Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability

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Abstract

The composition of a peatland plant community has considerable effect on a range of ecosystem functions. Peatland plant community structure is predicted to change under future climate change, making the quantification of the direction and magnitude of this change a research priority. We subjected intact, replicated vegetated poor fen peat monoliths to elevated temperatures, increased atmospheric carbon dioxide (CO_2), and two water table levels in a factorial design to determine the individual and synergistic effects of climate change factors on the poor fen plant community composition. We identify three indicators of a regime shift occurring in our experimental poor fen system under climate change: nonlinear decline of *Sphagnum* at temperatures 8 °C above ambient conditions, concomitant increases in *Carex* spp. at temperatures 4 °C above ambient conditions suggesting a weakening of *Sphagnum* feedbacks on peat accumulation, and increased variance of the plant community composition and pore water pH through time. A temperature increase of +4 °C appeared to be a threshold for increased vascular plant abundance; however the magnitude of change was species dependent. Elevated temperature combined with elevated CO_2 had a synergistic effect on large graminoid species abundance, with a 15 times increase as compared to control conditions. Community analyses suggested that the balance between dominant plant species was tipped from *Sphagnum* to a graminoid-dominated system by the combination of climate change factors. Our findings indicate that changes in peatland plant community composition are likely under future climate change conditions, with a demonstrated shift toward a dominance of graminoid species in poor fens.

Introduction

Boreal peatlands provide globally important ecosystem functions such as the regulation and maintenance of the hydrological cycle, and carbon storage (Limpens *et al.*, 2008). In particular, the long-term accumulation of slowly decomposing plant material (peat) allows these ecosystems to store approximately 30% of the Earth's terrestrial soil carbon while only comprising approximately 3% of the Earth's land area (Gorham, 1991; Clymo *et al.*, 1998). The main mechanism of peat accumulation is slow decomposition rates regulated by saturated, anaerobic soils, and cool climate conditions associated with the relatively northern latitudes where peatlands are dominantly found (Yavitt *et al.*, 1997). In northern peatlands, *Sphagnum* mosses are fundamental to this carbon sequestration and are key to the stability and resilience of this system (Turetsky

et al., 2012). *Sphagnum* spp. comprises up to 90% of peat (Kuhry, 1997; Turetsky, 2003; Hájek *et al.*, 2011) because the recalcitrant and antibacterial nature of *Sphagnum* inhibits decomposition (Painter, 1991; Kroken *et al.*, 1996), particularly when compared to the relatively decomposable tissues of vascular plants (Hobbie, 1996). This accumulation of peat changes the local hydrology and pore water biogeochemistry, making environmental conditions generally more advantageous for *Sphagnum*; as a result, *Sphagnum* is often considered an ecosystem engineer (van Breemen, 1995) contributing to peatland ecosystem resilience to perturbation (Waddington *et al.*, 2014). The importance of the *Sphagnum*-dominated peatland vegetation community is consistently highlighted in the literature as a key component of many ecosystem functions, including carbon storage (Weltzin *et al.*, 2000; Limpens *et al.*, 2008; Bragazza *et al.*, 2013; Kuiper *et al.*, 2013). Thus, changes in peatland plant community composition, especially ones that reduce *Sphagnum* dominance in favor of vascular vegetation, particularly graminoids,

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would be expected to have significant effects on carbon storage.

Anthropogenic-driven climate change (i.e. postindustrial elevated temperature and atmospheric CO_2 concentrations) has the potential to significantly change northern ecosystems, particularly peatlands (IPCC, 2007). Fenner *et al.* (2007) proposed that increased temperature and atmospheric CO_2 concentrations will increase vascular plant growth leading to a decrease in *Sphagnum* spp. cover, while stimulating belowground microbial activity through increased labile carbon in vascular plant root exudates, and a release from the inhibitory polyphenol compounds exuded by the *Sphagnum* spp. (Fenner & Freeman, 2011; Bragazza *et al.*, 2013). The increased abundance of vascular plants and microbial activity is subsequently expected to alter soil nutrient content and pH conditions to further reinforce this increase in vascular plants. Further consequences of this change are increased decomposition rates, increased CO_2 release, and changes to dissolved organic carbon (DOC) quality. Forecasted elevated temperatures at northern latitudes are also anticipated to increase evapotranspiration rates, lowering the water table relative to the ground surface (Rouse *et al.*, 1997). This lower water table would further favor vascular plants and potentially challenge *Sphagnum* spp. that rely on capillarity for moisture supply, further reinforcing changes in biogeochemical processes (Bragazza & Iacumin, 2009; Eppinga *et al.*, 2009; Fenner & Freeman, 2011; Jassey *et al.*, 2013).

Peatlands are not a singular type of ecosystem, but range from more groundwater-connected, minerotrophic, and graminoid-dominated rich fens, to purely precipitation-fed, ombrotrophic, and moss-dominated bogs. The intermediate stage(s) between a rich fen and a bog is generally described as a poor fen (Kuhry *et al.*, 1993). A poor fen, often considered a successional precursor to a more ombrotrophic bog, will become increasingly dominated by *Sphagnum* mosses over time, which in turn will develop the peat profile and move toward hydrological isolation (van Breemen, 1995; Klinger, 1996). During the poor fen stage, the presence of *Sphagnum* mosses and the physico-chemical conditions that they promote will tend to lower species diversity relative to more mineral-rich peatlands (Vitt *et al.*, 1995). Weltzin *et al.* (2000) demonstrated that changing climate conditions, in particular elevated temperature, could competitively advantage dominant rich fen species and revert a poor fen to a rich fen-like state with high graminoid abundance. From a carbon perspective, this reversion of a poor fen to a rich fen squanders the carbon accumulating potential of the system as rich fens do not accumulate carbon at the same rate as a bog (Thormann *et al.*, 1999). As such, understanding how poor fens will respond to climate

change pressures is central to anticipating changes in carbon sequestration in peatlands as a whole.

Turetsky *et al.* (2012) identified temperature, water table position, and atmospheric CO_2 concentrations as important interactive climate change stressors that can alter the resilience and stability of peatlands. Losses in the key individual functional types (e.g. *Sphagnum* mosses) can lead to further shifts in vegetation communities and the weakening of key ecosystem functions such as carbon accumulation. As such, it is important to understand both individual species responses and the community-level properties to identify mechanisms that may govern key feedbacks, and be indicators of (impending) state shift (Weltzin *et al.*, 2000). These shifts are foreshadowed by increased variance in ecosystem parameters (Carpenter & Brock, 2006), and demonstrated nonlinear responses in abundance or growth of constituent species (Guttal & Jayaprakash, 2008). For instance, de Mazancourt *et al.* (2013) suggested that reductions in plant species richness, concomitant with changes to overall community-level biomass are warning signs of ecosystem instability. In peatlands, the direction and magnitude of responses of vascular plant species and *Sphagnum* mosses to environmental changes are the indicators of a shift in plant community composition and ecosystem functions (Dise, 2009). There are no studies, to the best of our knowledge, that have addressed the interactive effects of all of the main climate change factors (changes in temperature, CO_2, and water table position as a result of increased evapotranspiration and potentially reduced precipitation) that affect peatland vegetation communities identified by Turetsky *et al.* (2012), despite the potentially dramatic alteration of functions identified by this important article that would accompany a transition from a moss-dominated to a vascular plant-dominated ecosystem.

The overall objective of the work presented here was to experimentally quantify the impacts of elevated temperature and CO_2, and changes in water table position on a poor fen peatland plant community. Specifically, we seek to test the hypothesis that climate change factors will produce a shift in plant community composition, with an increase in abundance of graminoids and a decrease in abundance of *Sphagnum* spp., accompanied by indicators of instability that would suggest a trajectory toward a shift in stable state.

Materials and methods

Study site

The peatland from which the experimental mesocosms were taken is a 4.5 ha pristine poor fen near White River, Ontario, Canada (48°21′N, 85°21′W) that is part of a long-term experi-

mental site (White River Experimental Watershed Study) maintained by the Ontario Ministry of Natural Resources – Ontario Forest Research Institute (see Webster & McLaughlin, 2010 for detailed description). The 26 year annual average precipitation and temperature is 980 mm and 2.1 °C, respectively (Webster & McLaughlin, 2010). The poor fen is dominated by a typical assemblage of vegetation including *Sphagnum* mosses, ericaceous shrubs, and conifers. The shrub community generally consists of *Chamaedaphne calyculata* (L.) Moench (leatherleaf), *Ledum groenlandicum* (Oeder) (Labrador tea), and *Andromeda polifolia* L (bog rosemary). The dominant trees are *Picea mariana* (Mill.) B.S.P. (black spruce) and *Larix laricina* (Du Roi) K. Koch (tamarack).

Experimental design

In August 2012, 100 intact cylindrical peat monoliths (30 cm diameter × 35 cm deep) were collected from the study peatland. The sampling locations were selected such that each mesocosm would include a representative species assemblage, including mosses, vascular groundcovers, small ericaceous shrubs (with at least one *C. calyculata* as it is the dominant shrub in these systems) and graminoids. All efforts were made to sample from uniform lawns dominated by *Sphagnum magellanicum* Brid.; other *Sphagnum* species that occurred in the system (<20%) include *S. angustifolium*, *S. fallax*, *S. cuspidatum*, and *S. fuscum*. Graminoids at the time of sampling were not an obvious feature of the plant community but included *Carex magellanica* Lam. (boreal bog sedge) and *Carex disperma* Dewey (softleaf sedge).

The peat monoliths were carefully cut using a 40 cm narrow-blade saw, lifted carefully, and placed into individual 5 gallon pails (30.5 cm diameter, 18.93 l). After returning the mesocosms to the University of Western Ontario's Biotron Institute for Experimental Climate Change, a tapered hole was drilled 2 cm from the bottom of each mesocosm, and a 25 cm length of perforated, 16 mm diameter PVC pipe was inserted into the bottom peat to serve as a bottom drain. A ½ inch threaded ABS barbed fitting was screwed into the sidewall, coupling with the drain. A 30 cm length of clear vinyl tubing was then connected to this fitting to control water level in the mesocosm (discussed below) and for water sampling. These mesocosms were then all placed in a staging greenhouse under ambient growing conditions for 10 weeks to stabilize under the new environmental conditions.

In December 2012, 12 randomly selected mesocosms were destructively sampled for initial above- and belowground biomass, peat chemistry, and biodiversity studies that are not reported here. Four additional mesocosms were set aside due to visually apparent disturbance that was considered unrepresentative. The remaining 84 mesocosms were numbered and randomly divided among six environmentally controlled greenhouses (6.1 m × 3.4 m = 98.1 m^3) under a full factorial experimental design (3 × temperature, 2 × CO_2, and 2 × water table treatments, × 7 replicates). The six experimental greenhouses are south facing, and located on the roof of the five-story Biotron building, flanked on either side by staging greenhouses to ensure even temperature and solar radiation regimes in the experimental systems. Relative humidity, temperature, and atmospheric CO_2 concentrations were automatically controlled and monitored using a computerized environmental control system (ARGUS Control Systems Ltd., White Rock, BC, Canada). Across all treatments over the entire experiment, relative humidity was set to a minimum of 60%, and all treatments received ambient solar radiation, with uniform midday shading to control daytime temperature fluctuations from solar gain. Vegetation surveys were performed initially at the end of the recovery period (December 2012), and every 4 months for 1 year to capture one full growing season (peak = April 2013 – August 2013).

Temperature. The experimental greenhouses were run with two temperature programs, depending on time of year. From May 1 to October 31 (growing season) temperature in the ambient greenhouse pair were programmed to temperature set points equal to the 5 year running mean daily maximum and minimum temperatures (and the corresponding timing of those averages) with a constant ramp between set point temperatures. The +4 °C and +8 °C greenhouse pairs were programmed in an identical fashion, but with the respective offsets. As the infrastructure in the experimental greenhouses cannot be reliably operated at <10 °C, the experimental greenhouse temperatures were set at a constant temperatures between November 1 to April 30. The ambient greenhouse pair was set to 11.5 °C, which is the mean growing season temperature for the experimental poor fen from which the samples were taken. The +4 °C and +8 °C greenhouse pairs were programmed in an identical fashion, but with the respective offsets.

Carbon dioxide. In one of each of the temperature treatments, the CO_2 concentrations in experimental greenhouse air reflected the ambient exterior air in the vicinity of the building (mean = 427.8 ppm, S.D. 3.55) and were not adjusted in any way experimentally. In the second of each of the temperature treatments, the greenhouse CO_2 concentrations were set at 750 ppm. This additional CO_2 was supplied by a compressed CO_2 source, and the elevated CO_2 condition was maintained dynamically by the environmental control system. The CO_2 regulating system was calibrated weekly against a known gas standard.

Water table. In each of the experimental greenhouses, seven replicate mesocosms were randomly selected for a higher water table treatment (~5 cm from the peat surface) with the remaining seven subjected to a lower water table treatment (~25 cm from the peat surface). The two water table treatments were held constant at their respective levels throughout the experiment to isolate the main effects that could be confounded by interactions among temperature, plant community changes, and evapotranspiration. Water levels were set in each of the mesocosms by fixing the end of the clear vinyl drain tube at the appropriate level on the outside of the mesocosm. This allowed for visual inspection of the water table position in the mesocosm, and prevented overwetting beyond the target water table level as excess water would simply drain until

the level in the mesocosm was level with that in the overflow tube. Water was added to all of the mesocosms evenly over the course of the experiment. To mimic the total water and nutrient delivery in rainfall and to not artificially disadvantage *Sphagnum* through ionic or pH effects, 700 ml of Rudolph's Solution (diluted by a factor of 4 and adjusted to pH 5.8; see Faubert & Rochefort, 2002) was added evenly over the vegetation twice weekly. On alternate days, small additions of reverse osmosis water were made at the edge of the mesocosms if the water level in the sight tube was below the target.

Vegetation and pH analyses

Plant species were identified and enumerated in all of the mesocosms every 4 months. Plant identification was based on Newmaster *et al.* (1997) and Legasy (1995). For *Sphagnum* spp. and *Carex disperma* that could not be counted individually because of density or size, percent cover was recorded using an adapted Braun-Blanquet scale as recommended by Rochefort *et al.* (2013). Water was sampled monthly from the drain tubes in each mesocosm, and pH was measured almost immediately after sampling using a calibrated standard pH glass electrode.

Data analyses

A three-way, repeated measures analysis of variance (RM-ANOVA) with a Tukey *post hoc* test was used to test for changes in absolute and percent change in plant species abundance and for species richness under the different experimental conditions (Statistica 7, StatSoft. Inc., 2004). As increased variance in ecosystem parameters and nonlinear responses in plant species abundance are considered precursors to shifts in ecosystem stability, the variance of species abundance and pH measures were calculated from within-treatment replicates. At the community level, we quantified total variability (or dissimilarity) for main experimental effects using SIMPER analysis in Primer 5 (Primer-E Ltd., 2001). This test calculates a community compositional similarity coefficient within and between mesocosm treatments based on species abundance data using the methods described by Bray & Curtis (1957). Plant community compositional data (11 dominant plant species) were analyzed using principle components analysis (PCA) in Statistica 7.0. Case scores for the first two principal components were analyzed with an ANOVA for the main effects of temperature, CO_2 concentration, and water table level, and by regression for pH to determine species-specific response to different variables. Factor coordinates based on species correlations were used to interpret the PCA. Product-moment correlations were performed on plant abundance at each time point. Analysis of similarities (ANOSIM) was performed on total plant community composition among treatments.

Results

A total of 16 plant species were observed across all mesocosms and sampling times (Table S1). There was no initial difference in richness [December 2012 average = 7.3 ± 0.1 (S.E.) species] across mesocosms in all treatments, however richness increased over the summer season (August 2013 average = 7.8 ± 0.2 species; $F_{3,216} = 6.018$, $P < 0.001$). No significant relationship was found among species richness and any of the main climate change factors (temperature, $F_{2,72} = 2.637$, $P = 0.079$; water table position, $F_{1,72} = 1.268$, $P = 0.264$; CO_2 concentrations, $F_{1,72} = 2.143$, $P = 0.148$), or their interactions.

There was no difference in *Sphagnum* spp. cover between the ambient and +4 °C treatments, however it decreased significantly at +8 °C ($F_{2,72} = 5.492$, $P = 0.006$; $F_{4,144} = 2.625$, $P = 0.037$) (Fig. 1a). *Carex disperma* increased in cover over time in all treatments, however the +8 °C treatment showed a much greater increase in cover over time ($F_{2,72} = 5.486$, $P = 0.006$; $F_{6,216} = 3.348$, $P = 0.004$) (Fig. 1b). Although mesocosms were allocated to the experimental treatments using a fully randomized scheme, the mesocosms in the +4 °C and +8 °C treatments had, on average, a higher initial abundance of the large graminoid Carex agellanica than ambient. Despite this, a significant pattern over time is clear. Carex magellanica abundance was unchanged under ambient temperatures, but
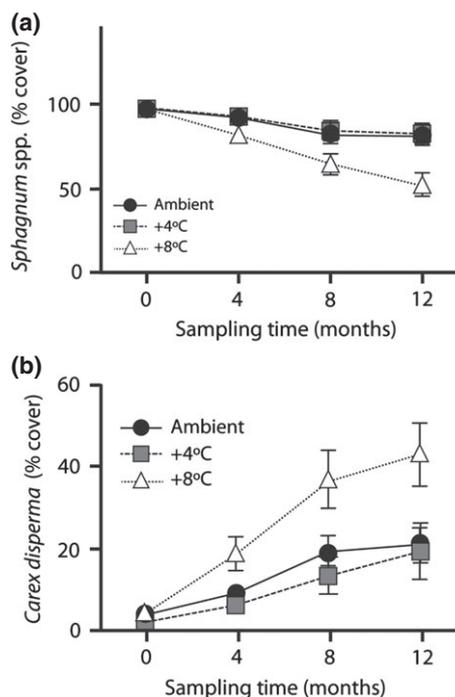
Fig. 1 Changes in peatland vegetation (a) *Sphagnum* spp. and (b) *Carex disperma* percent cover (mean ± SE) under elevated temperature conditions from December 2012 (T_0) to December 2013 (T_{12}) in experimental mesocosms.

increased significantly by 8 months under both +4 °C and +8 °C ($F_{2,72} = 8.640$, $P < 0.001$; $F_{6,216} = 6.384$, $P < 0.001$) (Fig. 2a). Interactive effects of the experimental treatments on the dominant plant species were only observed for *C. magellanica*; this species significantly increased under elevated temperature (+8 °C) and elevated CO_2 conditions ($F_{6,216} = 2.762$, $P = 0.013$) during the first 8 months of the experiment ($T_0 - T_8$ change in abundance $F_{2,72} = 5.280$, $P = 0.007$) resulting in 15 times greater abundance than under ambient temperature and CO_2 (Fig. 2b). *Sphagnum* was significantly negatively correlated with the abundance of *C. disperma* at all sampling times (T_4: $R = -0.753$, $P < 0.001$; T_8: $R = -0.753$, $P < 0.001$; T_{12}: $R = -0.600$, $P < 0.001$), but had no relationship with *C. magellanica* abundance.

Water table position and CO_2 concentration also showed main and interactive effects but only for the less abundant species. The ericaceous shrub *Kalmia polifolia* Wangenh (bog laurel) significantly increased in abundance under lower water table conditions ($F_{3,216} = 8.502$, $P < 0.001$). *Ledum groenlandicum* increased in abundance under ambient (temperature and CO_2) and lower water table conditions ($F_{6,216} = 3.783$, $P = 0.001$). Elevated CO_2 conditions decreased *Vaccinium myrtilloides* Michx (blueberry) ($F_{6,216} = 2.813$, $P = 0.012$) abundance at 8 months, but only under ambient temperature. *Chamaedaphne calyculata* increased by one or two individuals under elevated temperature by the end of the experiment ($F_{6,216} = 4.502$, $P < 0.001$).

The first two PCA components explained 31% of the variance (16.6% and 14.7%, respectively). Case scores of PC 1 were significantly related to pH ($R^2 = 0.242$, $P < 0.001$), whereas PC 2 was significantly related to temperature ($F_{2,79} = 4.043$, $P = 0.021$) (Fig. 3). Species driving PC 1 were *Sphagnum* spp. (0.64), *C. magellanica* (0.64) associated with acidic conditions, and *C. disperma* (−0.66) associated with higher pH conditions. For PC 2, *A. polifolia* (0.65), *V. myrtilloides* (0.46), and *Lycopodiella inundata* (L.) Holub (northern bog club moss) (0.44) were associated with ambient temperatures, while *Vaccinium oxycoccos* L. (bog cranberry) (-0.52) was associated with elevated (+8 °C) temperatures. ANOSIM revealed significant differences in community composition between water table positions (Global $R = 0.027$, $P = 0.042$) and temperature (Global $R = 0.091$, $P = 0.010$) whereby communities under ambient temperature were significantly different from +4 and +8 °C (pairwise comparisons $P = 0.030$, 0.020, respectively).

System variance

Variance in *C. magellanica* abundance increased after 8 months in elevated temperature treatments (Fig. 2c).
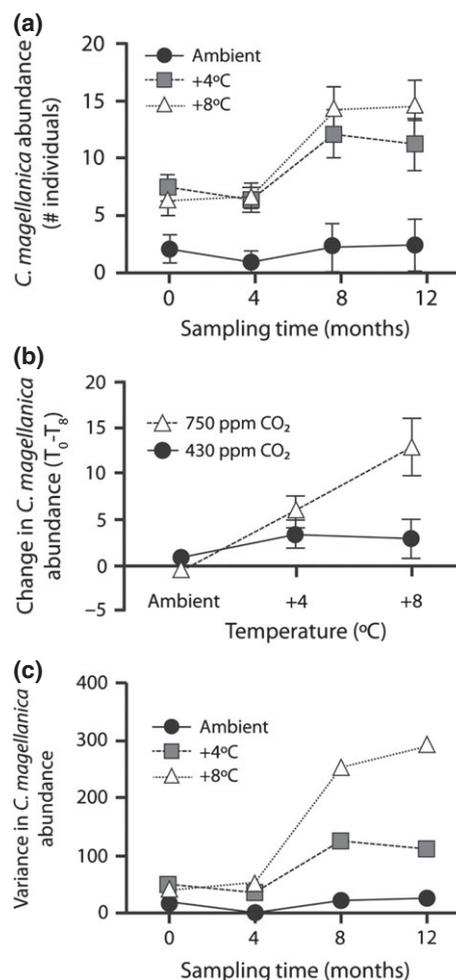
Fig. 2 (a) *Carex magellanica* abundance (mean ± SE) under elevated temperature conditions from December 2012 (T_0) to December 2013 (T_{12}) in experimental mesocosms, (b) change in *C. magellanica* abundance over the first 8 months (T_0–T_8) under elevated temperature and CO_2 conditions, and (c) variance in *C. magellanica* abundance under elevated temperature in experimental mesocosms over the duration of the experiment.

The SIMPER test corroborated greater total community variability (dissimilarity) within +8 °C elevated temperature mesocosms (ambient = 38%, +4 °C = 35%, +8 °C = 46% dissimilar). As expected for poor fen peat, the pH of all of the experimental mesocosms at all times was acidic (4.2 – 4.6); pH was higher under ambient temperatures than other treatments ($F_{2,69} = 20.44$, $P < 0.001$). Over time, there was an increase in variance in pH across the experimental system, increasing from 0.03 early in the experiment to 0.24 at the end of 12 months. There was an interactive effect of temperature and CO_2 on pH at the last sample time, where all mesocosms at +8 °C increased in pH ($F_{14,483} = 2.431$, $P = 0.03$).
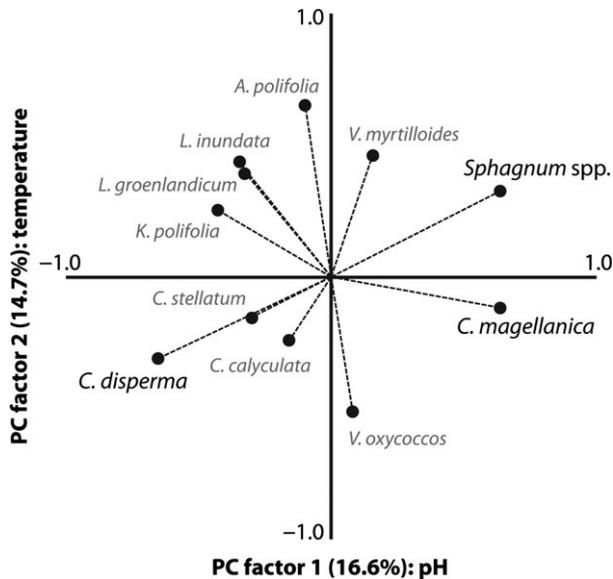
Fig. 3 Plot of the first and second principal components (PC) with percent explained variation for poor fen plant community based on abundance of 11 species collected from experimental mesocosms under elevated temperature, elevated CO_2, and water table manipulation. Positive PC 1 axis loading is associated with low pH conditions; positive axis loadings for PC 2 are ambient temperature conditions, while negative axis 2 loadings are associated with +8 °C conditions.

Discussion

Boreal peatlands depend on the presence of *Sphagnum* spp. for carbon accumulation and ecosystem-level hydrological and biogeochemical stability (Waddington *et al.*, 2014). Particularly at the poor fen stage of peatland development, *Sphagnum* promotes a positive feedback that inhibits decomposition and reinforces the likely successional trajectory toward a stable, ombrotrophic bog. Temperature, moisture, and CO_2 concentrations have been identified as direct controls on *Sphagnum* productivity (Turetsky *et al.*, 2012). Here, we demonstrate that elevated temperature is the main driver of *Sphagnum* decline; we posit that this is due to the loss of competitive advantage over vascular plant species (graminoids). While drought and elevated atmospheric CO_2 conditions have been shown to affect the structure and productivity of peatlands plant communities (Heijmans *et al.*, 2002; Strack & Waddington, 2007), temperature effects are often identified as the dominant driver of change (Weltzin *et al.*, 2000; Breeuwer *et al.*, 2008; Heijmans *et al.*, 2013). We found that temperature increases of +4 °C or higher, particularly when combined with elevated atmospheric CO_2 concentrations, stimulated the growth of *C. magellanica*. For the shorter, denser *C. disperma*, elevated temperatures

of +8 °C were the tipping point, and the expansion of this species is the driver of *Sphagnum* decline in our experiment.

In peatlands, a shift toward a more shrub-dominated system driven by warmer and drier conditions has been well articulated in the literature (Oechel *et al.*, 2000; Weltzin *et al.*, 2000; Breeuwer *et al.*, 2009; Molau, 2010; Bragazza *et al.*, 2013). We measured only minor changes in the shrub species; however we would not expect to have observed significant changes in these slower growing/propagating plants over the course of one experimental growing season. Other studies have considered changes in peatland vegetation abundance (Breeuwer *et al.*, 2010), percent cover (Ballantyne *et al.*, 2013), and biomass (Weltzin *et al.*, 2000) in response to environmental change, but few consider measures of species richness. Generally, changes in plant species richness would be expected to occur over longer time-scales (Menéndez *et al.*, 2006; Suttle *et al.*, 2007). The experimental design here is short term and precludes dispersal and colonization events that would influence natural patterns of species richness. Given the significant change in abundance in *Carex* and *Sphagnum*, one might expect this to be reflected in measures of richness as well; however none were observed under any of the experimental treatments.

Experimental climate conditions created three trajectories of the peatland plant community: ambient conditions maintained *Sphagnum* dominance, but elevated temperature pushed the system toward the expansion of two different graminoid communities; one of which co-occurred with *Sphagnum*, while the other displaced it. Primarily through pore water acidification and the promotion of anoxia under waterlogged conditions, *Sphagnum* spp. maintain a competitive advantage over rooted species under nominal conditions (Malmer *et al.*, 1994, 2003; van Breemen, 1995). Intermediate temperature increases combined with elevated CO_2 conditions benefitted the sparser, taller *C. magellanica* with little effect on the underlying *Sphagnum*. The *C. magellanica* trajectory was associated with more acidic conditions in the elevated temperature and CO_2 treatment, indicating that the favorable temperature and CO_2 conditions for the vascular *C. magellanica* outweighed the inhibitory effects of acidic pH. Under the +8 °C temperature, the densely growing *C. disperma* displaced *Sphagnum*, and was accompanied by a slight shift toward less acidic pore waters, suggesting a stronger trajectory toward a more intermediate fen-like state. Most surprising, this was observed within a single growing season, indicating a latent seed-bank and/or rapid rhizomal expansion under favorable environmental conditions. Fenner *et al.* (2007) is one of the few other studies that has quantified the interactive and

synergistic effects of elevated temperature and CO_2 in simplified peatland plant communities, and found that the percent cover of *Carex* increased most under this interactive treatment. We confirm these findings here in a natural plant community assemblage, and importantly demonstrate that the species of *Carex* that becomes dominant is very important in determining whether *Sphagnum* cover can be maintained. The ecosystem-level implications of a shift away from a *Sphagnum*-dominated to a *Carex*-dominated peatland are significant. Significant increases in *Carex* abundance are expected to substantially increase belowground biomass as well as the nutrient and carbon contributions made to the soil matrix from the rhizosphere (Hobbie, 1996; Fenner *et al.*, 2007; Bragazza *et al.*, 2013; Jassey *et al.*, 2013). This increase in nutrient and labile carbon quantity in both the litter and soil matrix will further promote vascular plants, promote microbial growth and activity, and lead to a degradation of the carbon stock (van Breemen, 1995; Berendse *et al.*, 2001; Larmola *et al.*, 2013).

Competition for light and moisture are the main variables that can tip the competitive advantage from mosses to vascular plants, but these dynamics are expected to play-out over decades (Turetsky *et al.*, 2012). While water table was manipulated in this experiment, biweekly top watering and fertilization precluded moisture from being a limiting factor for *Sphagnum* maintenance and growth. Rather, our main effect variables of elevated temperature and CO_2 enrichment gave vascular plants a competitive advantage, rather than disadvantaging *Sphagnum*. Under forecasted climate change conditions, we would expect these competitive factors to be at play simultaneously, further increasing ecosystem instability and movement toward a stable-state shift. Increased variance in pore water pH, graminoid abundance, and overall plant community composition measured here further suggested incipient ecosystem instability and possible state transition.

Identifying and understanding critical thresholds in ecosystems is a critical area of new knowledge in ecological sciences (Moritz & Agudo, 2013; Sutherland *et al.*, 2013). Despite the obvious interest in identifying these thresholds, the challenges and lack of experimental control in field studies obfuscate changes in key variables (Moritz & Agudo, 2013). Under highly controlled environmental conditions such as those described here, we were able to identify the key climate change drivers of plant community composition in poor fen peatland, and importantly identify threshold temperature changes that led to shifts away from *Sphagnum* toward graminoid dominance. The very rapid shift in *Sphagnum* and graminoid abundance observed in this study suggest that ecosystem shifts in peatlands may occur much more quickly than previously thought once temperature thresholds are exceeded, particularly in transitional peatland types like poor fens.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. A summary of the plant species observed throughout the 12 month study. The average frequency describes the average number of mesocosms ($n = 84$ total) which contained the associated species throughout the experiment. The average abundance/percent cover describes the average number of individual or cover which was observed across all mesocosms for a species. The presence of *Vaccinium oxycoccos* L., *Carex disperma* Dewey, *Sphagnum* spp., *Gaultheria hispidula* (L.) Muhl. ex Bigelow, and *Campylium stellatum var. stellatum* (Hedw.) were all recorded in terms of percent cover. All remaining species were monitored by changes in abundance.