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Drainage reduces the resilience of a boreal peatland

Lorna I Harris1,2, Nigel T Roulet1 and Tim R Moore1

1 Department of Geography, McGill University, Burnside Hall, 805 Sherbrooke Street West, Montreal, Quebec H3A OB9, Canada
2 Department of Renewable Resources, University of Alberta, South Academic Building 348, Edmonton, Alberta, T6G 2G7, Canada
E-mail: lorna.harris@mail.mcgill.ca

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Abstract

Drier conditions caused by drainage for infrastructure development, or associated with global climate warming, may test the resilience of carbon-rich northern peatlands. Feedbacks among biological and hydrological processes maintain the long-term stability of peatlands, but if hydrological thresholds are passed, these feedbacks may be weakened, causing a shift in ecosystem state and potentially large losses of carbon (C). To determine peatland response to hydrological change, we examined the structure (vegetation composition and hydrology) and biogeochemical function (carbon dioxide exchange) of a pristine bog and a bog subject to ∼7 years localised drainage (caused by regional groundwater drawdown due to mine dewatering) in the Hudson Bay Lowland, Canada. Water tables at the drained bog were ∼1 m below the hummock surface at the time of study compared to ∼0.3 m at the pristine bog. For hummocks and intermediate microforms at the drained bog, plant production was significantly less than at the pristine bog, most likely due to small changes in vegetation structure (reduced Sphagnum cover and smaller shrub leaf:stem ratios) caused by deeper water tables and significantly reduced moisture content of surface peat. Despite these changes in vegetation and hydrology, net ecosystem production (NEP) remained positive (C sink) for these microforms at the drained bog. Dry pools with mostly bare peat at the drained bog had negative NEP (C source to atmosphere), in stark contrast to Sphagnum- and sedge-dominated pools at the pristine bog with small but positive NEP. Our study shows that dry pools now occupy an unstable state, but the hydrological thresholds for a shift in ecosystem state have not yet been reached for hummocks and intermediate microforms at the drained bog. However, weak or no relationships between water table depth, peat surface moisture content, and plant production for these microforms at the drained bog, suggest that drainage has weakened the hydrological feedbacks regulating peat production, causing peat accumulation to slow. If drier conditions prevail, this reduced resilience increases the potential for a shift in ecosystem state and raises the risk of large C loss due to continued decomposition of deeper peat in oxic conditions, and wildfire.

Introduction

Northern peatlands store a large portion of the global soil carbon (∼500 to 1050 Gt C - Yu et al 2010, Nichols and Peteet 2019). These ecosystems are widespread in boreal and subarctic regions, where a cool and wet climate has sustained the slow accumulation of organic matter (peat) over the past 10,000 years (Tarnocai and Stolbovoy 2006, Yu et al 2010). Peatlands have contributed to a net cooling effect on global climate, but climate warming now poses a significant threat to the stability of these vast carbon (C) stores (Frolking et al 2011). Drier conditions associated with human disturbance (e.g. drainage for infrastructure development) or global climate warming may alter peatland ecohydrological structure and biogeochemical function, testing the effectiveness of feedbacks among hydrological and biological processes that facilitate the long-term stability of peatland...
ecosystems (Hilbert et al. 2000, Belyea and Baird 2006, Belyea 2009, Eppinga et al. 2009a, Waddington et al. 2014). If these feedbacks are weakened or broken, the resilience of peatland ecosystems to further environmental change may be reduced (Page and Baird 2016). Reduced peatland resilience with the continued drying effects of climate warming not only increases the potential for increased C loss to the atmosphere as carbon dioxide (CO₂), but also C loss through more frequent and extensive wildfires (Turetsky et al. 2011, Kettridge et al. 2015, Granath et al. 2016, Page and Baird 2016). As these C losses could amplify global climate warming, understanding the effect of drier conditions on peatland structure and function, and potential changes to peatland resilience, is critical (Intergovernmental Panel on Climate Change, IPCC 2014, IPCC 2019).

The accumulation of organic matter in peatlands is dependent on shallow water tables that limit decomposition relative to production (Clymo 1984). Microforms (raised hummocks and relatively lower hollows) develop where feedbacks among vegetation, hydrology, and nutrients cause differential rates of peat accumulation (Malmer and Wallén 1999, Belyea and Clymo 2001, Rietkerk et al. 2004). Hummocks, intermediate ‘lawns’, hollows, and pools comprise different species of Sphagnum moss that are adapted to small variations in the long-term average depth to water table (Rydin and McDonald 1985, Bengtsson et al. 2016). Woody shrubs and trees are also typically more abundant on hummocks with deeper water tables, allowing aeration of roots (Belyea and Clymo 1998). The presence of vegetation communities with variable functional traits (e.g. green biomass, leaf area) across different microform types is a significant control for biogeochemical function, including CO₂ exchange (Laine et al. 2012, Goud et al. 2017). These differences in microform structure and function mean hummocks and hollows occupy alternate stable states within peatlands, with hummocks representing a dry stable state, and hollows a wet stable state (e.g. Hilbert et al. 2000, Eppinga et al. 2009b, Page and Baird 2016).

The presence of alternate ecosystem states at the microform scale increases peatland resilience to disturbance, by allowing shifts between microform states to occur when the environmental conditions change (Belyea and Clymo 2001, Belyea and Malmer 2004, van Nes and Scheffer 2005, van de Leemput et al. 2015). For example, drier and warmer conditions can increase vascular plant cover and cause production to exceed decomposition, transforming drier hollows to lawn or hummock communities (Belyea and Clymo 2001, Breeuwer et al. 2009). However, it is not certain if the hydrological thresholds (e.g. depth of water table, surface peat moisture content) for these shifts in stable ecosystem states at the microform scale may be exceeded in future drier climate conditions. In bogs that depend on precipitation for water and nutrients, warmer and drier climate conditions with prolonged periods of drought will likely result in deeper water tables and much drier surface peat through a loss in surface tension (Hilbert et al. 2000, McCarter and Price 2014, McLaughlin and Webster 2014, Wu and Roulet 2014, Thompson et al. 2017). If hydrological thresholds for existing stable states are exceeded, we may observe shifts to non-peatland vegetation communities (e.g. Laine et al. 1995), and coupled with biogeochemical changes, a potentially significant effect on ecosystem function (Rietkerk et al. 2004, Scheffer et al. 2012, Lindenmayer et al. 2016).

Here, we examine the ecological effects of hydrological change (drainage) in peatlands in the Hudson Bay Lowland (HBL), Canada (figure 1(a)). The HBL peatlands extend over 250,000 km² and contain approximately 6% of the northern soil carbon pool, making them important C stores (Riley 2011, Packalen et al. 2014). The HBL peatlands are currently net C sinks (Humphreys et al. 2014) but global climate warming may alter this status, with the effects likely intensified by warmer regional temperatures caused, in turn, by the reduction of sea-ice on Hudson Bay (Gagnon and Gough 2005, Ruhland et al. 2013, Delidjakova et al. 2016). The HBL peatlands are also at risk from land-use change and disturbance, particularly drainage, from existing and proposed economic development (e.g. mining and transportation) within this remote region (Far North Science Advisory Panel 2010). Changes to peatland ecohydrological structure and biogeochemical function caused by these development pressures may reduce the resilience of these ecosystems, increasing their vulnerability to the effects of global climate warming.

We compare a pristine ombrogenous bog with a bog that has been subject to drainage for approximately seven years prior to and during our study (figures 1(b) and 1(c)). At the time of our study the water table at the drained bog was ∼1 m below the hummock surface compared to ∼0.3 m at the pristine bog. We examine differences in peatland structure (vegetation and hydrology) and biogeochemical function (net ecosystem production, NEP) to determine whether short-term drainage has caused a shift in ecosystem state. We hypothesise that in a bog with deeper water tables and drier surface conditions, there will be (1) less Sphagnum cover and greater cover of vascular plants (particularly woody shrubs), (2) smaller or potentially negative NEP (i.e. C emission), and (3) these changes in structure and function represent a shift to a potentially unstable ecosystem state or loss of resilience (as indicated by no relationship between NEP and water table depth).
Methods

Site description
We collected data from two research sites in the HBL, located approximately 90 km west of the town of Attawapiskat on the coast of James Bay in northern Ontario, Canada: (1) a pristine ombrogenous bog (52°41′36″ N, 83°56′41″ W; ∼93 m a.s.l.; Humphreys et al 2014, Ulanowski 2014), and (2) a bog subject to drainage for ∼7 years prior to our study starting in 2012 (Whittington and Price 2012; figure 1). The pristine reference bog is located ∼13 km south of De Beers Canada Victor Mine (52°49′06″ N, 83°54′18″ W; ∼83 m a.s.l.), and includes a 1.5 km raised boardwalk and two eddy covariance (EC) towers installed by the Ontario Ministry of Environment, Conservation and Parks (MECP) (Humphreys et al 2014). The drained bog is located approximately 3 km from Victor Mine, and within 100 m of a bioherm, a fractured limestone outcrop formed from an ancient coral reef (Cowell 1983; figure 2). Peatlands in the HBL are underlain by low permeability marine sediments (Riley 2011), but bioherms represent a hydrological connection to the regional groundwater due to reduced or no cover of marine sediment. Consequently, a drop in regional groundwater levels due to dewatering at the mine has caused a significant but localised (<50 m from the bioherm) decrease in peatland water tables (Whittington and Price 2012, Whittington and Price 2013). Bedrock water levels in the bioherms dropped by 2 to 4 m from 2007 to 2010, with water tables in the peatland surrounding the bioherm 20 to 80 cm deeper than peatlands surrounding a remote bioherm unaffected by dewatering at the mine (Whittington and Price 2012).

Vegetation surveys completed as part of the Impact Assessment for De Beers Canada Victor Mine indicate no significant difference in species composition at the pristine bog and the drained bog prior to construction of the mine and the onset of drainage (AMEC 2004, Riley 2003). Data for our study were therefore collected from plots representing similar vegetation-microform types at each site (e.g. Sphagnum-sedge pool, Sphagnum-spruce hummock—table 1 and figure 3), with most plots established along transects parallel to and within a short distance of raised boardwalks.

Temperatures in this part of the HBL range from −22.3 °C in January to 17.2 °C in July (daily averages), with an annual mean of −1.3 °C (1971–2000, Lansdowne House, 280 km WSW—Environment Canada 2016). The area receives ∼700 mm mean annual precipitation, falling predominantly as snow in all months except July and August. During our study in 2013 and 2014, the sites received ∼410 mm and ∼600 mm precipitation, respectively, with growing season rain (June through August) of 178 mm in 2013 and 142 mm in 2014. Coinciding with the end of snow melt, the sites received more spring rainfall (April/May) in 2014 than in 2013. Prior to our study, the sites received ∼750 mm precipitation in 2011 and ∼370 mm precipitation in 2012. Mean annual (and June through August) temperature in 2013 and 2014 was −2.3 °C (14.6) and −2.6 °C (15.0), respectively (MECP EC tower, data not shown).
CO₂ exchange

Three collars, each of 0.055 m² area, were installed in the same vegetation-microform types at the pristine bog and the drained bog in summer 2012 (table 1 and figure 3), with all measurements (N = 1059) completed on an approximately weekly basis during the 2013 and 2014 growing seasons (June through to August). CO₂ fluxes for each collar were measured using clear Plexiglas chambers (27 L volume) fitted with fans and a cooling unit. CO₂ concentration (ppm) in the chamber headspace was measured with a portable CO₂ gas analyser (EGM-4 Environmental Gas Analyser, PP Systems). Photosynthetic photon flux density (PPFD, μmol m⁻² s⁻¹) was measured at the same time as CO₂ using a quantum sensor (PAR-1, PP Systems). Measurements were recorded at 10-s intervals for the first minute and at 30-s intervals for the final 2 min, and repeated for full-light, half-light, and dark conditions by placing mesh and opaque shrouds over the chamber (Bubier et al 1998, Strack et al 2006, Pelletier et al 2011).

CO₂ flux rates (net ecosystem production, NEP μmol m⁻² s⁻¹) were calculated from the linear change in CO₂ concentration in the chamber headspace with time, as a function of chamber volume and temperature (Bubier et al 1998). For NEP, the sign convention is positive for CO₂ uptake and negative for CO₂ release to the atmosphere. Data with \( r^2 < 0.5 \) were checked for measurement errors caused by equipment malfunction or weather conditions and removed if necessary.

The relationship between NEP and PPFD was determined using a rectangular hyperbola curve in SigmaPlot 12.0 (equation (1), Frolking et al 1998).

\[
\text{NEP} = \frac{\text{GP}_{\text{max}} \cdot \alpha \cdot \text{PPFD}}{(\alpha \cdot \text{PPFD})} + \text{ER},
\]

where \( \text{GP}_{\text{max}} \) is the maximum gross photosynthetic CO₂ (μmol m⁻² s⁻¹) captured at maximum PPFD, \( \alpha \) is the photosynthetic quantum efficiency (μmol m⁻² s⁻¹ per μmol PPFD m⁻² s⁻¹), and ER is dark ecosystem respiration (μmol m⁻² s⁻¹). Maximum rates of photosynthesis (PSN\(_{\text{max}}\) μmol m⁻² s⁻¹) were calculated from all gross primary production (GPP) with PPFD greater than 1000 μmol m⁻² s⁻¹ (Bubier et al 2003).

Vegetation

Plant community composition and structure were measured at fixed plots (including NEP plots) in July-August 2014 using the point-intercept method (n = 47 quadrats at the pristine bog and 40 quadrats at the drained bog). We recorded the number of times a metal rod (radius ~3 mm) ‘hit’ each plant species and component (for shrub leaf:stem ratio) for 25 grid points within 0.5 m² quadrats (Larmola et al 2013). Canopy height of vascular plants was also recorded. All vegetation was identified to the species level, with nomenclature for vascular plants as Flora of North America (1993+), and nomenclature for lichens as Brodo et al (2001) (table S1 is available online.

Figure 2. Simplified diagram showing a cross-section of the bioherm and surrounding peatland with the approximate depth of the drained peatland water table. The approximate depth of peatland water table at a remote bioherm not affected by the regional groundwater drawdown is shown as ‘control bioherm’ (Whittington and Price 2012).
Table 1. Plot characteristics for vegetation-microform types for CO₂ exchange measurements at the pristine bog and the drained bog.

| Site         | Vegetation-Microform Type     | Vascular Plants          | Nonvascular       | VGA (m² m⁻²) | WTD (cm) | 2013 | 2014 | pH     |
|--------------|-------------------------------|--------------------------|------------------|-------------|----------|-------|-------|--------|
| PRISTINE     | Sphagnum-only pool            | —                        | Sphagnum majus   | 0.1 (0.0)   | 1.1 (0.2) | 2.2 (0.4) | 4.4 (0.1) |
|              | Sphagnum-sedge pool           | Scheuchzeria palustris   | S. majus         | 2.2 (0.4)   | 1.2 (0.2) | -0.8 (0.6) | 4.4 (0.1) |
|              |                               | Carex oligocephala       | S. papillorum    |             |          |       |       |        |
|              |                               | Carex limosa             |                  |             |          |       |       |        |
|              |                               | Carex pauciflora         |                  |             |          |       |       |        |
|              | Eriophorum-tussock intermediate | Eriophorum vaginatum   | Sphagnum rubellum| 5.8 (1.8)   | -6.8 (1.2)| -1.1 (0.5) | 4.1 (0.1) |
|              |                               | Vaccinium oxycoccos      | S. papillorum    |             |          |       |       |        |
|              | Sphagnum-shrub intermediate   | Rubus chamaemorus        | S. rubellum      | 1.6 (0.4)   | -19.6 (0.4)| -8.7 (0.5)| 4.1 (0.1) |
|              |                               | V. oxycoccos             |                  |             |          |       |       |        |
|              |                               | Andromeda glaucophylla   |                  |             |          |       |       |        |
|              | Sphagnum-spruce hummock       | Picea mariana            | Sphagnum fuscum  | 3.9 (1.0)   | -30.9 (0.4)| -22.9 (0.9)| 4.1 (0.1) |
|              |                               | Chamaedaphne calyculata  | Sphagnum capillifolium |       |          |       |       |        |
|              |                               | Rhododendron groenlandicu|                  |             |          |       |       |        |
|              |                               | Matanthesmus trifolium   |                  |             |          |       |       |        |
| DRAINED      | Bare peat pool                | —                        | —                | —           | -38.1 (0.6)| -28 (1.0) | 4.9 (0.0) |
|              | Eriophorum-tussock intermediate | E. vaginatum            | S. rubellum      | 3.2 (0.5)   | -56.6 (1.0)| -32 (0.7) | 4.4 (0.0) |
|              |                               | V. oxycoccos             |                  |             |          |       |       |        |
|              | Sphagnum-shrub intermediate   | R. chamaemorus           | S. rubellum      | 1.4 (0.2)   | -77.7 (4.0)| -62.9 (3.4)| 4.5 (0.1) |
|              |                               | V. oxycoccos             |                  |             |          |       |       |        |
|              | Sphagnum-spruce hummock       | P. mariana               | S. fuscum        | 1.7 (0.2)   | -114.7 (3.9)| -114.2 (2.6)| 4.0 (0.0) |
|              |                               | C. calyculata            |                  |             |          |       |       |        |
|              |                               | B. groenlandicum         |                  |             |          |       |       |        |

Standard error in parentheses. Dominant vascular plants and nonvascular bryophytes within collar are listed. Mean (combined 2013 and 2014) vascular green area (VGA) index within collar for each vegetation-microform type (triplicates). Mean 2014 pH recorded in summer (June to August) for vegetation-microform types at each site. Mean values for 2013 and 2014 summer (June to August) water table depth (WTD, cm below surface) recorded at same time as all gas flux measurements and in additional plots at each site.
Bare peat and litter were also recorded for each quadrat.

We measured the vascular green area (VGA) index for each NEP collar by measuring the width and length of 20 leaves per species (or all leaves if less than 20) and recording the total number of leaves per species (non-destructive sampling according to Wilson et al. 2007, with Lai et al. 2014 and Goud et al. 2017 as examples). Species-specific formulae based on leaf geometry were applied to determine average leaf size (Wilson et al. 2007). The green area index of a vascular plant species (m$^2$ m$^{-2}$) for the measurement period (mid-July to mid-August) was determined by multiplying the average leaf size by the number of leaves, then dividing by the collar surface area. The VGA index (m$^2$ m$^{-2}$) of each collar was calculated by summing the green area index of all vascular plants present.

Ancillary measurements

We measured air and peat temperature at 10 and 20 cm below the surface, peat moisture content, and water table depth, at the same time as all NEP sampling runs and in additional plots at both study sites. Water table depth below the surface was measured in wells (slotted PVC tubes with a mesh cover) installed at each location, either manually, or from continuous logger measurements using capacitance water level probes (Odyssey, Dataflow Systems, New Zealand). Moisture content of peat at 20 cm depth (volumetric water content, VWC %) was measured using a Hydrosense 2 Soil Moisture Sensor fitted with a CS658 water content sensor (20 cm probe length, Campbell Scientific). Volumetric moisture content (%) was calculated from the period (μs) using a custom linear calibration curve of gravimetric moisture content (GWC, % of dry weight) for vegetation and peat samples from plots at each site.

Statistical analyses

Unless noted otherwise, all statistical analyses were conducted in R version 3.5.1 (R Core Team 2018). To examine differences in vegetation species composition and abundance between sites and for microforms within each site, we used non-metric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix calculated from percentage cover in the R-library vegan (Oksanen et al. 2016). Species associations for different sites and microform types within sites were determined from hierarchical clustering using average linkage methods and the Kendall coefficient of concordance (W) (Legendre 2005). Species richness (total number of species per plot, alpha diversity), Simpson Diversity (D) and Shannon-Weiner Diversity (H’) (evenness) were calculated for each individual quadrat. We used general linear models (GLM) to determine the significance of site (drainage) and microform type for species richness, diversity, vegetation abundance and shrub leaf:stem ratio, with posthoc multiple pairwise comparisons using the Tukey-Kramer test in the R-library emmeans (Lenth 2020).
We used generalised linear mixed effect models (GLMMs) in the R-library lme4 (Bates et al 2015) to determine the significance of vegetation and environmental factors (peat temperature, peat moisture, water table depth) for GPP, ER, and NEP. The models were fit with gamma distribution and log link, with collar (plot) as a random effect and date as repeated measures. We completed posthoc multiple pairwise comparisons using the sequential Sidak method in the R-library emmeans to determine differences among microforms at each site, and for the same vegetation-microform type at the drained and pristine site. We used the same GLMM model structure and posthoc multiple pairwise comparisons to determine differences in water table depth among microforms at each site, and for the same vegetation-microform type at the drained and pristine site. GLMMs for peat temperature and peat moisture were fit with a gaussian distribution and with repeated measures, followed by the same post hoc multiple pairwise comparisons. The best model fit for each response variable was determined using Akaike’s Information Criterion (AIC). Significant interactions between main effects in each GLMM were determined using the Likelihood Ratio Test (LRT).

**Results**

**Hydrology and peat temperature**

Water tables were significantly deeper for all microforms at the drained bog than the pristine bog in both 2013 and 2014 (GLMM p < 0.001; table 1). Hummock water tables (mean WTD below surface) at the drained bog were 84 cm lower than at the pristine bog in 2013, and 88 cm lower than at the pristine bog in 2014. In both 2013 and 2014, the distribution of WTD for pools at the drained bog ranged from ~ −20 to −50 cm below the surface, matching the range for hummock WTD at the pristine site (figure 4), with no significant difference in WTD for hummocks at the pristine bog and pools at the drained bog (GLMM 2014 p = 0.999, 2013 p = 0.993). Water tables in pools at the pristine bog remained at or near the *Sphagnum* surface in both 2013 and 2014.

Surface peat (upper 20 cm) was significantly drier for all microforms at the drained bog than the pristine bog (GLMM p < 0.001), with a mean VWC (% ± standard error, 2014 data) of 48 ± 0.3% and 65 ± 1.4% for *Sphagnum*-spruce hummocks at the drained bog and pristine bog respectively. Mean VWC for pools was 76 ± 0.8% at the drained bog and 92 ± 0.4% at the pristine bog.

Pools were 1.3 °C warmer at the drained bog (mean 12.9 ± 0.2 °C) than the pristine bog (mean 11.6 ± 0.2 °C, combined vegetation types, 2014 data). Hummock peat temperature (at 20 cm depth, combined vegetation types) did not differ significantly between sites (< 0.5 °C difference in means, GLMM p = 0.971), but there were significant differences depending on vegetation type. Peat temperatures in *Sphagnum*-spruce hummocks were 4.1 °C warmer at the pristine bog (mean 12.6 ± 0.2 °C) than the drained bog (mean 8.5 ± 0.2 °C), whereas the difference in peat temperature was only 1.0 °C in lichen-covered hummocks at the drained bog (mean 7.0 ± 0.4 °C) than at the pristine bog (mean 6.0 ± 0.4 °C). Peat temperatures in pools and intermediate microforms were warmer than hummocks at both sites (GLMM p < 0.001).

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![Figure 4. Distribution of water table depth (WTD, daily means of continuous water level logger measurements) for hummocks and pools at the pristine bog and the drained bog for July through August 2014.](image-url)
Vegetation

An NMDS ordination of plant community composition showed no distinction between the pristine bog and the drained bog, except for pool communities (figures S1, and 3 examples). Species richness and Shannon’s diversity (evenness) were significantly less in pools at the drained bog than the pristine bog, but there were no significant differences for hummocks or intermediate microforms (figure S2). *Sphagnum* spp. cover was slightly less for hummocks and intermediate microforms at the drained bog than at the pristine bog, although the difference was not statistically significant (figure 5(a)). Forb cover (e.g. *Rubus chamaemorus*, *Maianthemum trifolium*) was also less for hummocks at the drained bog than the pristine bog but there were no significant differences for intermediate microforms (figure 5(b)). *Sphagnum* spp., and forbs were not recorded in pools at the drained bog.

Although there were no significant differences in percent shrub cover (e.g. *Chamaedaphne calyculata*, *Rhododendron groenlandicum*) between sites, shrub leaf:stem ratios were significantly smaller for hummocks...
and intermediate microforms at the drained bog (figures 5(c) and (d)). Vascular green area (VGA) was also smaller for all microforms at the drained bog (e.g. mean VGA = 3.9 and 1.7 for Sphagnum–spruce hummocks at pristine and drained, table 1). There were no differences in percent cover of graminoids, lichens, or trees between sites. Litter cover was significantly greater in Sphagnum–shrub intermediate microforms (GLM and Tukey-Kramer test \( p < 0.01 \)) and pools (GLM and Tukey-Kramer test \( p < 0.001 \)) at the drained bog than the pristine bog, but there was no difference for hummocks.

**CO₂ exchange**

GLMMs showed a significant interaction between site and microform, indicating the effect of drainage on GPP, NEP, and ER differs for microform types. Mean gross primary production (GPP, \( \mu \text{mol m}^{-2} \text{s}^{-1} \pm \text{standard error} \)) was significantly smaller for Sphagnum–spruce hummocks (2.1 \( \pm \) 0.1 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) and Sphagnum–shrub intermediate microforms (1.9 \( \pm \) 0.1 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) at the drained bog than the pristine bog (3.9 \( \pm \) 0.2 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for Sphagnum–spruce hummocks and 2.9 \( \pm \) 0.2 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for Sphagnum–shrub intermediate) (figure 6 and table S2). GPP did not differ between sites for Eriophorum–tussocks or for pools. Smaller GPP for Sphagnum–spruce hummocks and Sphagnum–shrub intermediate microforms corresponds to significantly reduced NEP for these microforms at the drained bog (<1 \( \mu \text{mol m}^{-2} \text{s}^{-1} \pm 0.1 \mu \text{mol m}^{-2} \text{s}^{-1} \)). Although ecosystem respiration (ER) was greater for Eriophorum–tussocks at the drained bog than the pristine bog, NEP did not differ between sites. However, larger ER coupled with small GPP resulted in negative NEP for bare peat pools at the drained bog (mean \(-0.4 \pm 0.08 \mu \text{mol m}^{-2} \text{s}^{-1} \)).

GLMMs showed vascular green area (VGA) was the most significant predictor for GPP, ER, and NEP at both sites, with a larger VGA corresponding to greater GPP, ER, and NEP (table 2). The models showed water table depth (WTD) was weakly significant for GPP at the pristine bog but not the drained bog, with deeper water tables corresponding to greater GPP at the pristine bog. The weak negative relationship between ER and WTD at the pristine bog indicates deeper water tables have greater ER. At the drained bog, the model coefficient is significant but very small indicating a weak positive relationship where deeper water tables (>1 m below the surface) have smaller ER. Although statistically significant, volumetric water content (VWC) was a weak predictor for GPP at the pristine bog (larger VWC have smaller GPP) and this relationship was weaker at the drained bog. Smaller VWC and warmer soil temperatures corresponded to greater ER at the drained bog but not at the pristine bog.

**Discussion**

To determine peatland response to hydrological change that may occur as a result of human disturbance (drainage) and/or a warming climate, we compared the ecological conditions of a bog subject to drainage (~7 years), with a pristine bog. Our results show the ecological response to drainage to be significant, but that this response differs among microforms, highlighting the importance of peatland microforms with different ecosystem states for overall ecosystem stability.

Species composition for hummocks and intermediate microforms did not differ between sites, but there was a stark contrast between Sphagnum–sedge pools at the pristine bog and dry pools at the drained bog with mostly bare peat and litter. Pool species such as S. majus (that forms floating Sphagnum mats) are slow to recover from prolonged desiccation (Rydin and McDonald 1985, Højek and Vícherová 2014), and so their absence in a dry pool is not surprising. We did not record greater graminoid cover (sedges) in any microforms at the drained bog, most likely due to the deeper water tables at this site being outside the range of tolerance for most peatland species (Weltzin et al 2003, Talbot et al 2010, Laine et al 2012). Mean peat moisture at the surface (~20 cm depth) was 67% for Eriophorum tussocks at the drained bog (compared to 92% at the pristine bog), slightly drier than the range (>70%) noted for increased E. vaginatum growth at an extracted peatland in Quebec (Lavoie et al 2005). Although frequently observed for disturbed bogs and fens (Tuittila et al 2000, Lavoie et al 2005), deeper water tables and reduced peat moisture content at the drained site may prevent the expansion of E. vaginatum or other sedge species within the bare peat pools.

The smaller shrub leaf:stem ratio and vascular green area (VGA) for Sphagnum hummocks at the drained bog suggests reduced water availability is having an adverse effect on hummock vegetation structure, including species that are tolerant of deeper water tables such as S. fuscum (Rydin and McDonald 1985, Toet et al 2006, Højek and Vícherová 2014). These small changes in vegetation structure, the absence of forbs such as Maianthemum trifolium, and slightly reduced Sphagnum cover explain the smaller gross primary production (GPP) at the drained bog. Smaller GPP at the drained bog may also be due to low peat moisture contents at the surface of hummocks and intermediate microforms, causing periods of water stress and decreased photosynthesis in S. fuscum and S. rubellum (Wallen et al 1988, Silvola 1990). GPP for Eriophorum tussocks (E. vaginatum) in intermediate microforms did not differ between sites, suggesting the photosynthesis of
established Eriophorum tussocks with a deep root system is maintained at the drained bog despite deeper water tables (Wein 1973).

GPP in pools at the drained bog was small owing to the collars containing only bare peat and litter (no vegetation cover) but there was no difference when compared to Sphagnum-only pools (collars with no sedges) at the pristine bog (GPP at both sites < 1 μmol m⁻² s⁻¹). Although Sphagnum GPP is typically small (generally less than 2 μmol m⁻² s⁻¹, e.g. Street et al. 2012), it is possible that shallow water tables and greater surface ponding in pools at the pristine bog in 2014 had a negative impact on photosynthesis of S. majus, thereby reducing GPP (Weltzin et al. 2000, Pelletier et al. 2011). At the drained bog, we also observed small dark patches of possibly algae or lichen on the surface of the dry pond but as this was often indistinguishable from litter, it was

Figure 6. Differences in GPP, ER, and NEP (mean ± standard error) for (a) Sphagnum-spruce hummocks, (b) Sphagnum-shrub intermediate microforms, (c) Eriophorum-tussocks (intermediate microforms), and (d) Sphagnum-sedge, Sphagnum-only, and bare peat pools, at the pristine bog and the drained bog. Different uppercase letters indicate there is a statistically significant difference in GPP, ER, or NEP for the same vegetation-microform type (or different vegetation types for pools) at the pristine and drained bog (GLMM p < 0.05).
recorded as such. This may be a reason for the small GPP in collars with no apparent vegetation cover in pools at the drained bog.

**Potential shifts in ecosystem state and loss of resilience**

According to the two-layer model of peat structure and growth, peat is added to the upper oxic catotelm and therefore peat growth, but is limited by water stress at both shallow and deep water tables (Belyea and Clymo 2001, Clymo 1992, Hilbert et al. 2000). Peat growth is therefore optimal in peat with moderate water tables, or intermediate acrotelm thickness (Hilbert et al. 2000, Belyea and Clymo 2001). Our results showed net ecosystem production (NEP) was largest where water tables were ~30 cm below the surface, and that NEP declines as the water table (shown as deepest recorded water table as an estimate of acrotelm thickness according to Clymo 1992) is more or less than this optimum range (figure 7). If we assume NEP as an indicator of peat growth, our results support the described relationship.

Our results showed NEP is positive for both pools and hummocks at the pristine bog, so we assume production exceeds decomposition and that these microforms represent a stable wet state and a stable dry state as shown on our conceptual model (figure 8 - Hilbert et al. 2000, Belyea and Clymo 2001, Eppinga et al. 2009a, 2009b, Scheffer et al. 2012, Lindenmayer et al. 2016). Although the acrotelm thickness for dry pools at the drained bog was within the same range as hummocks at the pristine bog (see figure 4), NEP was negative. We also found indicators of advanced peat decomposition in these dry pools (data not shown), which suggests decomposition is likely to exceed production and that these pools now represent an unstable state with the potential for a shift to a alternative ecosystem state (position B—figure 8). NEP was positive for hummocks at the drained bog and we did not find any indicators of advanced decomposition (data not shown), which suggests these hummocks occupy a stable dry state but with reduced resilience (R2 or R3 - figure 8).

This loss of resilience is indicated by the lack of a relationship between production (GPP) and water table depth, and the weak relationship between production and surface peat moisture at the drained bog (table 2). These data suggest the hydrological feedbacks regulating production at the drained bog are weakened, causing peat accumulation to slow (Hilbert et al. 2000, Belyea and Clymo 2001).

Hydrological thresholds for vegetation change have been passed for dry pools at the drained bog, but thresholds for vegetation change in hummocks and intermediate microforms have not been reached, or there is a delayed vegetation response. Vegetation succession in peatlands can be slow, often taking decades, even in response to external forcing (e.g. change in climate) (Nordbakken 2000, Hughes and Barber 2004). Whether dry pools at the drained bog are eventually colonised by peatland hummock species (e.g. Chamaedaphne calyculata, S. fuscum) or undergo succession to forest species (e.g. Populus spp., Alnus spp., Geocaulon lividum, and

### Table 2. Generalised linear mixed effect model (GLMM) results for gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) at the pristine bog and the drained bog.

| Model Term | PRISTINE | | | DRAINED | | |
|------------|----------|------------|------------|----------|------------|
|            | F | Coefficient (SE) | t | p-value | F | Coefficient (SE) | t | p-value |
| GPP Model  | 24.7 | 0.151 (0.04) | 3.95 | 0.001 | 49.9 | 0.222 (0.02) | 8.11 | 0.001 |
| VGA Model  | 15.6 | -0.021 (0.00) | -3.29 | 0.001 | 65.8 | 0.002 (0.00) | -1.51 | 0.130 |
| WTD Model  | 10.8 | -0.011 (0.00) | -1.80 | 0.003 | 7.0 | -0.008 (0.00) | -2.65 | 0.009 |
| VWC Model  | 3.2  | -0.053 (0.02) | -2.30 | 0.074 | 2.9  | 0.022 (0.01) | 1.70 | 0.090 |
| Peat temperature | 5.3 | -0.055 (0.02) | -2.30 | 0.074 | 2.9  | 0.022 (0.01) | 1.70 | 0.090 |
| ER Model   | 14.5 | 0.148 (0.07) | 2.07 | 0.042 | 17.7 | 0.126 (0.03) | 4.20 | 0.001 |
| VGA Model  | 4.3  | -0.041 (0.01) | -3.49 | 0.001 | 20.9 | 0.002 (0.00) | 4.56 | 0.001 |
| WTD Model  | 12.2 | -0.007 (0.01) | -0.64 | 0.521 | 50.0 | -0.011 (0.00) | -7.07 | 0.001 |
| VWC Model  | 0.0  | -0.013 (0.04) | -0.30 | 0.760 | 274.2 | 0.095 (0.00) | 16.55 | 0.001 |
| Peat temperature | 0.4 | -0.003 (0.02) | -0.45 | 0.565 | 20.7 | -0.019 (0.00) | -4.54 | 0.000 |

Standard error for model coefficient in parentheses. * = significant.

Model terms = vascular green area (VGA), water table depth (WTD), peat volumetric water content (VWC) at 20 cm depth, and peat temperature at 10 cm depth.
Pleurozium spp. from the nearby raised bioherm, will determine the shift to a stable peatland dry state or an alternative ecosystem state (Figure 8). Over time, deeper water tables may also cause compression of the peat and subsidence, therefore reducing distance to the water table (Price and Schlotzhauer 1999, Strack et al 2006). This feedback could potentially mediate the effects of drainage by increasing peat surface moisture and Sphagnum growth, and thus preventing shifts to non-peatland states.

**Conclusion**

Our study shows that although large areas (hummocks and intermediate microforms) of the drained bog remain a C sink, dry pools are a C source to the atmosphere and the resilience of the peatland has been reduced by relatively short-term (∼7 years) drainage. Long-term drainage and/or further decreases in peatland water table due to mine dewatering or other hydrological disturbance may further reduce peatland resilience, as a decline in Sphagnum and forb cover on hummocks reduces production and deeper peat is subject to continued
decomposition in oxic conditions. Shrub and tree species tolerant of drier conditions (e.g. *Picea mariana*, *Rhododendron groenlandicum*, *Empetrum nigrum*) may slowly increase cover but this would likely lead to slower rates of peat accumulation and a potential shift to a non-peatland state. However, we suggest even short-term drainage could have significant consequences for these large C stores, with reduced *Sphagnum* cover and a drier peat surface more vulnerable to fire ignition, greater burn severity, and prolonged peat smouldering (Turetsky et al. 2011, Kettridge et al. 2015). As the frequency of wildfires in large parts of Canada’s boreal continue to increase in a drier and warmer climate, drained peatlands with reduced resilience could be at significant risk of large C losses.

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**Author contributions**

LIH conceived the ideas, designed the methodology, collected and analysed the data, and wrote the manuscript. NTR and TRM contributed critically to the ideas, methodology, and data interpretation. All authors contributed to the draft manuscript and gave final approval for publication. The authors declare no conflicts of interest.

**Data accessibility**

The data presented in this manuscript are available from the Dryad Digital Repository: DOI (doi:10.5061/dryad.x69p8czfr).

**ORCID iDs**

Lorna I Harris  [https://orcid.org/0000-0002-2637-4030](https://orcid.org/0000-0002-2637-4030)

Nigel T Roulet  [https://orcid.org/0000-0001-9571-1929](https://orcid.org/0000-0001-9571-1929)

Tim R Moore  [https://orcid.org/0000-0001-7472-7569](https://orcid.org/0000-0001-7472-7569)

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