Title

Wetland Flux Controls: How does interacting water table levels and temperature influence carbon dioxide and methane fluxes in Northern Wisconsin?

Authors

Carolyn A Pugh[1], David E Reed[2,3], Ankur R Desai[2], Benjamin N Sulman[4]

1 University of Virginia, Department of Environmental Science, Charlottesville, VA
2 University of Wisconsin-Madison, Department of Atmospheric and Oceanic Sciences, Madison, WI
3 Michigan State University, Center for Global Change and Earth Observations, East Lansing, MI
4 Princeton University, Program in Atmospheric and Oceanic Sciences, Princeton, NJ

Key Points

1) Temperature is the primary control on ecosystem CO_2 fluxes at seasonal time scales and CH_4 fluxes at annual time scales

2) Hydrology affects ecosystem respiration , but primary production is controlled by temperature at annual time scales

3) Long-term observations are needed to quantify hydrological effects on CO_2 and CH_4 fluxes

Abstract

Wetlands play a disproportionately large role in global terrestrial carbon stocks, and from one year to the next individual wetlands can fluctuate between carbon sinks and sources depending on factors such as hydrology, temperature, and land use. Although much research has been done on short-term seasonal to annual wetland biogeochemical cycles, there is a lack of experimental evidence concerning how the reversibility of wetland hydrological changes will influence these cycles over longer time periods. Five years of drought-induced declining water table at Lost Creek, a shrub fen wetland in northern Wisconsin, coincided with increased Ecosystem Respiration (R_{eco}) and Gross Primary Production (GPP) as derived from long-term eddy covariance observations. Since then, however, the average water table level at this site has increased, providing a unique opportunity to explore how wetland carbon fluxes are affected by interannual air temperature differences as well as changing water table levels. Water table level, as measured by water discharge, was correlated with R_{eco} and GPP at interannual time scales. However, air temperature had a strong correlation with R_{eco}, GPP, and Net Ecosystem Productivity (NEP) at monthly time scales and correlated with NEP at inter-annual time scales. Methane flux was strongly temperature-controlled at seasonal time scales, increasing an order of magnitude from April to July. Annual methane emissions were 51 g C m^{-2}. Our results

demonstrate that over multi-year timescales, water table fluctuations can have limited effects on wetland net carbon fluxes and instead at Lost Creek annual temperature is the best predictor of interannual variation.

1. Introduction

Wetlands play a disproportionately large role in global terrestrial carbon storage, and climate change is expected to affect wetland carbon fluxes through changes in ecosystem respiration and photosynthesis (Gorham 1991). Changes in precipitation, temperature, and nutrient availability impact ecosystem productivity, which in turn influences carbon uptake from the atmosphere (Denman et al. 2007). Ecosystem respiration rates, on the other hand, are influenced by factors such as soil moisture, temperature, and microbial communities (Denman et al. 2007). According to the IPCC Fifth Assessment Report (Stocker et al. 2013), higher latitudes are expected to experience an increase in precipitation, mean daily temperatures, and length of the growing season, ultimately changing wetland hydrology.

Although much research has been done on wetland biogeochemical cycles, there is a lack of consensus in the literature concerning how changes in wetland hydrology influence these cycles. In northern wetlands, water table drawdowns are expected due to increased temperatures and evapotranspiration (Gorham 1991), and wetlands are expected to alternate between low and high water table levels. Previous studies of wetland carbon cycle responses to water table changes have yielded equivocal results. Changes in the water table have been shown to drive both Net Ecosystem Productivity (NEP) and Gross Primary Production (GPP), but not Ecosystem Respiration (R_{eco}), in an eddy covariance study of a boreal bog Strachan et al. (2016). Similar connections between net primary productivity and water table have been shown in southeastern floodplain forests using leaf litterfall, wood production, and groundwater table depth measurements Megonigal et al. (1997). Both R_{eco} and GPP were connected to water table changes in an eddy covariance study of temperate lowland peatlands Helfter et al. (2015), although these responses have been shown to vary by peatland ecosystem type and nutrient status Humphreys et al. (2006). A study of a constructed, impounded freshwater wetland suggested that GPP responds more than R_{eco} to drought and rewetting (Anderson et al. 2016), while in an temperate peatland, NEP was shown to be driven by changes in R_{eco} (Wilson et al. 2016). A long-term study of a Scottish peatland showed that NEP responded to variations in both R_{eco} and GPP driven by both water table and growing season length (Helfter et al. 2015). A shortcoming of many studies is the lack of long-term data to evaluate these responses. As a result, a knowledge gap exists in understanding the consequences of short and long term disturbances, as few studies have records of more than 5 years Peichl et al. (2014).

In addition, methane fluxes should not be overlooked when considering the carbon cycle. Global atmospheric methane concentrations have been rising for the past decade, in part due to wetland emissions (Dlugokencky et al. 2009; Nisbet et al. 2014), which are the largest natural source for global CH_4 emissions (Bridgham et al. 2013; Whiting & Chanton 2001). Along with temperature, water table levels are one of the strongest environmental controls on CH_4 production rates for temperate wetlands (Bridgham et al. 2006; Frolking et al. 2011; Nykänen et al. 1998). Moore and Knowles (1989) found that decreased water levels led to decreased CH_4 production rates in wetlands. Water table fluctuations have been shown to sometimes have legacy effects on CH_4 emissions (Brown et al. 2014; Goodrich et al. 2015; Sturtevant et al. 2016), while sometimes the impact has no delay (Chamberlain et al. 2016). Secondary factors such as soil pH and nutrient inputs influence CH_4 production rates as well (Moore & Knowles 1989; Nykänen et al. 1998), and primary productivity has been shown as an important controlling factor Whiting and Chanton (1993). Due to these regionally variable factors, the ecosystem response to lowering water tables may differ slightly depending on the characteristics of the area. A better understanding of wetland carbon cycling responses to changes in hydrology is needed for improved regional and global carbon budget modeling (Blodau 2002).

One significant uncertainty related to changes in hydrology that can be addressed with multi-year data including both carbon dioxide and methane fluxes is the persistence and reversibility of wetland carbon flux responses to water table changes over multi-year time scales. In one relevant case study, *Sulman et al*. (2009) analyzed the effect of a declining water table at Lost Creek, a shrub wetland in northern Wisconsin, USA, on ecosystem respiration and ecosystem production. over a period of six years. They found that declining water tables coincided with increased ecosystem respiration and productivity (Sulman et al. 2009). Since then, the average water table level at Lost Creek has begun increasing again. This affords the unique opportunity to explore how wetland carbon fluxes are impacted by drought recovery. This study compared downstream water discharge to gross primary production (GPP) and aerobic ecosystem respiration (R_{eco}), as well as to methane emission rates. The following hypotheses were tested: 1) Higher discharge (indicating higher water table) is correlated with decreased aerobic respiration (R_{eco}) and GPP, as measured using CO_2 fluxes. 2) Higher discharge is correlated with increased anaerobic ecosystem respiration, as measured using CH_4 production.

2. Methods

2.1 Site Description

Eddy covariance fluxes and auxiliary data from a flux tower at the Lost Creek wetland site were analyzed for this study. Lost Creek (US-Los) is part of the Ameriflux network [Baldocchi et al., 2001] as well as the Chequamegon Ecosystem Atmosphere Study [Davis et al., 2003; Sulman et al., 2009]. The Lost Creek flux tower was established in September 2000 [Sulman et al., 2009], and the surrounding shrub fen wetland is located in the Northern Highlands State Forest in North Central Wisconsin, USA at 485 meters above sea level (46° 4.9' N, 89° 58.7' W).

Lost Creek has a northern continental climate characterized by relatively warm, wet growing seasons and cold, dry winters. The growing season in the area is typically June through August. The average annual precipitation from 1961-1990 was 818 mm, with an average annual temperature of 4.8 °C. Based on aerial photographs, the site has remained a shrub wetland since at least 1950 (R. Hewett, Wisconsin Department of Natural Resources, unpublished). The vegetation canopy is composed primarily of alder (*Alnus incana ssp. rugosa*) and willow (*Salix sp.),* with an average height of 1-3 meters (Sulman et al. 2009). The understory is dominated by sedges (*Carex sp.)*. Lost Creek's floodplain creates the saturated conditions that allow peat to accumulate. Soils are classified as hydric histosols, and include Seelyeville and Markey soils with 0 to 1 percent slopes.

2.2 Measurements

Half hourly eddy covariance fluxes were calculated from 3-D wind speeds using a sonic anemometer (CSAT3, Campbell Scientific, USA, 2000-present), and CO_2/ H_2O gas concentrations from either a closed (LI-6262, LI-COR, USA, 2000-2010) or open (LI-7500A, LI-COR, USA, 2014-present) path infrared gas analyzers, while CH_4 gas concentrations were made on an open path gas analyzer (LI-7700, LI-COR, USA, 2014-present). Due to funding limitations, eddy covariance observations were not recorded from 2011-2013. One-minute air temperature was measured with a slow response sensor and averaged every 30 minutes (HMP45, 2000-2014, Vaisala, Finland; CS215, 2014-present, Campbell Scientific, USA). Eddy covariance data were recorded at 10 Hz at a height of 10.2 meters above the soil surface and averaged every 30 minutes.

Eddy covariance fluxes were calculated using nighttime NEP observations to partition R_{eco} and GPP following the methods of Desai et al. (2005) and then measurements were quality-controlled and gap-filled by the Ameriflux Management Project as part of the FLUXNET 2015 data release (Papale et al. 2006; Reichstein et al. 2005; Vuichard & Papale 2015). Carbon flux into the land surface was defined as a positive NEP value. Further information on the data processing methods can be found at the FLUXNET 2015 web site (http://fluxnet.fluxdata.org/data/fluxnet2015-dataset/data-processing/).

Discharge from a U.S. Geological Survey (USGS) station at Bear River was used as a proxy for water table levels, due to inaccuracies and large data gaps in water table levels at Lost Creek from the data record after 2008. Bear River is located downstream from Lost Creek, 12 miles south at 46° 2.93' N, 89° 59.07' W. The USGS gauge has a drainage area of 211 km^2. To accurately compare discharge to water table level values, only daily water table values above -10 cm (with negative water table values indicating a water table below the soil surface) were compared to daily discharge values since zero discharge conditions at the USGS station were associated with a large range of negative water table levels at the Lost Creek site (Figure 1a).

As an alternate estimate of ecosystem productivity, we used MODIS-derived normalized difference vegetation index (NDVI) centered on the Lost Creek tower site. Data were accessed from the Oak Ridge National Laboratory MODIS server (https://modis.ornl.gov/fixedsite/).

Relationships between environmental drivers (air temperature and discharge) and fluxes (GPP, R_{eco}, and NEP) were calculated using ordinary least squares linear regression (using the Python statsmodels package (Seabold & Perktold 2010)). At the monthly time scale, months with mean air temperature less than 5ºC and months with less than 75 percent measured and gapfilled data were excluded. At annual time scales, we averaged summer (June, July, August) fluxes because those months were available for the greatest number of years after 2010. Availability of non-summer fluxes was limited in 2010-2013. Summer fluxes were compared with mean annual temperatures, because growing season fluxes have been previously shown to respond to temperatures prior to the growing season [Peichl et al. 2014]. Annual comparisons with discharge used the mean discharge in the month with the highest discharge rate. This was a better indicator of interannual variability than mean annual or growing season discharge due to the uneven annual pattern of discharge, which was characterized by short periods of high flow occurring each year (Fig. 1c).

3. Results

3.1 Climate and water table trend

Precipitation across the state of Wisconsin was lower than average in 2003 and, according to the Wisconsin State Climatology Office (http://www.aos.wisc.edu/~sco/), drought conditions began in 2005 with persistent low precipitation lasting through 2009. Local water level sensors were in place at the site from 2001-2008, but had to be corrected for peat subsidence that occurred during the dry period (Sulman et al. 2009). Daily water table measurements from 2001-2008 correlated well with discharge data from Bear River when water table was above -10 cm ($R^2 = 0.63$, $p<0.001$) (Figure 1a). Below that threshold, discharge values at the USGS gauge approached zero and did not capture variations in Lost Creek water table. At annual time scales water table level and discharge tracked each other well ($R^2 = 0.95$, $p=0.00015$) (Figure 1b).

The period of low precipitation from 2005-2009 led to a decline in stream flow in Bear Creek (Figure 1c). Maximum annual discharge rates at Bear Creek declined 86% from 13.3 $m^3\ s^{-1}$ in 2002 to 1.8 $m^3\ s^{-1}$ in 2007, before rising again from 2008-2015, to a maximum annual flow of 8.9 $m^3\ s^{-1}$ in 2015, while mean annual flows showed similar trends, declining 72% from 2.8 $m^3\ s^{-1}$ in 2002 to 0.8 $m^3\ s^{-1}$ in 2007.

The drought had little effect on the overall greenness of Lost Creek, with NDVI during the growing season remaining relatively constant from year to year (Figure 1d). Maximum NDVI values for each year did not show an effect from changes in discharge ($p>0.05$). During the drought, only temperatures in 2005-2007 were 2-3 °C higher than average (Wisconsin State Climatology Office, Supplemental Figure 1).

3.2 CO_2/CH_4 flux responses to environmental factors

Eddy covariance measurements were used to quantify ecosystem GPP, R_{eco}, and NEP starting in 2001, in order to monitor ecosystem response to drought (Supplemental Figure 1). At monthly time scales R_{eco}, GPP, and NEP flux values all were significantly correlated with air temperature

(Figure 2a, c, and e) with a threshold between winter and growing seasons at approximately 5 °C. Above that threshold, both R_{eco} and GPP increased rapidly with temperature. A multiple linear regression model with predictors of discharge and temperature was fit to data above the 5 °C threshold. R_{eco} had a significant declining relationship with discharge (p=0.004) in addition to temperature (p<0.001; R^2=0.89 for model including both temperature and discharge) at temperatures greater than 5ºC. Color-coded lines in Figure 2a,b show the statistically significant relationships binned by the second variable. Only temperature had a significant relationship with NEP (R^2=0.87) and GPP (R^2=0.67). While the relationship between R_{eco} and discharge was statistically significant, most of the variation at seasonal time scales was explained by temperature. A temperature-only model had a higher Akaike information criterion (AIC) value (112.5) than a model with both discharge and temperature (105.5), indicating that adding discharge information improved the model.

Monthly average CH_4 flux was influenced by temperature (Figure 2g) and a sharp increase in flux occurred after mean air temperatures increased above 5 °C, while CH_4 flux had no significant correlation with monthly average discharge at Bear River (Figure 2h). Methane flux remained about the same throughout the winter, with a mean monthly average of 3.0 mg C m^{-2} day^{-1} from January to April, when temperatures were low, and increased to a maximum of 35.7 mg C m^{-2} day^{-1} in the peak of the growing season.

Mean summer (June-August) fluxes were examined as functions of average annual temperature and annual maximum of mean monthly discharge, as average temperatures prior to the growing season have been shown to influence mean summer fluxes. NEP was negativity correlated with annual average temperature (Figure 3e, p=0.03; R^2=0.46), indicating that in warmer years, the carbon sink was weaker at Lost Creek. R_{eco} and GPP were not significantly correlated with annual average temperature. Mean summer NEP was not correlated with discharge. However, both summer average R_{eco} and GPP were significantly correlated with annual maximum monthly-average discharge (Figure 3b,d R_{eco}: p=0.047, R^2=0.41; GPP: p=0.046, R^2=0.41).

4. Discussion

The first hypothesis of this work stated that higher water table levels should be correlated with decreased ecosystem aerobic respiration (R_{eco}). Previous results from this study site suggested that ecosystem respiration was controlled by the water table depth in addition to temperature and that respiration increased 44% during a period of regional drought and declining water tables (Sulman et al. 2009). Additional site-years were consistent with this relationship, with the very wet 2014 having low summer R_{eco} and relatively dry 2008 and 2010 having higher summer R_{eco} (Figure 3). However, at seasonal time scales R_{eco} was largely controlled by temperature, with hydrology only driving slight changes in flux magnitude. Previous studies in artic wetlands have suggested enhanced decomposition processes during drought (Ise et al. 2008; Oechel et al. 1993), however the timing, severity and duration of drought periods are all important factors for carbon cycling in more temperate sites (Lund et al. 2012). The interactions between the effects from changes in water table depth and temperature were also explored by Sonnentag et al. (2010) in a minerotrophic fen wetland. They found little impact on R_{eco} from changes in water table depth and concluded that R_{eco} was largely controlled by temperature. While wetland type and mean climate state, including non-growing season effects on soil hydrology and roots, may be a mitigating factor influencing differences among these studies, our study also confirms that the lack of longer-term observations also limits comparability, as responses of wetlands over short periods with a monotonic trend may not reflect the actual decade-scale response to longer-term fluctuations in temperature or hydrology.

Hypothesis 1 also stated that increases in water table levels would lead to a decrease in photosynthesis at the site. Reductions of wetland productivity due to drought (Arneth et al. 2002; Sonnentag et al. 2010) as well as periodic flooding (Megonigal et al. 1997) have been noted in the literature. While we did not observe water table changes having an effect on GPP at monthly time scales, there was a significant negative relationship between summer average GPP and annual maximum monthly-average discharge, likely caused be limited photosynthesis during wet years from diffusional limitations due to stomatal closure and to metabolic inhibition of photosynthesis (Pezeshki 2001). Summer GPP was not correlated with average temperature at annual time scales, although seasonal patterns were consistent with the expected temperature response of GPP (Berry & Bjorkman 1980; Braswell et al. 1997).

A change in site greenness was not observed in this study, suggesting that water availability was never low enough to limit leaf growth even during drought. Average plant biomass was noted to increase throughout the water table level decline, as noted via species composition changes (J. Thom, personal communication), potentially explaining the increase in GPP.

At inter-annual time-scales, R_{eco} and GPP were both negatively correlated with discharge, but the hydrological effects canceled, leaving inter-annual variations in NEP to be primarily controlled by temperature. During wetter years, both R_{eco} and GPP were suppressed, leading to smaller NEP annual value, but no connection between discharge and NEP. As a result, interannual variations in NEP were dominated by higher C losses in warmer years driven by higher R_{eco}. Compounding this effect was the fact that warmer years tended to be drier as well, which was also connected with higher levels of R_{eco}. Note that, due to data availability limitations, our analysis used downstream water discharge as a proxy for water table depth. This could have introduced error into our results, since some interannual variations in discharge were driven by short-term high-flow events. Furthermore, discharge rates were unable to capture water table variations during very dry time periods. However, discharge was well correlated with monthly and interannual variations in water table (Fig. 1) and our results were consistent with previous analysis of this site that used direct measurements of water table (Sulman et al., 2009).

When the temporal aspect of NEP was considered, Strachan et al. (2015) showed annual wetland NEP to be determined primarily by respiration from spring, fall and winter. As expected, we saw a strong R_{eco} response to monthly-scale air temperatures, as well as a similar GPP response (Berry & Bjorkman 1980), and an overall connection between annual mean temperatures and summer NEP.

However, CO_2 fluxes alone do not characterize wetland carbon cycling and hypothesis 2 stated that higher water table levels should be correlated with increased anaerobic ecosystem respiration. Wetlands are known to be the largest natural source of atmospheric methane (Meng et al. 2012) and eddy covariance flux as well as chamber flux studies are beginning to quantify the responses and drivers of wetland methane fluxes. This work shows methane fluxes at our site having a strong temperature-controlled seasonal cycle, with average monthly fluxes varying between near-zero flux in the winter and 39.0 mgC m^{-2} day^{-1} in the growing season. The total yearly methane emission was found to be 51 g C m^{-2}, which is comparable to emissions from a boreal sedge marsh (41.7–42.9 g C m^{-2} $year^{-1}$ (Song et al. 2011)), boreal reed marsh (20–123 g C m^{-2} $year^{-1}$ (Kankaala et al. 2004)) and the temperate Winous Point marsh (37.1–49.2 g C m^{-2} $year^{-1}$ (Chu et al. 2014)) and significantly lower than that of cool-temperate freshwater marsh (117 ± 19 g C m^{-2} year-1 (Strachan et al. 2015))

While lacking methane flux data over the long-term drought, our results showed no significant correlation with hydrological fluctuations at the seasonal time scale. Instead, we observed a strong temperature response at monthly timescales. Several studies show methane emissions to be connected to increases in temperature, either measured as air (Strachan et al. 2015), shallow soil (Song et al. 2011), or deep soil temperatures (Chu et al. 2014). Using regional-scale modeling, Watts et al. (2014) showed that methane emissions decreased in sub-Arctic ecosystems during cooler and drier summers, while methane emissions increased in the Artic due to wetter and warmer summers.

Luan and Wu (2014) showed a connection between photosynthesis and methane, with GPP explaining nearly half (44%-47%) of the temporal variation in methane. This connection was also significant in the context of spatial variations in methane fluxes. Luan and Wu (2014) showed that water table depth and soil moisture explained half of the spatial variation (40%-63%) in methane fluxes. Strachan et al. (2015) showed increased methane emissions using chambers from vegetation, relative to water surfaces or unvegetated mats in a freshwater cold-temperate marsh. Our results were from ecosystem-scale observations, but both GPP and methane flux being strong functions of monthly temperature and hence high in the summer season support the connection between methane and photosynthesis found at other sites (Anderson et al. 2016).

The carbon dioxide balance at our site was near-neutral over the course of the study, with the effects of hydrology and temperature potentially pushing the site to either a net source or sink year to year. Methane fluxes amounted to a small amount of carbon loss from the ecosystem compared to NEP, with approximately 20 times the carbon dioxide flux relative to methane. However, the strong long-term radiative forcing effect of methane makes even smaller fluxes significant in the greenhouse gas context (Frolking et al. 2011; Whiting & Chanton 2001). With increasing long-term records of methane fluxes, studies of methane responses to drought are beginning to show that methane production is as sensitive as carbon dioxide production to warming. Due to the greater greenhouse warming potential of methane (Neubauer & Megonigal 2015), the source/sink dynamics of carbon dioxide can be secondary to methane emissions from wetlands on short timescales (20 years) (Whiting & Chanton 2001). At longer timescales (greater than 100 years), the relative warming potential of methane is reduced as the cumulative effects of changes in CO_2 flux accumulate. Many wetlands have a net climatic cooling effect on a lifetime basis due to carbon sequestration in peat (Frolking et al. 2011), but new wetlands or disturbed wetlands could cause net warming effects due to methane emissions or carbon losses. Because carbon sequestration and climate regulation are important wetland ecosystem services, quantifying and understanding dynamics of net carbon balance of wetlands can have long term implications on the relative warming potential of wetland ecosystems.

5. Conclusions

With predicted increases in variability of precipitation along with increases in temperatures, North American wetland ecosystems are projected to be under increasing drought stress, over both seasonal and multi-year time scales. While droughts are expected to drive carbon losses from vegetation and soil pools at the landscape level, wetlands may act as a buffer to drought related regional climate change impacts on carbon cycling. With canceling effects of hydrological variations on R_{eco} and GPP, the net result is a weak connection between hydrological variations and NEP. However, temperature was shown to be the primary control on C fluxes, and increasing annual temperatures were shown to weaken the net carbon sink. This suggests that warming may be more important than declining water table as a driver of changes in wetland C balance in the future.

Acknowledgements

The authors would like to thank Jonathan Thom for technical field help at US-Los and Yost R. for dogged assistance throughout analysis. Flux data is archived as part of the FLUXNET 2015 data release, discharge data is archived by the USGS and MODIS NDVI data is archived by Oak Ridge National Laboratory. This work was supported National Science Foundation Atmospheric and Geospace Sciences Postdoctoral Fellowship Program (#GEO-1430396), the U.S. Department of Energy (DOE) Office of Biological and Environmental Research (BER), National Institute for Climatic Change Research (NICCR) Midwestern Region Subagreement 050516Z19, and Department of Energy Lawrence Berkeley National Laboratory Ameriflux Network Management Project Subcontract to ChEAS Core Site Cluster. B. Sulman is supported by award NA14OAR4320106 from the National Oceanic and Atmospheric Administration, U.S.

Department of Commerce. The statements, findings, conclusions, and Recommendations are those of the author(s) and do not necessarily reflect the views of the National Oceanic and Atmospheric Administration, or the U.S. Department of Commerce.

Figures

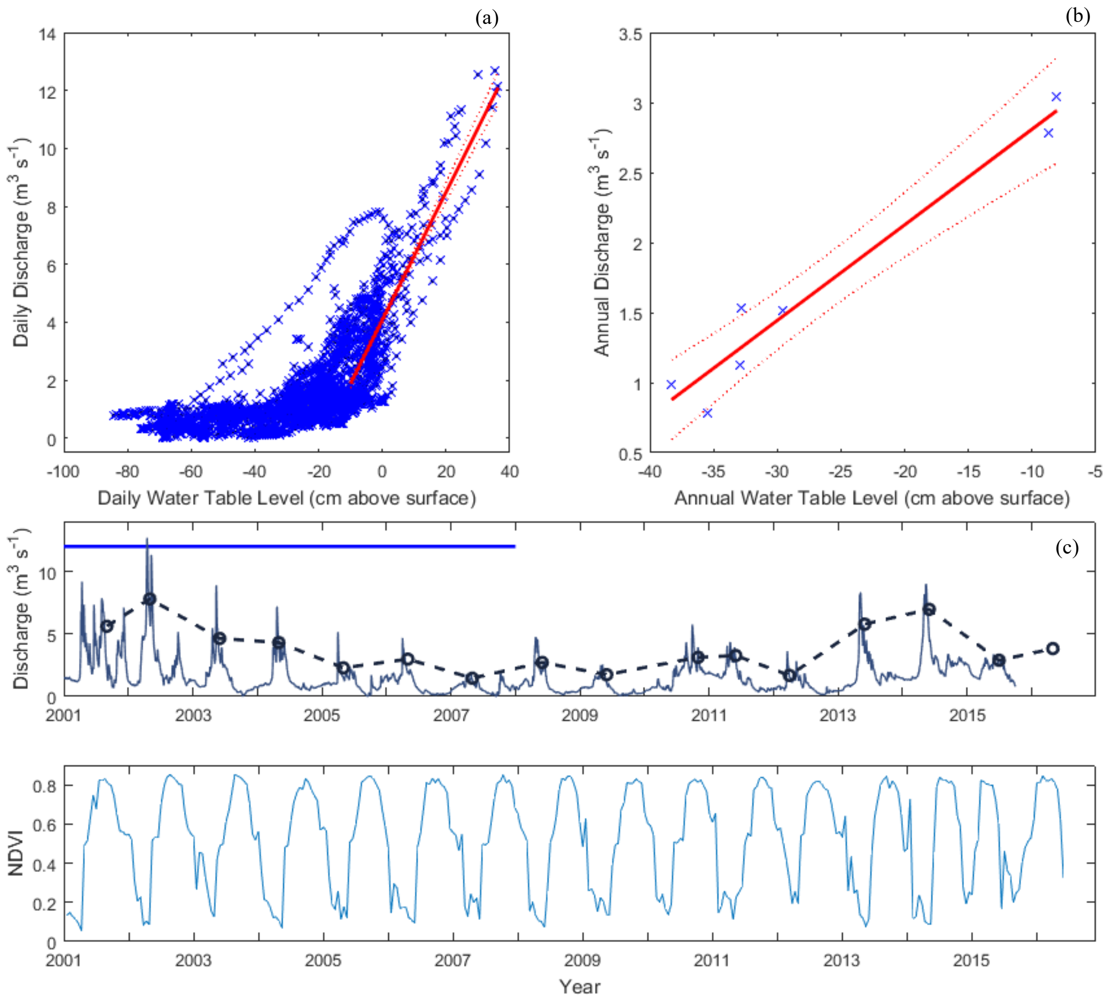

Fig. 1. Daily (panel a) and annual (panel b) average water table level vs average discharge at Bear River. Existing water table data and discharge at Bear River were correlated both at annual ($R^2 = 0.954$, *p-value* = 0.0002, 95% CI shown) and daily ($R^2 = 0.628$, *p-value* < 0.0001, 95% CI shown) scales, when using daily data above low discharge threshold. Time series of water discharge at Bear River at Lost Creek Wetland from 2001-2015, with circles showing the average discharge of the month with the highest average in each year and solid line showing

period when water table depth data was available (panel c). NDVI at Lost Creek wetland from 2000-2016 based on MODIS observations (panel d).

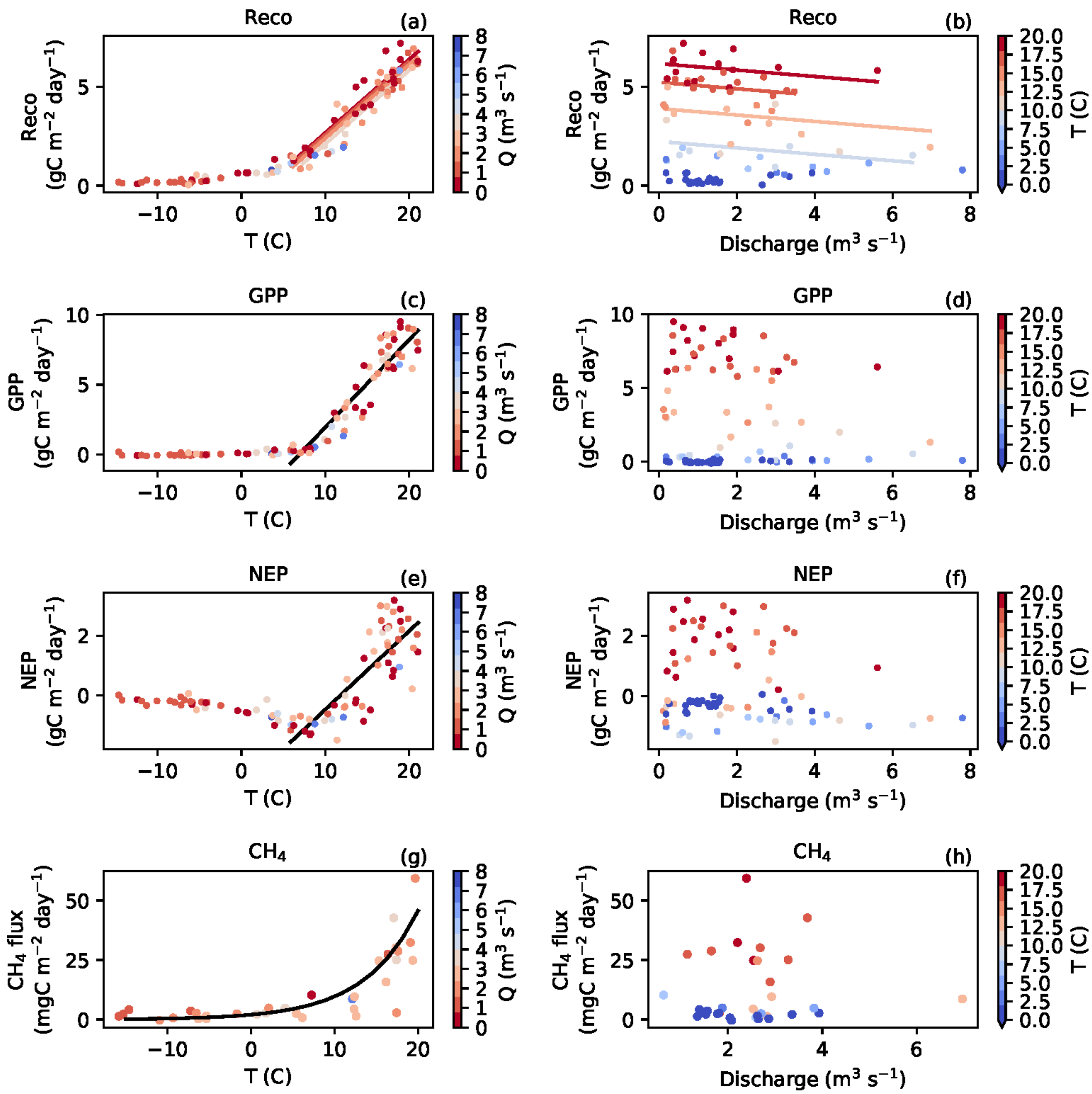

Fig. 2. Monthly R_{eco}, GPP and NEP from 2000-2010 and 2014-2015 as functions of monthly air temperature (panels a, c, and e) and discharge (panels b, d, and f). Average monthly CH_4 flux from 2014-presnt as a function of air temperature (panel g) average monthly discharge (panel h). Black lines show significant regressions, linear for CO_2 fluxes and an exponential fit for CH_4 flux. For R_{eco}, both discharge and temperature were significant and lines show relationships with binned and color-coded secondary variables (discharge, panel a; temperature panel b).

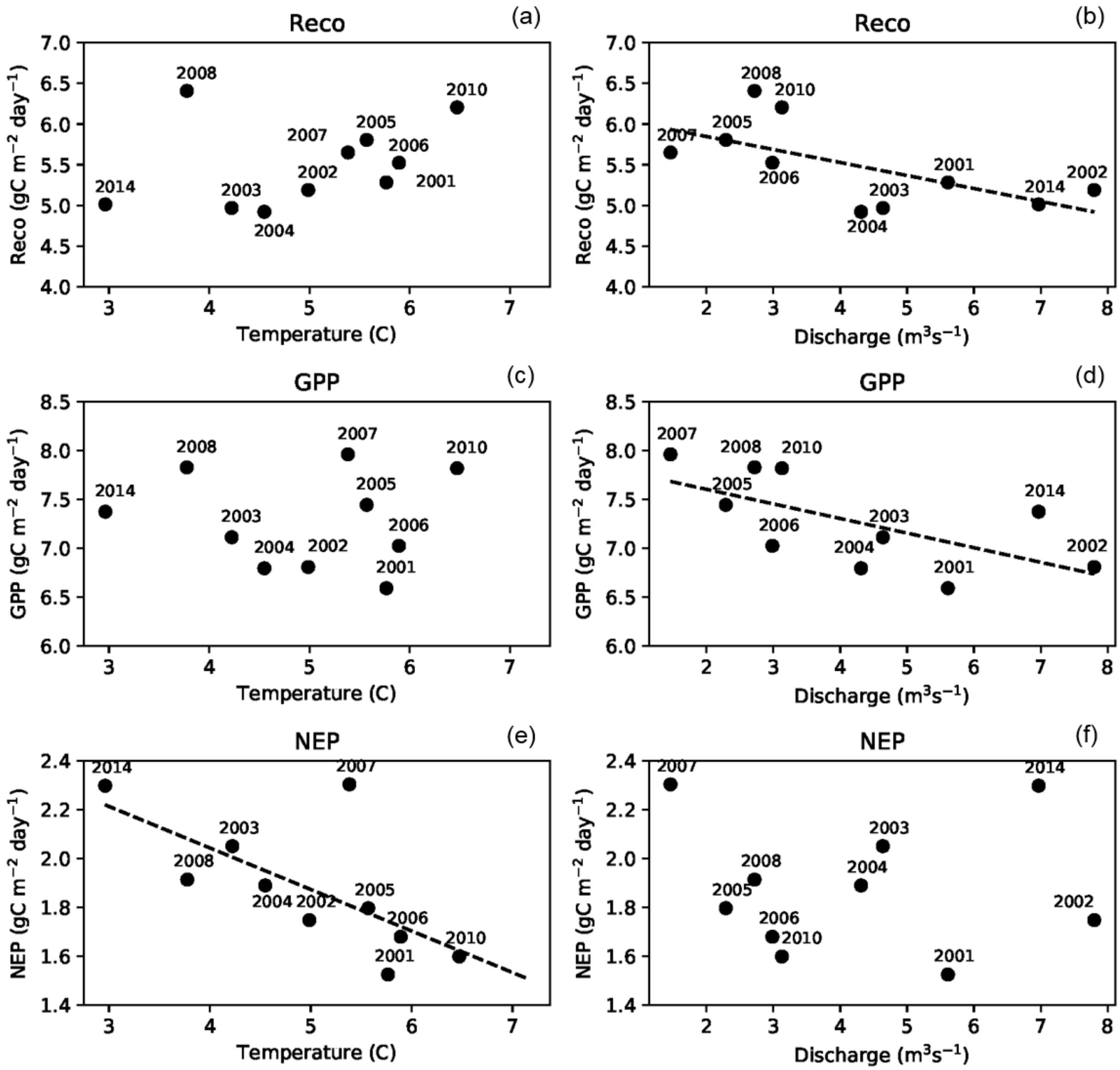

Fig. 3. Summer average fluxes as a function of mean annual temperature (a-c) and maximum monthly-average discharge (d-f). CH_4 flux not included due to <2 years of data.

References

Anderson FE, Bergamaschi B, Sturtevant C, Knox S, Hastings L, Windham-Myers L, Detto M, Hestir EL, Drexler J, Miller RL, Matthes JH, Verfaillie J, Baldocchi D, Snyder RL, Fujii R (2016) Variation of energy and carbon fluxes from a restored temperate freshwater wetland and implications for carbon market verification protocols. Journal of Geophysical Research: Biogeosciences 121(3): 777-795

Arneth A, Kurbatova J, Kolle O, Shibistova OB, Lloyd J, Vygodskaya NN, Schulze ED (2002) Comparative ecosystem–atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability of CO_2 fluxes. Tellus B 54(5): 514-530

Berry J, Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Annual Review of Plant Physiology 31(1): 491-543

Blodau C (2002) Carbon cycling in peatlands — A review of processes and controls. Environmental Reviews 10(2): 111-134

Braswell B, Schimel DS, Linder E, Moore B (1997) The response of global terrestrial ecosystems to interannual temperature variability. Science 278(5339): 870-873

Bridgham SD, Cadillo-Quiroz H, Keller JK, Zhuang Q (2013) Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. Global Change Biology 19(5): 1325-1346

Bridgham SD, Megonigal JP, Keller JK, Bliss NB, Trettin C (2006) The carbon balance of North American wetlands. Wetlands 26(4): 889-916

Brown MG, Humphreys ER, Moore TR, Roulet NT, Lafleur PM (2014) Evidence for a nonmonotonic relationship between ecosystem-scale peatland methane emissions and water table depth. Journal of Geophysical Research: Biogeosciences 119(5): 826-835

Chamberlain SD, Gomez-Casanovas N, Walter MT, Boughton EH, Bernacchi CJ, DeLucia EH, Groffman PM, Keel EW, Sparks JP (2016) Influence of transient flooding on methane fluxes from subtropical pastures. Journal of Geophysical Research: Biogeosciences 121(3): 965-977

Chu H, Chen J, Gottgens JF, Ouyang Z, John R, Czajkowski K, Becker R (2014) Net ecosystem methane and carbon dioxide exchanges in a Lake Erie coastal marsh and a nearby cropland. Journal of Geophysical Research: Biogeosciences 119(5): 722-740

Denman KL, Brasseur GP, Chidthaisong A, Ciais P, Cox PM, Dickinson RE, Hauglustaine DA, Heinze C, Holland EA, Jacob DJ (2007) Couplings between changes in the climate system and biogeochemistry. Climate change 2007: The physical science basis:

Desai AR, Bolstad PV, Cook BD, Davis KJ, Carey EV (2005) Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. Agricultural and Forest Meteorology 128(1–2): 33-55

Dlugokencky EJ, Bruhwiler L, White JWC, Emmons LK, Novelli PC, Montzka SA, Masarie KA, Lang PM, Crotwell AM, Miller JB, Gatti LV (2009) Observational constraints on recent increases in the atmospheric CH_4 burden. Geophysical Research Letters 36(18): n/a-n/a

Frolking S, Talbot J, Jones MC, Treat CC, Kauffman JB, Tuittila E-S, Roulet N (2011) Peatlands in the Earth's 21st century climate system. Environmental Reviews 19(NA): 371-396

Goodrich J, Campbell D, Roulet N, Clearwater M, Schipper L (2015) Overriding control of methane flux temporal variability by water table dynamics in a Southern Hemisphere, raised bog. Journal of Geophysical Research: Biogeosciences 120(5): 819-831

Gorham E (1991) Northern Peatlands - Role in the Carbon-Cycle and Probable Responses to Climatic Warming. Ecological Applications 1(2): 182-195

Helfter C, Campbell C, Dinsmore KJ, Drewer J, Coyle M, Anderson M, Skiba U, Nemitz E, Billett MF, Sutton MA (2015) Drivers of long-term variability in CO₂ net ecosystem exchange in a temperate peatland. Biogeosciences 12(6): 1799-1811

Humphreys ER, Lafleur PM, Flanagan LB, Hedstrom N, Syed KH, Glenn AJ, Granger R (2006) Summer carbon dioxide and water vapor fluxes across a range of northern peatlands. Journal of Geophysical Research: Biogeosciences 111(G4): n/a-n/a

Ise T, Dunn AL, Wofsy SC, Moorcroft PR (2008) High sensitivity of peat decomposition to climate change through water-table feedback. Nature Geoscience 1(11): 763-766

Kankaala P, Ojala A, Käki T (2004) Temporal and spatial variation in methane emissions from a flooded transgression shore of a boreal lake. Biogeochemistry 68(3): 297-311

Luan J, Wu J (2014) Gross photosynthesis explains the 'artificial bias' of methane fluxes by static chamber (opaque versus transparent) at the hummocks in a boreal peatland. Environmental Research Letters 9(10): 105005

Lund M, Christensen TR, Lindroth A, Schubert P (2012) Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland. Environmental Research Letters 7(4): 045704

Megonigal JP, Conner WH, Kroeger S, Sharitz RR (1997) Aboveground production in southeastern floodplain forests: a test of the subsidy–stress hypothesis. Ecology 78(2): 370-384

Meng L, Hess P, Mahowald N, Yavitt J, Riley W, Subin Z, Lawrence D, Swenson S, Jauhiainen J, Fuka D (2012) Sensitivity of wetland methane emissions to model assumptions: application and model testing against site observations. Biogeosciences 9(7): 2793-2819

Moore, Knowles R (1989) The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Canadian Journal of Soil Science 69(1): 33-38

Neubauer SC, Megonigal JP (2015) Moving Beyond Global Warming Potentials to Quantify the Climatic Role of Ecosystems. Ecosystems 18(6): 1000-1013

Nisbet EG, Dlugokencky EJ, Bousquet P (2014) Methane on the Rise—Again. Science 343(6170): 493-495

Nykänen H, Alm J, Silvola J, Tolonen K, Martikainen PJ (1998) Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochemical Cycles 12(1): 53-69

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent Change of Arctic Tundra Ecosystems from a Net Carbon-Dioxide Sink to a Source. Nature 361(6412): 520-523

Papale D, Reichstein M, Aubinet M, Canfora E, Bernhofer C, Kutsch W, Longdoz B, Rambal S, Valentini R, Vesala T, Yakir D (2006) Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. Biogeosciences 3(4): 571-583

Peichl M, Öquist M, Löfvenius MO, Ilstedt U, Sagerfors J, Grelle A, Lindroth A, Nilsson MB (2014) A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen. Environmental Research Letters 9(5): 055006

Pezeshki SR (2001) Wetland plant responses to soil flooding. Environmental and Experimental Botany 46(3): 299-312

Piao S, Ciais P, Friedlingstein P, Peylin P, Reichstein M, Luyssaert S, Margolis H, Fang J, Barr A, Chen A (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature 451(7174): 49-52

Reichstein M, Falge E, Baldocchi D, Papale D, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Gilmanov T, Granier A, Grünwald T, Havránková K, Ilvesniemi H, Janous D, Knohl A, Laurila T, Lohila A, Loustau D, Matteucci G, Meyers T, Miglietta F, Ourcival J-M, Pumpanen J, Rambal S, Rotenberg E, Sanz M, Tenhunen J, Seufert G, Vaccari F, Vesala T, Yakir D, Valentini R (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Global Change Biology 11(9): 1424-1439

Seabold S, Perktold J Statsmodels: Econometric and statistical modeling with python. In: Proceedings of the 9th Python in Science Conference. 2010. vol 57. p 61

Song C, Sun L, Huang Y, Wang Y, Wan Z (2011) Carbon exchange in a freshwater marsh in the Sanjiang Plain, northeastern China. Agricultural and Forest Meteorology 151(8): 1131-1138

Sonnentag O, Van Der Kamp G, Barr AG, Chen JM (2010) On the relationship between water table depth and water vapor and carbon dioxide fluxes in a minerotrophic fen. Global Change Biology 16(6): 1762-1776

Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (2013) Climate change 2013: The physical science basis. Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5)(Cambridge Univ Press, New York):

Strachan, Nugent KA, Crombie S, Bonneville M-C (2015) Carbon dioxide and methane exchange at a cool-temperate freshwater marsh. Environmental Research Letters 10(6): 065006

Strachan IB, Pelletier L, Bonneville M-C (2016) Inter-annual variability in water table depth controls net ecosystem carbon dioxide exchange in a boreal bog. Biogeochemistry 127(1): 99-111

Sturtevant C, Ruddell BL, Knox SH, Verfaillie J, Matthes JH, Oikawa PY, Baldocchi D (2016) Identifying scale-emergent, nonlinear, asynchronous processes of wetland methane exchange. Journal of Geophysical Research: Biogeosciences:

Sulman, Desai A, Cook B, Saliendra N, Mackay D (2009) Contrasting carbon dioxide fluxes between a drying shrub wetland in Northern Wisconsin, USA, and nearby forests. Biogeosciences 6(6): 1115-1126

Vuichard N, Papale D (2015) Filling the gaps in meteorological continuous data measured at FLUXNET sites with ERA-Interim reanalysis. Earth Syst. Sci. Data 7(2): 157-171

Watts JD, Kimball JS, Bartsch A, McDonald KC (2014) Surface water inundation in the boreal-Arctic: potential impacts on regional methane emissions. Environmental Research Letters 9(7): 075001

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. Nature 364(6440): 794-795

Whiting GJ, Chanton JP (2001) Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. Tellus B 53(5): 521-528

Wilson D, Farrell CA, Fallon D, Moser G, Müller C, Renou-Wilson F (2016) Multiyear greenhouse gas balances at a rewetted temperate peatland. Global Change Biology 22(12): 4080-4095