organic matter is primarily protected electrochemically due to low redox potential and chemically due to the low nutrient content and high chemical recalcitrance of peatland vegetation.

Soil oxygen directly enhances GHG production by acting as electron acceptor in metabolic reactions that produce CO₂ and N₂O (i.e., heterotrophic microbial respiration and nitrification). Indirectly, soil oxygen increases other substrates required by heterotrophic microbial respiration and nitrification by directly enhancing organic matter breakdown leading to higher dissolved organic matter content and NH₄⁺ content. Furthermore, soil oxygen indirectly increases heterotrophic respiration by promoting vascular plant communities that increase litterfall rates and quality, which in turn provide high quality substrates for soil microbes. By enhancing dissolved organic matter content and nitrification, soil oxygen has also an indirect positive effect on denitrification, causing N₂O production. Soil oxygen availability is associated with water unsaturated conditions, which—by increasing diffusion rates—promote CO₂ emissions and incomplete reduction of NO₃⁻ leading to N₂O volatilization.

The effect of rewetting on these processes are described in more detail in the following section, and their relations are illustrated by a set of causal loop diagrams.

### 3.2.1 Soil Water Content, CO₂ Uptake, and Litterfall Rate

Soil water content is the main control of soil oxygen content by limiting gas exchanges as pores become saturated (Skopp et al., 1990; Sierra et al., 2015, 2017). In drained organic soils, rewetting through ditch blocking decreases lateral outflow, increasing soil water content, raising the water table, and ultimately decreasing soil oxygen content (Silins and Rothwell, 1999; Lohila et al., 2011).

Lowering soil oxygen content indirectly decreases CO₂ uptake by limiting plant productivity compared to drained peatlands (Kozlowski, 1986; Gyimah et al., 2020). Water saturation limits root respiration and thus root activity affecting plant growth (Ben-Noah and Friedman, 2018; Bhanja and Wang, 2021) and restricting most species associated with productive forestry (Arnold et al., 2005). Diminished plant growth decreases litterfall (Neumann et al., 2018; Giweta, 2020), which represents the main carbon and nitrogen input to the soil (Janssens et al., 2010; Lohila et al., 2011; Soylu et al., 2014; Bhanja and Wang, 2021).

However, decreasing lateral outflow in drained peatlands can ultimately decrease leaching, which can limit losses of mineral nutrients and dissolved organic carbon that could otherwise be stabilized into soil organic matter (Haapalaho et al., 2014; Nieminen et al., 2018).

Rewetting previously forested drained peatlands decreases ecosystem productivity and carbon inputs to the soil. The main causal pathways and mechanistic understanding relating soil water content to CO₂ uptake by vegetation and litter production are illustrated in Figure 1.

### 3.2.2 Soil Oxygen, Soil pH, Nutrient Contents, and Litterfall Quality

Plant community composition controls litterfall quality. Long-term water saturation caused by rewetting promotes gradual changes in plant communities (Urbanová and Bártá, 2020). Peat soils characterized by high mineral nutrient, medium pH, low soil oxygen content and high soil water content promote plant communities dominated by specialized vascular plants such as wetland sedges (Carex spp.) and some forbs species (Robroek et al., 2015; Laine et al., 2015). In contrast, peat soils characterized by low mineral nutrient content, low pH, low soil oxygen content and high soil water content enhance plant communities dominated by peat mosses (Sphagnum spp.) (Bragazza and Gerdol, 2002; Gлина et al., 2019; Bengtsson et al., 2021).

Increased Sphagnum mosses dominance in the plant community decreases overall litterfall quality (Bragazza et al., 2009). Vascular plant litter can be almost three times more labile than Sphagnum litter when measured through decomposition rates, because Sphagnum litter is characterized by low nutrient and high phenolic contents (Bragazza et al., 2009).

In poor and acidic peats, rewetting can promote plant communities characterized by calcifuge litter. The main causal pathways and mechanistic understanding relating soil oxygen content, pH and nutrient contents to litterfall quality are illustrated in Figure 2.

### 3.2.3 Soil Oxygen, Soil Water Content, and Carbon and Nitrogen Mineralization Rates

Litterfall rate and litter quality control soil organic matter content and quality, by affecting organic matter breakdown and nutrient retention during decomposition (Luo and Zhou, 2006; Horwath, 2015; Normand et al., 2021). Organic matter breakdown transforms particulate organic matter into dissolved organic matter available for microbial consumption (Eijssackers and Zehnder, 1990; Reddy and DeLaune, 2008b; Horwath, 2015). During decomposition, nutrients are immobilized if substrate is nutrient poor, or released if it is nutrient rich in mineral form, resulting in typical trajectories of decreasing substrate C:N:P through time (Manzoni et al., 2010). The breakdown rate is enhanced by temperature, soil water content (below soil field capacity), soil oxygen content (above soil field capacity), and is regulated by chemical composition and enzymatic activities (Luo and Zhou, 2006; Horwath, 2015).

Peatlands are characterized by high soil organic matter content, and frequently by low soil organic matter quality (Heller et al., 2015; Szajdak et al., 2020). Rewetting decreases soil oxygen content which inhibits microbial activity by requiring microbes to use less energetically efficient electron acceptors, thus resulting in low decomposition rates and carbon accumulation (Skopp et al., 1990; Sierra et al., 2015, 2017). Moreover, low soil oxygen decreases oxygenases activity which are enzymes capable of breaking resistant organic compounds. Low oxygen limits substrate for oxygenases mediated reactions and limits microbial metabolisms capable of oxygenases synthesis (Freeman et al., 2001; Reddy and DeLaune, 2008b; Sinsabaugh, 2010; Plante et al., 2015). Furthermore, hydrolase enzymes, which are not limited by oxygen,
might be further inhibited by phenolic compounds commonly found in Sphagnum litter (Freeman et al., 2001), thus contributing to soil organic matter accumulation rates in peatland ecosystems, although this remains disputed (Wen et al., 2019; Urbanová and Hajek, 2021). Hydrolases and oxygenases content increases as microbial metabolism increases but decreases with high dissolved organic matter content (Allison and Vitousek, 2005).

Rewetting decreases organic matter breakdown by acting directly on soil oxygen content and indirectly on microbial and enzyme composition and activity. The main causal pathways and mechanistic understanding relating soil water content, soil oxygen content and organic matter breakdown are illustrated in Figure 3.

3.2.4 Carbon Mineralization Pathways
Dissolved organic carbon derived from organic matter breakdown is mineralized into CO₂ and CH₄ by different microbial groups. Simultaneously, CO₂ and CH₄ can also be
consumed (Horwath, 2015; Robertson and Groffman, 2015; Feng et al., 2020). Soil redox potential is primarily regulated by soil water content in peatlands (Lin et al., 2021), and in turn it regulates the dominant metabolic pathway through which carbon is mineralized (Reddy and DeLaune, 2008b).

Low oxygen content associated with water saturation decreases CO₂ production by hindering root respiration and heterotrophic aerobic microbes (Horwath, 2015). Microbial heterotrophic aerobic metabolism is controlled by soil oxygen and soluble organic matter availability (Dalal et al., 2008; Lin et al., 2021), which explains reports of low CO₂ emissions in water saturated peatlands and high CO₂ emissions in drained organic soils (Wilson et al., 2016).

In contrast, water saturation associated with rewetting increases CH₄ in soil by removing soil oxygen, which is toxic for most methanogenic microbes (Reddy and DeLaune, 2008b). This explains high sensitivity of CH₄ emissions to water table fluctuations reported in both rewetted and pristine peatlands (Koskinen et al., 2016; Ritson et al., 2017).

In saturated peatlands, methanogenesis occurs through different pathways. Aceticlastic and hydrogenotrophic methanogenesis dominate in peatlands (Galand et al., 2005; Bräuer et al., 2020). Aceticlastic methanogenesis uses acetate generated by acetogenic bacteria and vascular plants as substrate and produces CO₂ besides CH₄ (Ye et al., 2012; Bräuer et al., 2020). Hydrogenotrophic methanogenesis uses CO₂ and H₂ generated from fermentative bacteria as substrate (Reddy and DeLaune, 2008b). Both acetogenic and fermentative bacteria respond positively to decreases in soil oxygen associated with rewetting (Galand et al., 2005; Bräuer et al., 2020). Methanogenic activity is enhanced by organic substrate availability, therefore is highly dependent of plant community through litterfall quantity and quality (Putkinen et al., 2018; Urbanová and Bárt, 2020).

Acetoclastic methanogenesis is thought to account for 2/3 of methane production in peatlands (Bräuer et al., 2020). However, some hydrogenotrophic methanogens respond better to nutrient poor and acidic conditions which explain their importance in bogs (Galand et al., 2005; Bräuer et al., 2020). Furthermore, some hydrogenotrophic methanogens seem to be more tolerant to oxygen giving them an advantage in drained or not fully restored peatlands (Urbanová and Bárt, 2020).

However, CH₄ produced in peatlands can be consumed and oxidized into CO₂ by autotrophic methanotrophs in the presence of oxygen (Agethen et al., 2018; Grodnitskaya et al., 2018). This process can be important in peat upper layers when unsaturated conditions or high oxygen diffusion through plant roots take place (Agethen et al., 2018).

Despite water saturation and low soil oxygen content conditions, peatland methanogenesis can be inhibited by more efficient non-aerobic heterotrophic microbial metabolism in the presence of other electron acceptors such as SO₄²⁻ and NO₃⁻ (Blodau et al., 2007; Ye et al., 2012; Agethen et al., 2018). Moreover, low pH directly down-regulates the activity of organisms involved in methanogenesis and fermentation (Ye et al., 2012). Oxidized-sulfur containing compounds produced by Sphagnum and low pH associated with bogs partially explain lower methane emissions in bogs compared to fens (AminiTabrizi et al., 2020).

Nevertheless, water table is the main control of carbon mineralization pathways in peatlands. The main causal

![Causal loop diagram of the main effects of water table management in mineralization rates. An arrow with a plus sign (blue) indicates a change in the variable affected that is in the same direction as the change in the driving variable, an arrow with a minus sign (red) indicates a change in variable affected that is in the opposite direction as the change in the driving variable.](image-url)
pathways and mechanistic understanding relating soil water content, soil oxygen, CH$_4$ production and CO$_2$ production are illustrated in Figure 4.

### 3.2.5 Nitrogen Mineralization Pathways

N$_2$O is mostly an intermediate product of both nitrification and denitrification. Soluble organic nitrogen derived from organic...
matter breakdown is mineralized into ammonium (NH$_4^+$) by microbes which is in turn transformed into NO$_3^-$ through nitrification and into N$_2$ through denitrification.

Pathways of N$_2$O production in nitrification are not fully understood, especially for nitrifying archaea (Tzanakakis et al., 2019), however there is evidence that nitrification is an important source of N$_2$O in forested drained peatlands (Liimatainen et al., 2018). Rewetting hinders nitrification by reducing O$_2$ availability which is required by nitrifiers to oxidized NH$_4^+$.

Lower soil oxygen caused by rewetting might also decrease NH$_4^+$ content through lower organic nitrogen mineralization rates (Khalil et al., 2004; Pauletta et al., 2013). However, lower soil oxygen content can also reduce microbial nitrogen demand by decreasing microbial C-use efficiency, leading to NH$_4^+$ mineralization and NH$_4^+$ accumulation in soil. Therefore, critical C:N ratios leading to mineral nitrogen immobilization are higher in water saturated environments such as pristine and rewetted peatlands (Reddy and DeLaune, 2008c).

Being mostly an anaerobic process, denitrification increases when soil oxygen content decreases (Seitzinger et al., 2006; Yang et al., 2020). However, denitrification requires soluble organic carbon, protons (H$^+$) and nitrate (NO$_3^-$) (Seitzinger et al., 2006; Reddy and DeLaune, 2008c; Wang Cong et al., 2021). Nitrification, which decreases when soil oxygen content is reduced, is the main source of soil nitrate (NO$_3^-$) in non-fertilized systems such as most of the aforessted and not managed peatlands. However, atmospheric deposition can be an important source of NO$_3^-$. Even though denitrification increases N$_2$O in soil, many denitrifiers produce the enzyme N$_2$O reductase which further reduces N$_2$O into N$_2$ (Robertson and Groffman, 2015). N$_2$O reductase activity increases when soil oxygen decreases (Baggs, 2011; Wan et al., 2012). High soil copper (Cu) availability and high pH might also promote N$_2$O reductase activity in northern peatlands (Liimatainen et al., 2018). Microbial community composition also explain N$_2$O reductase activity, for example denitrifying fungi are not capable of synthetizing N$_2$O reductase (Baggs, 2011; Wan et al., 2012).

Organic matter nitrogen content has been proposed as the main control for N$_2$O emissions in northern drained peatlands (Klemedtsson et al., 2005). High emissions of N$_2$O in drained peatlands are associated with nitrogen-rich organic matter, with C:N ratios lower than 30 (Klemedtsson et al., 2005; Liimatainen et al., 2018). Drainage and afforestation of peatlands tends to generate relative N enrichment, decreasing C:N ratios through peat degradation and increasing N mineralization (Krüger et al., 2015; Lasota and Błońska, 2021). Moreover, drained peatlands tend to have higher bulk density and lower porosity than pristine peatlands, which can lead to rapid saturation after rain, causing N$_2$O pulses due denitrification associated with temporary anoxic conditions and high NO$_3^-$ availability (Reay et al., 2004; Cui et al., 2016; Liu et al., 2019).

Due to the contrasting effect of soil oxygen content on nitrification and denitrification dependence of nitrification byproducts, N$_2$O production optimum water filled pore space varies between 50 and 90% in boreal peats (Regina et al., 1998). When considering the mean annual water table depth as predictor of N$_2$O production instead of soil saturation, the optimum depth is around ~25 cm (Jungkunst et al., 2004). Main causal pathways and mechanistic understanding relating soil water content, soil oxygen and N$_2$O production are illustrated in Figure 5.

### 3.2.6 Gas Transport

GHG transport can occur via gas transport processes such as diffusion or convection in soils (Blagodatsky and Smith, 2012) or via plant mediated transport in the xylem or aerenchyma, and exchange through the stomata (Bhullar et al., 2013; McNicol et al., 2017). GHG transport is affected directly and indirectly by water content and therefore rewetting (Segers, 1998; Reddy and DeLaune, 2008a) as is illustrated in Figure 6.

GHG diffusion is controlled by gaseous concentration gradients; therefore, diffusion rates are enhanced by GHG concentration in soil. Diffusion rates decrease with soil water content and increases with soil porosity and pore connectivity (Blagodatsky and Smith, 2012; Ball, 2013). Peat soils are characterized by high porosity, typically around 80% in the upper 30 cm (Rezanezhad et al., 2016). Rewetting peatlands decreases diffusion rates by increasing soil water content. However, long term drainage decreases total porosity and thus the relative abundance of large pores that promote pore connectivty (Wang Mairoun et al., 2021). Diffusion is likely the main pathway of CO$_2$ and N$_2$O emission to the atmosphere in drained peatlands. High diffusion rates might hinder the complete reduction of N$_2$O during denitrification by releasing N$_2$O before it can be consumed partially explaining high N$_2$O emissions in drained peatlands with high nutrient content.

Mass flow is a convective movement of gases, so it depends of total pressure differences between the soil and the atmosphere (Reddy and DeLaune, 2008a; Ball, 2013; Kreba et al., 2017). Mass flow is enhanced when atmospheric pressure decreases which can be caused by wind movement (Reddy and DeLaune, 2008a). Under waterlogged conditions such as those in rewetted and pristine peatlands, CH$_4$ accumulation in soil can lead to mass flow events in forms of bubbles passing through water commonly referred as ebullition (Blagodatsky and Smith, 2012). Ebullition can account for 50–64% of total CH$_4$ flux in northern peatlands under water saturation (Tokida et al., 2007).

Plant mediated transport is driven by gas partial pressure differences between the plant tissue and the surroundings (Grosse and Frick, 1999). This process is facilitated by plant total porosity which reduces gas transport resistance (Reddy and DeLaune, 2008a). Plant total porosity is a function of several properties such as leaf area and the pore density of specific type tissue (e.g., aerenchyma) and can be limited by temporary reduction of leaf gas exchanges by stomatal closure (Reddy and DeLaune, 2008a). Under water saturated and high nutrient availability conditions, like those found in some rewetted and pristine peatlands, vegetation communities with high plant tissue porosity can dominate, which facilitates plant mediated transport (Bhullar et al., 2013; Valiranta et al., 2017). Plant mediated transport can be an important pathway for methane and nitrous oxide emissions (Greenup et al., 2000; Agethen et al., 2018), but also
for soil oxygen replenishment, increasing methane oxidation in the rhizosphere (Agethen et al., 2018). Some studies indicate that methane oxidation might dominate over methane facilitated transport (Bhullar et al., 2013).

3.3 Theoretical Effect of Rewetting Forested Peatlands on Greenhouse Gas Fluxes Over Time

Peatland restoration through rewetting seems to require between 15 and 30 years to yield ecosystem functions typical of pristine peatlands. However, both incomplete empirical data and process understanding hinder our knowledge about rewetting effect through time. Rewetting effect is highly dependent on local characteristics and site history (Kreyling et al., 2021). Moreover, peatland restoration is often done by clear cutting and ditch blocking, but it can include active vegetation transfer, mulching and microtopography modifications (Gorham and Rochefort, 2003). Initial hydrological properties, peat degradation, nutrient status and restoration approach are likely to affect the revegetation and hydrological responses to increased water table. This would likely affect restoration trajectory and, subsequently, GHG fluxes over time (Nugent et al., 2019; Purre et al., 2020). Higher nutrient availability associated with fens might lead to a faster and more dynamic response to rewetting. However, simpler hydrology associated with bogs might increase the likelihood of successful restoration. Here we conceptualize the consequences of rewetting on GHG fluxes over time by separating restoration in three phases in relation to peat hydrological and ecological properties.

3.3.1 Restoration Phases

The first restoration phase is characterized by an increase in water table due to lower tree transpiration and reduced lateral water outflow. Initially, in this phase the water table might be lower than in a pristine state (Menberu et al., 2016), however mean annual water table might recover fast (Haapalehto et al., 2011). Water table variability is likely higher than in the pristine state because lower soil macroporosity and higher bulk density developed after long term drainage have a negative effect on hydraulic conductivity and water storage capacity (Ahmad et al., 2020; Liu et al., 2020; Kreyling et al., 2021). High organic substrate availability is expected due to rewetting associated disturbances, tree residues, turnover of tree roots and its associated microbial biomass and expansion of wetland vascular plants (Rigney et al., 2018; Vestin et al., 2020). High nutrient availability due to low plant nutrient demand is expected which, added to rewetting associated disturbances, might promote high nutrients exports often reported after rewetting (Koskinen et al., 2017; Nieminen et al., 2020). Due to enhanced decomposition, this phase might be characterized by high dissolved organic matter concentrations (Negassa et al., 2021). Vegetation during this phase is patchy (Hedberg et al., 2012) and growth of mosses such as Sphagnum is likely limited by high water table variability (Kim et al., 2021). Proliferation of wetland associated vascular plants is likely due to nutrient availability, however the specific species will likely be influenced by pH (Kozlov et al., 2016).

The second phase of restoration is characterized by high water table due to effective water outflow control by years of ditch blocking. However, pore size distribution and bulk density are not
expected to be fully recovered (Kreyling et al., 2021), leading to high water table variability and oxic pulses especially in highly degraded peat (Kim et al., 2021). Water table variability might continue to inhibit Sphagnum proliferation and sustain vascular plants, leading to more labile litterfall compared to pristine conditions (Bragazza et al., 2009; Kim et al., 2021). Oxic periods promote the decomposition of recalcitrant peat, thereby increase nutrient content and labile organic substrate availability (Górecki et al., 2021). Vegetation cover and CO2 uptake capacity is expected to be recovered (Alderson et al., 2019; Lees et al., 2019). However, plant communities might not have the same composition as in a pristine state and are likely influenced by nutrient content and peat degradation at the moment of restoration (Hedberg et al., 2012; Kreyling et al., 2021).

The third phase of restoration is characterized by recovery of the ecological characteristics associated with pristine peatlands and soil physical properties are mostly restored alongside typical water table dynamics. During this phase vegetation cover is fully recovered and plant community is characterized by typical peatlands genera such as Sphagnum, Eriophorum and Carex. Final composition will likely be a function of nutrient content and pH (Laine et al., 2021). There is evidence of effective restoration of ecological properties through rewetting (Menberu et al., 2016; Alderson et al., 2019; Ahmad et al., 2020; Purre et al., 2020), but this process might require up to 30 years and for some systems might not be possible due to changes associated with long term drainage (Holden et al., 2004; Kreyling et al., 2021).

The time that each restoration phase would require is likely sensitive to site specific characteristics and restoration approach. However, recovery is expected to take between 10 and 30 years. The first phase is likely to take between 3 and 5 years, while the second phase might require between 5 and 25 years.

3.3.2 CO2 Emissions Through the Restoration Phases

Soil CO2 emissions are expected to be lower than in drained sites during the first restoration phase (Komulainen et al., 1999). However, the system will likely be a net source of CO2 (Petrone et al., 2001; Hambley et al., 2019; Creevy et al., 2020) (Figure 7). High rates of aerobic heterotrophic respiration sustained by organic substrate availability, mineral nutrient availability and oxic conditions in the upper layers of the peat are expected. Moreover, CO2 uptake rate is anticipated to be low due to sparse vegetation.

During the second phase of restoration, soil CO2 emissions are expected to be significantly lower compared with drained status because of increased water table (Wilson et al., 2016; Laine et al., 2019). Due to increased photosynthesis and decreased autotrophic respiration the system will be approaching to carbon neutrality during this phase (Laine et al., 2019; Purre et al., 2020).

The restored peatlands will be a net CO2 sinks during the third phase of restoration due to high anoxic conditions, proper restoration of peat forming vegetation communities and slow decomposition (Hambley et al., 2019; Creevy et al., 2020). Therefore, an overall transition from CO2 source to sink is expected during this phase.

3.3.3 CH4 Emissions Through the Restoration Phases

CH4 emissions will increase with time during the first phase due to labile organic substrate availability, mineral nutrient availability, increasing water table and progressive establishment of methanogenic microbes and associated microbial communities (e.g., fermentative bacteria) (Figure 8). CH4 emission will be higher than in a drained state even without a fully recovered water table (Komulainen et al., 1998; Urbanová et al., 2013). Water bodies created by ditch blocking might be important sources of CH4 emissions during this phase.
During the second phase of restoration, CH$_4$ emissions are expected to be higher than in the drained state and even higher than in the pristine state (Vanselow-Algan et al., 2015; Abdalla et al., 2016; Koskinen et al., 2016). High methane emissions are associated with labile litter availability related to vascular plant, mineral availability due to mineralization during oxic pulses and gas transport facilitation by plant communities with porous tissues (Vanselow-Algan et al., 2015; Lee et al., 2017; Rigney et al., 2018). However, if plant community recovering is low during this phase, lower CH$_4$ emissions compared to pristine state might occur due to low substrate availability associated with low litter inputs (Putkinen et al., 2018; Urbanová and Bára, 2020) and reduced proliferation of methanotrophs (Dunfield and Dedysh, 2014; Robroek et al., 2015).

The restored peatlands will be a source of CH$_4$ during the third phase, but emissions levels are expected to correspond to those reported for pristine sites (Laine et al., 2019; Creevy et al., 2020). Overall CH$_4$ emission are thus expected to increase after rewetting, but then decrease as restoration progresses and plant communities recover.

3.3.4 N$_2$O Emissions Through the Restoration Phases

N$_2$O emissions will decrease after rewetting due to lower diffusivity and the negative effect of lower oxygen on nitrification (Tauchnitz et al., 2015) (Figure 9). However, some emissions can be expected (Vestin et al., 2020) due to the positive effect of lower nutrient competition on nitrification and enhanced denitrification due to lower oxygen content.
During the second phase, \(\text{N}_2\text{O}\) emissions will be significantly reduced due to lower mineral nutrient availability caused by higher plant nutrient demand compared to the first phase. Some emissions might happen due to oxic pulses caused by water table variability.

In the long-term, the restored peatlands will be a negligible source of \(\text{N}_2\text{O}\) due to low oxygen content and low diffusivity associated with restored hydrological properties, comparable to pristine sites (Minkkinen et al., 2020). To summarize, \(\text{N}_2\text{O}\) emissions are expected to steadily decrease during the restoration.

**4 CONCLUSION**

Rewetting decreases soil related GHG emissions from drained and forested peatlands. However, considering fluxes from vegetation can alter the overall assessment of the GHG balance. The effect of rewetting on GHG fluxes is highly dependent on several factors such as nutrient status, soil physical properties and vegetation recovery. Water table restoration can turn a formerly drained peatland into a carbon sink, but recovering related ecosystem functions can take decades and has been scarcely reported. Long term monitoring of rewetted systems is thus required to fulfill observation gaps regarding the transient effect of rewetting on GHG fluxes.

Water table management changes soil oxygen content, which in turn directly and indirectly controls several processes that produce, consume, and transport GHG in peatlands. Soil oxygen directly affects plant growth, litterfall quality and quantity through plant community composition, organic matter breakdown rates, carbon mineralization pathways and rates, nitrification, denitrification and soil diffusivity which in turn control GHG fluxes. While these processes are relatively well understood in isolation, the complex relations among them make it difficult to scale up local and short-term GHG measurements to estimate the consequences of interventions at the landscape level and in the long-term.

Organic soil management is fundamental in the context of climate change. Long term integrated monitoring and dynamic modelling are necessary to improve our understanding regarding rewetting effects on GHG fluxes from organic soils and their sensitivity to local conditions and system definition. We hypothesized three different restoration phases for rewetted previously forested peatlands that could provide a framework to compare ongoing and future rewetting experiments based on restoration state rather than time **per se**, but could also support modelling exercises.

**AUTHOR CONTRIBUTIONS**

DE and SB designed the study. DE performed the study with constant support from SB and SM. DE wrote the article with constant support from SB and SM.

**FUNDING**

DE and SB had been supported by the project “A guide on how land-use management can convert high-emitting drained organic soils into areas with negative emissions” financed by FORMAS (project No 2019-01991). SM has been partly supported by the grant “Holistic management practices, modelling and monitoring for European forest soils” (H2020 Grant Agreement No 101000289).

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