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Plant community composition along a peatland margin follows alternate successional pathways after hydrologic disturbance

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ABSTRACT

Hydrological disturbances can alter the structure and function of ecosystems by changing plant species composition over time. Peatlands in the northern hemisphere are particularly sensitive to global change drivers related to soil water availability, such as drought and drainage, because of important ecohydrological feedbacks between species composition and water table position. Here, we examined the plant community structure and environmental drivers of species distributions over two growing seasons along a bog – margin gradient, pre- and post-disturbance by beaver activity. Pond drainage resulted in seasonal average water table depth 8–24 cm lower in the second season. Five plant communities corresponded to changes in water table depth and acidity: bog, poor fen, meadow, mudflat and pond. Plant cover increased in meadow and mudflat communities, decreased in the pond community and did not differ between years in bog and poor fen communities. Changes in species abundance between years showed signs of alternate successional pathways: one that favors *Sphagnum* moss and bog community expansion and another pathway that favors meadow and mudflat expansion. This study highlights the non-linear successional trajectory of plant communities with changes in water table depth, which has implications for land management goals that aim to conserve the ecological integrity of peatland ecosystems.

1. Introduction

Understanding the environmental drivers of plant community composition is a fundamental question that is increasingly relevant as global change drivers such as climate and land use change continue to impact the structure and function of natural ecosystems. Global change drivers related to soil water availability are of particular importance for many ecosystems due to the reliance on water for plant productivity. Such drivers include altered precipitation and temperature, which can lead to droughts, as well as hydrologic disturbances such as drainage and flooding. Peatlands in the northern hemisphere function as long-term carbon sinks (Loisel et al., 2014) and are particularly sensitive to changes in soil water availability because of important ecohydrological feedbacks between species composition and water table position (Malhotra et al., 2016). Thus, hydrological disturbances, either natural or anthropogenic, could modify the structure and function of peatlands by changing plant species composition over time. Species shifts have already been observed in peatlands experiencing hydrologic disturbances such as permafrost thaw (Johansson et al., 2006; Malhotra and Roulet, 2015) and drainage (Jukaine et al., 1995; Minkkinen et al., 1998; Talbot et al., 2014), and future shifts are predicted for peatlands that will experience warmer, drier conditions in response to increasing temperatures under climate change (Roulet et al., 1992; Strack et al., 2006b).

Under drier conditions (*e.g.*, drought, drainage), peatland water tables fall below the peat surface, which has corresponded to increased vascular plant cover (such as dwarf shrubs) and a reduction in the moss cover over long (*i.e.*, multi-year, decadal) (Munir et al., 2014; Strack et al., 2006a; Urbanová et al., 2012) and short timescales (*i.e.*, within a growing season) (Strack and Waddington, 2007). Alternatively, raising peatland water tables have been associated with both declining (Mitchell and Niering, 1993; Kelly et al., 1997) and increasing plant cover (Asada et al., 2006; Tuittila et al., 2000), often with species-specific responses. Thus, the direction of species shifts in response to hydrologic change is not generalizable across different peatland types (*e.g.*, bogs, fens), and likely varies among peatland types and successional stages.

Similar to other wetlands, peatlands can change from one type to another over successional time. For example, fens are minerotrophic peatlands that receive water and nutrients from precipitation and

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groundwater, and will typically develop over successional time into bogs when they become disconnected from mineral-rich groundwater. Bogs are ombrotrophic, nutrient poor peatlands raised above the water table that receive water and nutrients exclusively from precipitation. Bogs are potentially more sensitive to hydrologic changes because of this dependence on precipitation for both soil water and nutrients available for plant uptake. Therefore, an understanding of the successional stages of peatlands with hydrologic change is important when considering the direction of species shifts for any given peatland.

Although the importance of water table position on species composition has been emphasized in numerous peatland studies (*e.g.*, Bragazza et al., 2005; Glaser et al., 1990; Laine et al., 2007), less attention has been given to the ombrotrophic bog margin. The margin, or "lagg", is important for bog functioning by buffering the bog from mineral-rich waters and maintaining the water mound in the bog (Damman, 1986). Hydrologic conditions at the margin are distinct from the bog center because of variable water levels and nutrient conditions in combination with low summer flows and high winter runoff. Moreover, the margin can be subjected to unique disturbances, such as drainage and flooding. For example, beaver activity is a common disturbance along peatland margins that drastically changes the hydrologic regime and consequent plant community composition (Rosell et al., 2005).

Beaver activity affects not only hydrologic regimes but also fluvial processes and carbon dynamics (*i.e.*, patterns of carbon accumulation and greenhouse gas exchange of carbon dioxide and methane). Beaver maintain high water levels at the margins and within peatlands, which moderates water flow and vegetation patterns. Beaver disturbance follows a 10–15 year cycle of dam initiation, abandonment and recolonization. Dam initiation raises water levels, creating a pond and flooding the adjacent peatland margin. Dam abandonment and collapse allow water levels to recede, exposing substrate and allowing species to colonize previously submerged areas, or emerge from the buried seed bank (McMaster and McMaster, 2001). Dam recolonization consequently regresses plant succession to earlier submerged states (Little et al., 2012; McMaster and McMaster, 2001).

Plant colonization following beaver dam collapse may follow alternate successional pathways (Little et al., 2012; Mitchell and Niering, 1993; van der Valk, 1981), the direction of which has consequences for peatland structure and function. Here, we examined the plant community structure and environmental drivers of species distributions over two growing seasons (May–September of 2012 and 2013) in a temperate bog disturbed by beaver activity. We sampled along a gradient extending from ombrotrophic bog, through the bog margin, and into a beaver pond (hereafter referred to as a 'bog - margin gradient'). Logs were selectively removed from the beaver dam in October–November, 2012 to accelerate the process of dam abandonment and collapse, and pond water levels substantially fell and remained lower throughout the 2013 growing season. This allowed us to examine changes in plant species composition along a bog - margin gradient in response to hydrologic disturbance. We expected to find distinct plant communities along the bog - margin gradient corresponding to changes in average water table position and water chemistry (*e.g.*, acidity). We predicted aquatic plant species cover to decrease and graminoid (*e.g.*, grasses, rushes, sedges) cover to increase in response to lower water levels. We further predicted that lower water levels along the bog margin would encourage the expansion of bog species (*e.g.*, dwarf shrubs, ombrotrophic sedges and mosses) relative to fen (*e.g.*, dwarf shrubs, minerotrophic sedges and mosses) and marsh species (*e.g.*, minerotrophic graminoids and herbs), largely because of the loss of standing water and mineral-rich inputs that are important for fen and marsh species.

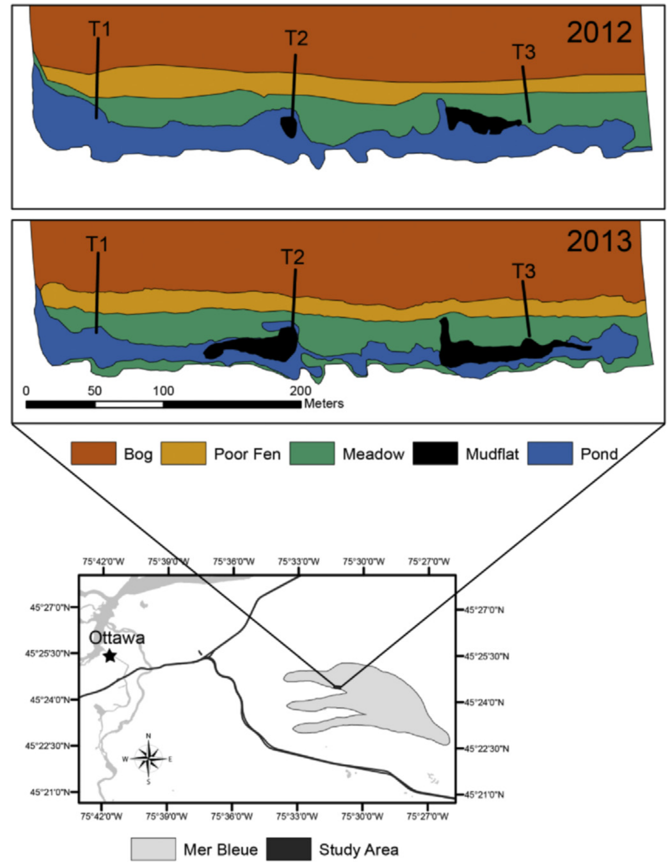

Fig. 1. Map showing the location of the Mer Bleue peatland and total cover between years for five plant communities along the bog – margin gradient in 2012 and 2013. Community cover for each year was extrapolated from transect data (T1-T3) and Google Earth imagery obtained for August 2012 and 2013. Open data for roads and waterbodies are licensed under the Open Government License, City of Ottawa, Ontario, Canada.

2. Methodology

2.1. Site description

Measurements were made along the margin of the Mer Bleue peatland in an area containing beaver ponds. Mer Bleue is a large (25 km^2) raised ombrotrophic bog ~10 km east of Ottawa, Ontario, Canada (Fig. 1). The climate of the area is cool-continental with a mean annual temperature of 5.8 °C and mean growing season temperature (May–October) of 15.5 °C. Mean annual precipitation is 910 mm and mean growing season precipitation is 491 mm (Lafleur et al., 2005). The bog center is dominated by dwarf shrubs such as *Chamaedaphne calyculata* (L.) Moench, *Kalmia angustifolia* L. and *Rhododendron groenlandicum* (Oeder) Kron & Judd, with a surface layer of *Sphagnum* mosses. Peat depths reach 5–6 m at the center of the bog and thins to 1–2 m towards the margins (Bubier et al., 2006).

2.2. Vegetation sampling

In May 2012, we established three transects (oriented North-South) that covered the major variation in plant species and water table depths including typical bog microtopography (hummocks, hollows), the peatland margin and beaver pond (Fig. 1). Boardwalks were constructed parallel to the transects to avoid damaging the vegetation and to allow easier access for data collection. Square vegetation plots (61 cm × 61 cm) were permanently installed every 2.5 m along the three transects. Transect 1 (T1) was closest to the beaver dam and