

REVIEW AND SYNTHESIS

Tundra ecosystems observed to be CO₂ sources due to differential amplification of the carbon cycle

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Abstract

Are tundra ecosystems currently a carbon source or sink? What is the future trajectory of tundra carbon fluxes in response to climate change? These questions are of global importance because of the vast quantities of organic carbon stored in permafrost soils. In this meta-analysis, we compile 40 years of CO₂ flux observations from 54 studies spanning 32 sites across northern high latitudes. Using time-series analysis, we investigated if seasonal or annual CO₂ fluxes have changed over time, and whether spatial differences in mean annual temperature could help explain temporal changes in CO₂ flux. Growing season net CO₂ uptake has definitely increased since the 1990s; the data also suggest (albeit less definitively) an increase in winter CO₂ emissions, especially in the last decade. In spite of the uncertainty in the winter trend, we estimate that tundra sites were annual CO₂ sources from the mid-1980s until the 2000s, and data from the last 7 years show that tundra continue to emit CO₂ annually. CO₂ emissions exceed CO₂ uptake across the range of temperatures that occur in the tundra biome. Taken together, these data suggest that despite increases in growing season uptake, tundra ecosystems are currently CO₂ sources on an annual basis.

Keywords

Carbon flux, tundra, climate change.

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INTRODUCTION

Over the past five decades, researchers have tried to determine whether high-latitude ecosystems will become a source of carbon (C) to the atmosphere, or remain a sink, as climate changes. This question is of global importance because these ecosystems cover large areas of the northern high latitudes and store vast quantities of organic C in their soils (Schuur *et al.* 2008; Tarnocai *et al.* 2009). Based on their large standing stocks of carbon, researchers have determined that these ecosystems have been, on average, a C sink for the past 10 000 years (Harden *et al.* 1992; Hicks Pries *et al.* 2012). The ability of tundra to sequester and store carbon is due to long, harsh winters and poorly drained permafrost soils, which create conditions that slow decomposition relative to plant production (Chapin *et al.* 1980; Miller *et al.* 1983; Billings 1987; Post 1990; Oechel & Billings 1992; Hobbie *et al.* 2000). But temperatures in high latitudes are rising (Chapin *et al.* 2005; IPCC 2007). The response of the carbon cycle to this climate forcing is of vital importance but the magnitude and timing of change is uncertain.

Two opposing feedbacks within the carbon cycle will determine the future C balance of tundra ecosystems. Rising temperatures resulting from increased atmospheric CO₂ concentrations could warm and thaw permafrost soils and stimulate decomposition and ecosystem respiration, resulting in a positive feedback to climate change by further increasing atmospheric CO₂ concentration (Shaver *et al.* 1992; Hobbie *et al.* 2000; Schuur *et al.* 2008; McGuire *et al.* 2009; Grosse *et al.* 2011). On the other hand, increases in temperature and CO₂ concentration could stimulate primary production. Stimulation effects could be direct through effects on plant physiology, or indirect through increases in plant-available nutrients

released from decomposing organic matter and/or lengthening of the growing season (Shaver *et al.* 1992; Johnson *et al.* 2000). If gross primary production exceeds ecosystem respiration, the ecosystem will sequester CO₂ from the atmosphere and act as a negative feedback to climate change.

Much effort has gone into quantifying the carbon balance of tundra ecosystems and understanding the controls over carbon uptake and emission. Previous studies of growing season CO₂ exchange have shown initial release of CO₂ in the 1980s (Oechel *et al.* 1993), followed by a longer term response of increased growing season CO₂ uptake (Oechel *et al.* 2000; Ueyama *et al.* in press). However, growing season patterns of CO₂ flux are only a part of the picture and by themselves do not provide complete information about the trajectory of tundra ecosystems. Winter CO₂ emissions have been recognised as an integral part of tundra carbon balance, and although there is considerably less winter data in the literature, recent efforts have improved our knowledge of the controls over winter CO₂ flux (Fahnestock *et al.* 1998, 1999; Welker *et al.* 2000; Grogan & Jonasson 2006; Nobrega & Grogan 2007; Sullivan *et al.* 2008; Rogers *et al.* 2011). However, a regional synthesis of winter CO₂ emission is missing.

In this meta-analysis, we compiled CO₂ flux observations from both growing season and winter time periods. Using linear models of temporal trends, we assess whether seasonal or annual CO₂ fluxes have changed over time. By comparing CO₂ fluxes from different sites, we investigated the response of the carbon cycle to local differences in climate. Our intent is to revisit the question of whether tundra ecosystems are sources or sinks of CO₂, and to determine if the available observational evidence supports either trajectory.

MATERIAL AND METHODS

Literature search

We compiled published observational data on CO₂ flux (gross primary production: GPP, ecosystem respiration: ER, net ecosystem exchange: NEE) from fifty-four studies (see Table S1 in Supporting Information) at 32 different sites (Fig. 1). NEE is the net exchange of CO₂ between the atmosphere and the ecosystem over a time interval (Baldocchi 2003) and is the balance of two strong, opposing processes during the growing season: CO₂ uptake by primary producers (GPP) and respiration losses of CO₂ by both primary producers and heterotrophs (ER). During winter, tundra vegetation is covered by snow and photosynthesis is negligible, therefore NEE is effectively equivalent to ER. We used the convention that negative values indicate CO₂ uptake by the ecosystem (Baldocchi 2003).

We gathered CO₂ flux data by searching ISI Web of Science and Google Scholar using the keywords 'carbon and tundra'. We only included studies containing CO₂ flux observations from tundra ecosystems. As a second line of investigation, we contacted all lead investigators identified during our initial literature search and inquired about any additional studies that were previously overlooked. As a second filter for our meta-analysis, we only included studies if flux measurements were distributed throughout the season (growing season or winter) and spanned the range of conditions encountered at each site. As a third filter, we only included studies from sites with 'tundra' vegetation, although we recognise that this category includes a variety of plant communities across a moisture gradient. We specifically excluded studies from high-latitude forests, as well as fens, bogs and mires, because these wetlands have different controls over carbon balance. We were interested in non-manipulated fluxes but also report control or ambient CO₂ flux estimates from experimental manipulations. For comparison, all data are reported as total seasonal fluxes in g C m⁻² for either growing

season or winter time periods (see Table S1). Because there was a wide range in the interpretation of what constitutes the growing season and winter, and to follow conventions comparable with previous meta-analyses (Oechel *et al.* 1993, 2000), we standardised the length of the growing season (100 days) and winter (245 days) by dividing seasonal estimates by the length of the reported season to estimate average daily (g C m⁻² day⁻¹) flux. We then multiplied daily estimates by the standardised growing season and winter length. We chose season lengths based on the average length of the seasons reported in our meta-analysis, which is why the length of the growing season (100 days) and winter (245 days) does not add up to a full year. During the remaining 20 days, at the season transitions, CO₂ fluxes are roughly balanced with GPP = ER (i.e. net flux is approximately zero), so excluding these periods does not alter estimates of annual flux derived by adding growing season and winter estimates. Data were gathered on climate corresponding to the year when CO₂ fluxes were measured (mean annual temperature: MAT, total annual precipitation: TAP) for each of the 32 sites sampled (Fig. 1 and see Table S1) from the University of Delaware precipitation and air temperature data set on NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, at <http://www.esrl.noaa.gov/psd/>. These weather data are a gridded interpolation of land station data and have a spatial resolution of 0.5 × 0.5 degrees, which may reduce data variation of nearby sites. If data were reported as an average of multiple sites, we report the average climate conditions.

Data analysis

To elucidate changes in the tundra carbon cycle over space and time, we explored both temporal trends in CO₂ fluxes and relationships among CO₂ fluxes and spatial differences in climate. First, we examined how seasonal CO₂ fluxes have changed over the last four decades, and estimated the historical annual CO₂ balance from our

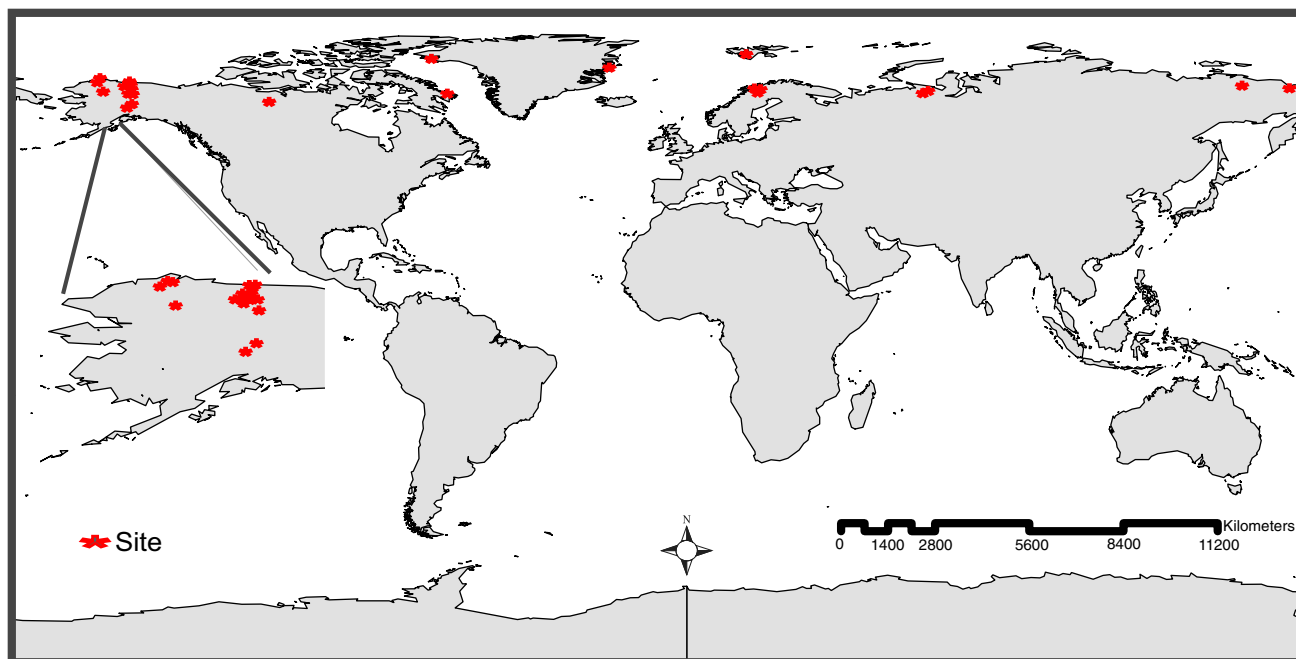


Figure 1 Map showing the 32 sites (stars) included in this meta-analysis.

temporal estimates. Temporal trends in growing season and winter CO₂ fluxes were estimated using a linear mixed effect model with site and site × year interaction as random effects to account for variation in the slopes with respect to time due to local site differences. There was a small but significant correlation between year and long-term average (1950–2000) temperature ($r = 0.21$; $P = 0.003$), and long-term average precipitation ($r = 0.32$; $P = 0.001$) for sites included in the analysis. An autoregressive (AR1) correlation structure was added to the model to account for temporal autocorrelation within sites. Flux estimates were aggregated by site for each year and weighted by the number of observations within each site-year combination. Simulations of the null hypothesis (no overall trend at the population level) suggested that this approach was anticonservative, with a type-I error rate of approximately 0.1 for a nominal P -value of 0.05; therefore, we used parametric bootstrapping to achieve an appropriately conservative estimate for the significance of the trend (Booth 1995). Because our winter data were insufficient to support such a complex analysis, we did not include the correlation structure in the winter model and only included site (not the site × year interaction) as a random effect. To calculate an annual estimate of tundra CO₂ balance, we fitted the growing season model to a restricted data set containing only sites sampled during winter (to avoid calculating an annual estimate from disparate sites). We then summed the predicted values from the restricted growing season and winter models to calculate the annual estimate. The variance of the annual estimate was estimated as the sum of the variances of the winter and growing season models (Lyons 1991). We used a Student's t -test of the differences in estimated slopes to determine significant seasonal differences in the rates of change through time.

Second, we used simple linear regressions to explore if the observed variation in CO₂ fluxes (NEE, GPP, ER) during the growing season and winter were related to spatial differences in climate (MAT & TAP). Because MAT and TAP were highly correlated ($r = 0.7$; $P < 0.001$) for sites in our analysis, and the observational record of temperature is much stronger, we present only results from MAT, recognising that responses to temperature and precipitation are strongly confounded (see Table S2 for full analysis and TAP results). We also explored the use of growing season (June to August) temperature to explain growing season trends in CO₂ fluxes, but found MAT explained more overall variation (higher adjusted R^2). In addition, slopes estimated with growing season temperature did not differ from MAT estimated slopes for either GPP or ER, and growing season temperature was a non-significant predictor of growing season NEE ($P = 0.47$); therefore, we use MAT in our analysis of both seasons. To determine if the growing season or the winter was responding more strongly to changes in MAT, we tested for the difference between slopes using a Student's t -test. Similar to the temporal analysis above, we calculated an annual response to temperature by adding estimated growing season and winter trends together. All models were fitted using the base and nlme (version 3.1-98: Pinheiro *et al.* 2011) packages; graphics were produced with the ggplot package (version 0.8.9: Wickham 2009) in R (R Core Development Team 2011).

RESULTS

Changes in CO₂ flux over time

Over the past four decades, tundra ecosystems measured during the growing season have been found to be both CO₂ sources and CO₂

sinks, but overall growing season NEE has been decreasing over time (i.e. net CO₂ uptake is increasing; Fig. 2). Seventy per cent of the total growing season NEE observations were below zero (net CO₂ uptake). Across the full data set, growing season NEE has decreased $-3.8 \pm 1.4 \text{ g C m}^{-2} \text{ year}^{-1}$ (standard F test $P = 0.007$; bootstrap adjusted $P = 0.03$). Due to the limited number of sites and sparse observations at individual sites during the 1980s, we

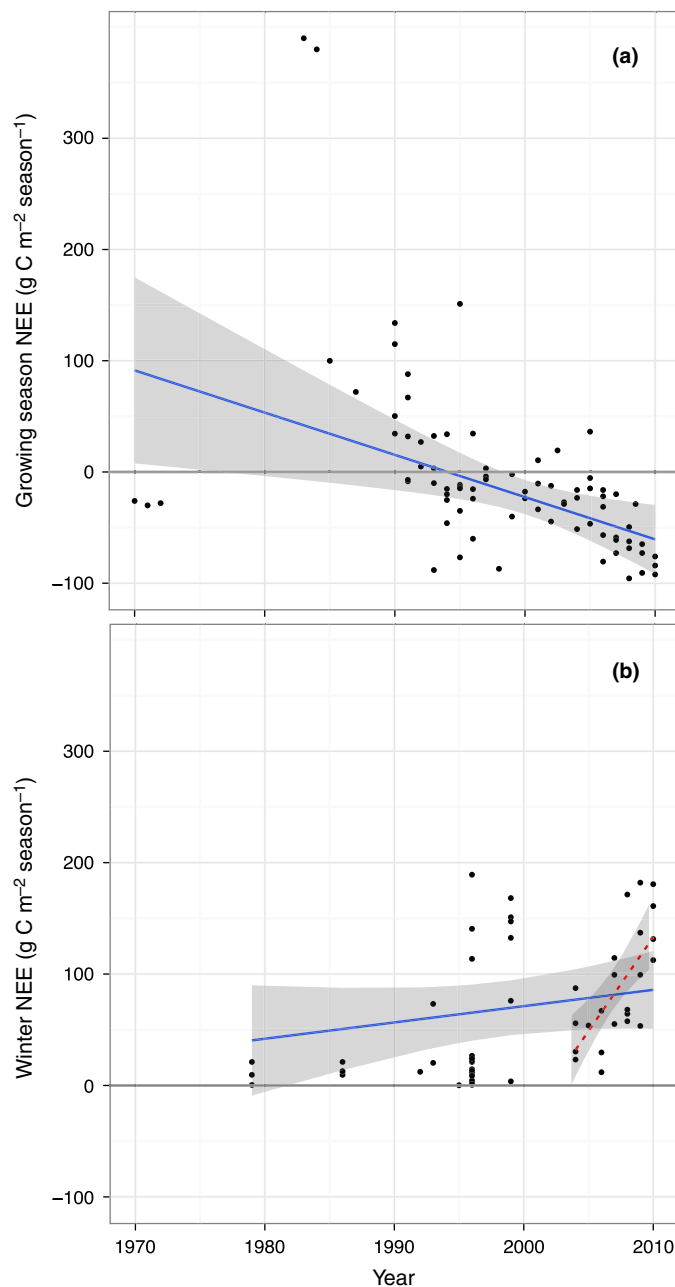


Figure 2 Temporal trends of net ecosystem CO₂ exchange ($\text{g C m}^{-2} \text{ year}^{-1}$) during the (a) growing season ($-3.8 \pm 1.4 \text{ g C m}^{-2} \text{ year}^{-1}$; $P = 0.03$), and (b) winter with the long-term winter trend ($1.5 \pm 1.1 \text{ g C m}^{-2} \text{ year}^{-1}$; $P = 0.18$) shown in solid blue and the most recent 7-year winter trend ($15.9 \pm 4.3 \text{ g C m}^{-2} \text{ year}^{-1}$; $P = 0.03$) in dashed red. Estimates of slopes are reported with standard errors; positive values denote a C source. The trend lines shown are from simple linear models, but slope estimates are based on the full mixed-effect models.

repeated this linear analysis using data collected post-1990, when the majority of observations were collected. The decreasing trend of growing season NEE for this period is $-4.5 \pm 0.9 \text{ g C m}^{-2} \text{ year}^{-1}$ (bootstrap adjusted $P = 0.005$), which amounts to an estimated cumulative increase of 90 g C m^{-2} of net growing season C uptake between 1990 and 2010. Before 1990, the limited number of sites and sparse observations do not allow for robust tests of trends through time; thus, the best-fit line extending through the whole data set is poorly constrained for the early decades of the data set.

The trend in winter CO_2 emissions over time ($1.5 \pm 1.1 \text{ g C m}^{-2} \text{ year}^{-1}$), across the entire winter data set (1979–2010) was much weaker and not statistically significantly different from zero (Fig. 2b; $P = 0.18$), when including a random intercept to control for among-site differences. However, the winter CO_2 flux data set overall has many fewer sites, and fluxes at individual sites are more sparsely quantified in comparison to growing season studies. Early records in the winter data set (Table S1) came from relatively cold sites only. The middle period (1995–2000) contains a wider range of sites, but come mostly from sites sampled only during 1 year. The most recent period of the record (from 2004 to 2010) contains sites that span the range of environmental conditions (MAT, MAP), and includes multiple sites monitored over several seasons that have more coherent with-site trends. In the latest period alone, we find a significant increase in winter CO_2 emissions over time, with an estimated increase of $15.9 \pm 4.3 \text{ g C m}^{-2} \text{ year}^{-1}$ ($P = 0.002$; Fig. 2b). This increase in recent CO_2 emissions could be due to a recent amplification of winter CO_2 emissions or to the stronger data record, which improved our ability to estimate temporal trends in winter CO_2 flux. However, the exact slope of the line may not be representative of longer term trends because it is fit to only 7 years of data.

Estimates of annual CO_2 flux based on combining growing season and winter regressions show that the mean flux across the data set ranged from an estimated net loss of $82 \text{ g C m}^{-2} \text{ year}^{-1}$ in 1979 to an estimated loss of $21 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2010 (Fig. 3). In 1980, it was not possible to determine if this net loss was statistically different from C neutral due to data scarcity. But for several decades from the early 1980s until the early 2000s, tundra ecosystems were a net source of CO_2 to the atmosphere, with a mean net loss of $76 \text{ g C m}^{-2} \text{ year}^{-1}$ in 1982 and a net loss of $36 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2002. By the mid 2000s, the overall declining but statistically insignificant annual trend (estimate = $-2.0 \pm 1.9 \text{ g C m}^{-2} \text{ year}^{-1}$; $P = 0.18$) pushed the estimated annual CO_2 flux towards net C neutrality. Clearly, observed increases in growing season CO_2 uptake are shifting tundra sites towards becoming a CO_2 sink on an annual basis. However, the magnitude of the more uncertain winter emissions also plays a role. The winter trend from the recent data intensive period (2004–2010; Fig. 3b) counterbalances the shift towards C neutrality and reverses the trend through time, resulting in a continued increase in CO_2 emissions on an annual basis (Fig. 3b). Although it is hard to know how trends documented over a 7-year period will change in the future, these results highlight the important role of winter CO_2 emissions in determining annual CO_2 exchange, and emphasise the need for more sustained winter CO_2 flux data from a variety of locations.

Relationships between CO_2 flux and spatial differences in climate

To identify potential factors driving temporal trends in CO_2 flux, we explored patterns among CO_2 fluxes and spatial differences in

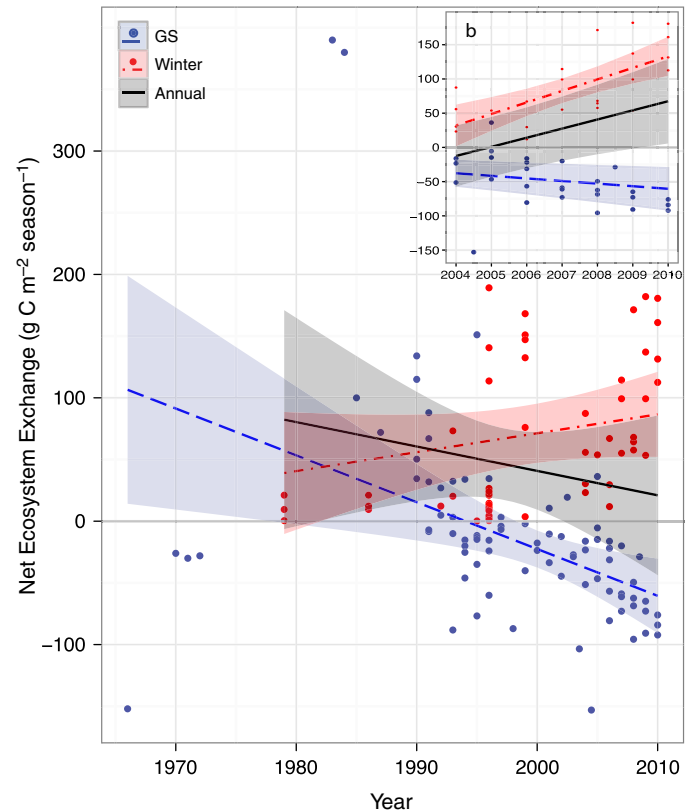


Figure 3 Estimates of temporal trends of net ecosystem exchange ($\text{g C m}^{-2} \text{ season}^{-1}$) of CO_2 (a) over the entire data record during the growing season (GS; blue), winter (red) and the annual period (black; produced by summing predicted values of seasonal trends and their variances). The subset within figure (b) shows temporal trends of GS, winter and annual periods estimated from the last 7 years of the record. Trend lines are reported with 95% confidence intervals and are based on predictions from full mixed-effect models; positive values denote a C source.

MAT. We recognise that MAT is highly correlated with precipitation at the sites included in our analysis, so we are using MAT as a proxy for the general climate influence on CO_2 flux. Both growing season CO_2 emissions (Fig. 4a) and CO_2 uptake (Fig. 4b) are greater at sites with higher temperatures, with an overall negative trend between MAT and growing season NEE. This corresponds to higher net growing season CO_2 uptake at sites with higher MAT (Fig. 4c). The slope of the growing season GPP trend is significantly greater than the slope of the growing season ER trend (est. = $-3.6 \pm 2.0 \text{ g C m}^{-2} \text{ year}^{-1}$; $P = 0.05$), indicating that growing season GPP responds more strongly than growing season ER to differences in MAT. In contrast to the analysis with time, there is no indication of positive growing season CO_2 fluxes (where respiration > plant uptake) across the range of MAT. This suggests that the period of growing season net CO_2 loss predicted by the regression model before 1990 in the analysis with time (Fig. 2) was driven by data scarcity and influential points early in the record rather than being a true feature of ecosystems pre-1990.

During the winter, when only heterotrophic respiration is occurring, sites with higher MAT exhibited greater CO_2 emissions (Fig. 4d). The estimate of predicted net annual (winter plus growing season) CO_2 flux is positive throughout the range of temperatures (Fig. 5), yet there was no statistical difference between the absolute

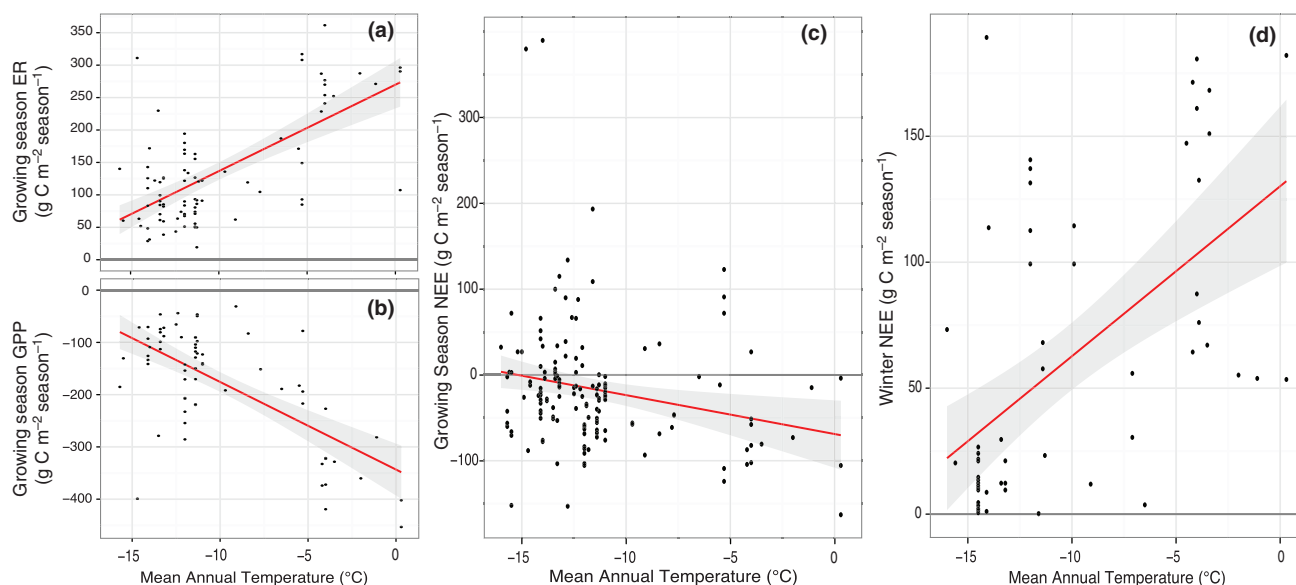


Figure 4 Linear relationships between mean annual temperature (°C) and (a) growing season ecosystem respiration (ER; est. = 13.3 ± 1.6 ; $P = 0.001$; adj. $R^2 = 0.45$), (b) growing season gross primary production (GPP; est. = -16.7 ± 2.3 ; $P = 0.001$; adj. $R^2 = 0.43$), (c) growing season net ecosystem exchange (NEE; est. = -4.5 ± 1.7 ; $P = 0.007$; adj. $R^2 = 0.04$) and (d) winter NEE (est. = 6.8 ± 1.3 ; $P = 0.001$; adj. $R^2 = 0.31$). Estimates of slopes are reported with standard errors; positive values denote a C source.

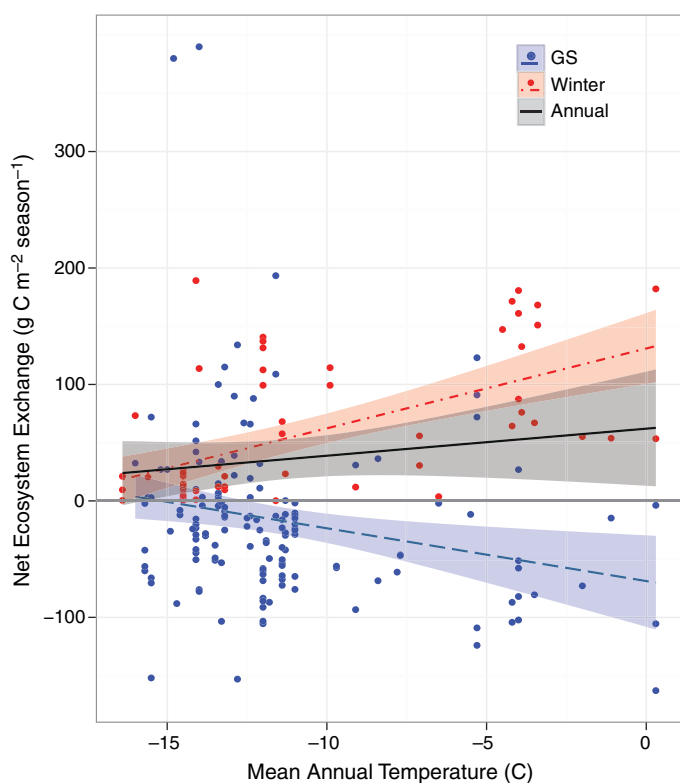


Figure 5 Estimates of linear relationships between mean annual temperature (°C) and net ecosystem exchange ($\text{g C m}^{-2} \text{ season}^{-1}$) of CO₂ during the growing season (GS; blue), and winter (red) with 95% confidence intervals, and the annual estimate (black) of the temperature relationship produced by summing predicted values of seasonal trends and their variances. Positive values denote a C source.

value of slopes of the growing season and winter trends (est. = $1.9 \pm 2.0 \text{ g C m}^{-2} \text{ year}^{-1}$; $P = 0.2$). This result suggests that both growing season and winter CO₂ flux have similar responses to changes in MAT, but the magnitude of the CO₂ emission exceeds CO₂ uptake. Based on predictions from the annual response, mean annual C emissions should range from 23 to 56 g C m^{-2} across the gradient of tundra temperatures, and a 1 °C increase in temperature would increase annual emissions by 2 g C m^{-2} . These results indicate that the recent amplification of arctic temperature should have increased both CO₂ uptake and CO₂ emission at a similar rate, but that ultimately the source strength of tundra ecosystems is greater on an annual basis.

DISCUSSION

In spite of the spatial variation in climate, soil characteristics, vegetation composition and site histories within the tundra biome (Callaghan *et al.* 2004), our meta-analysis detected an apparent regional amplification of the C cycle in recent decades. Growing season net CO₂ uptake has definitively increased since the 1990s, and trends point towards a potential increase in winter CO₂ emissions, at least in the last decade (Fig. 3). Changing temperature, and the factors that covary with it, may have played a role in this amplification. Based on the relationship with site MAT (Fig. 5), CO₂ emissions exceed CO₂ uptake across the range of temperatures that occur in the tundra biome, indicating a shift from the historical state of tundra as a CO₂ sink.

Early analysis of Alaskan tundra reported a shift in growing season CO₂ balance from a historical C sink to a C source in response to warming and drying (Oechel *et al.* 1993). As more flux data were compiled from Alaskan tundra, across-site CO₂ balance was measured as net CO₂ uptake during the growing season. It was hypothesised that tundra ecosystems could have initially lost CO₂ in

response to warming, then metabolically adjusted to continued warming while subsequently increasing CO₂ sink activity (Oechel *et al.* 2000). Our analysis using linear models does not allow us to quantify short-term fluctuations in source and sink activity, and data limitations preclude us from quantifying growing season trends in the early part of the record (pre-1990). However, the larger post-1990 data set clearly shows an increasing trend of growing season CO₂ uptake (Fig. 2a). Our meta-analysis over a longer time period and from 32 sites across the tundra biome shows a more gradual and continuing increase in CO₂ uptake during the growing season, on average, through the modern period. This amplification of growing season carbon uptake is in concordance with earlier reports, which showed increased sink activity over time (Oechel *et al.* 2000). However, growing season net carbon uptake, on average across tundra sites, appeared to be closer to C neutral (~1990) with no widespread evidence from other sites to support the magnitude of the largest net growing season losses reported for the early 1980s (Oechel *et al.* 1993).

Similar to our finding of increased net growing season CO₂ uptake, recent studies have reported that tundra was a growing season CO₂ sink during the past two decades (McGuire *et al.* 2012; Ueyama *et al.* in press), with increasing CO₂ uptake in a majority of tundra sites in the 2000s (McGuire *et al.* 2012). In addition, long-term (since the early 1980s) remote sensing observations show a greening Arctic (Myneni *et al.* 1997; Jia & Epstein 2003; Nemani *et al.* 2003; Goetz *et al.* 2005; Sitch *et al.* 2007; Jia *et al.* 2009) and increased shrub encroachment (Stow *et al.* 2004; Sturm *et al.* 2005), both suggesting a regional response of accelerated C uptake by tundra vegetation. By extrapolating our post-1990 growing season trend to the areal extent of tundra (10.5×10^6 km²; McGuire *et al.* 1997; Callaghan *et al.* 2004), we estimate that tundra on average sequestered 137 ± 80 Tg C during the growing seasons of the last few decades (1990–2006).

Winter CO₂ trends were less clear in our analysis across the entire data set (not significant at $P = 0.05$), but the last 7 years of the record where the data set is much stronger do show a strong and significant increase in CO₂ emissions over time (Fig 2b). The slope estimated from a 7-year trend are not likely to match decadal-scale trends; based on the entire record it appears that the 7-year slope may overestimate longer term winter trends (Fig 2b). Taken together, winter CO₂ emissions may have increased for more than just the past 7 years, but the sparsity of the data highlights the great need for additional sustained winter data to strengthen the record. Summing the growing season and longer term winter trend, we estimated that tundra sites were CO₂ sources during the 1990s, although we were unable to differentiate tundra from carbon neutral during the 2000s (Fig. 3). This finding supports the magnitude of annual net C loss reported in Oechel *et al.* (1993, 2000) with the addition of winter respiration losses enough to offset growing season uptake; a pattern that has been observed elsewhere as well (Oechel *et al.* 1997; Welker *et al.* 2000; Belshe *et al.* 2012; Euskirchen *et al.* 2012). Using only the more recent 7-year winter trend predicts increasing CO₂ emission annually for the most recent time period (Fig. 3b), and the increasing winter and annual temperature trends (Fig. 5) indicate that recent increases of arctic air temperature should lead to an increase in annual CO₂ emissions. While the analysis with time (Fig. 3) and with temperature (Fig. 5) are at some odds with one another in terms of the prediction of tundra as a sustained annual net C source, this is most likely due to data

scarcity in particular during the winter. Although we cannot refute the potential influence for other factors affecting annual CO₂ balance, the congruence of the MAT trends and the temporal analysis using more recent, data-robust 7-year period supports our conclusion that insufficient data are leading to the disparity between our temperature and long-term temporal predictions.

Several other lines of evidence support an amplification of the tundra C cycle in recent decades, but large uncertainty in past estimates have impeded the ability to accurately determine the annual C balance. Top-down atmospheric inversion studies show the Arctic as a C sink (-410 ± 400 Tg C year⁻¹) during the 1990s (Baker *et al.* 2006; McGuire *et al.* 2009), although recent inversion analyses were unable to distinguish Arctic tundra from C neutral in the 1990s (-13 ; range = -321 to 140 Tg C year⁻¹) or the 2000s (-117 ; range = -439 to 243 Tg C year⁻¹; McGuire *et al.*, 2012). Retrospective analyses from process-based models show an amplification of tundra C uptake and C emissions, but in the last few decades predict that tundra is a C sink. However, model predictions vary in sink strength and exhibit large temporal and spatial variability in source and sink activity (Clein *et al.* 2000; McGuire *et al.* 2000; Sitch *et al.* 2003, 2007; Grant *et al.* 2011). In a recent comparative analysis McGuire *et al.* (2012) found that summed estimates of annual C fluxes over the past few decades (1990–2006) from inversion models (-96 ; range = -331 to 173 Tg C year⁻¹) were C neutral, while regional (-177 ; range = -284 to -41 Tg C year⁻¹) and global (-86 ; range = -205 to -1 Tg C year⁻¹) process-based models predicted that tundra was a C sink, although sink strength could not be determined due to uncertainty in estimates. In addition, observationally based estimates of annual CO₂ balance over the last two decades ranged from C neutral (10 ; range = -10 to 28 Tg C year⁻¹) to a weak C sink (-82 ; range = -134 to -30 Tg C year⁻¹; McGuire *et al.* 2012). In contrast, our mean annual estimate (Fig. 3a) extrapolated to the areal extent of tundra from the same time period predicts tundra was a CO₂ source (462 ± 378 Tg C year⁻¹). The divergence of these observationally based estimates is likely due to the larger variation in vegetation types (including forest tundra, fens, bogs and mires) and sampling duration and frequency of studies included in that synthesis. Using a restricted group of dry/mesic tundra sites, McGuire *et al.* (2012) estimated tundra was annual carbon source, which is similar to our finding, although uncertainty in their estimate made it indistinguishable from carbon neutral. This suggests that increased variation as a result of including different vegetation/ecosystem types may have obscured overall trends, and also highlights the need to increase both the coverage and the standardisation of carbon flux observations in high-latitude ecosystems to resolve how the carbon cycle is responding to climate change.

For tundra to be a historical C sink over centuries to millennia, C uptake had to be greater than C emissions across the range of conditions within the biome. Yet, our annual temperature response based on the past several decades of measurements predicts that tundra sites are CO₂ sources across the range of temperatures (Fig 5). Within this range, tundra sites with warmer temperatures exhibit greater CO₂ fluxes (Fig. 4; Ueyama *et al.* in press) and both CO₂ uptake and CO₂ emissions are amplified by temperature by a similar amount. These results suggest a shift from the historical equilibrium, with C uptake and C emissions now of different magnitudes, with C emissions dominating across the range of conditions on an annual basis. These predictions are supported by recent flux

studies (2008–2010) from relatively warm (long-term MAT of -1°C) and cold (long-term MAT of -12°C) tundra sites, which report CO₂ losses in five out of six annual observations ranging from 13 to 78 g C m⁻² year⁻¹ and 2–82 g C m⁻² year⁻¹ respectively (Belshe *et al.* 2012; Euskirchen *et al.* 2012).

A combination of several factors may have shifted the C balance of tundra ecosystems in recent decades. Surface air temperature has increased 0.35 °C per decade since the 1970s, with dramatic increases since the 1990s (Polyakov *et al.* 2002; Hinzman *et al.* 2005; Serreze & Francis 2006; Euskirchen *et al.* 2007; McGuire *et al.* 2009), atmospheric CO₂ has increased by 50 ppm since 1980 (Keeling & Whorf 2004) NOAA/ESLR) and the rate and areal extent of permafrost thaw has dramatically increased (Jorgenson *et al.* 2001; Stow *et al.* 2004; Hinzman *et al.* 2005; Schuur *et al.* 2008; Osterkamp *et al.* 2009). This analysis indicates that tundra ecosystems are responding to these recent changes and are currently undergoing a multi-decade transition. Growing season net CO₂ uptake has definitely increased since the 1990s, and the data also suggest (albeit not definitively) the possibility of an increase in winter CO₂ emissions, especially in the last 7-year period. Our result of increased growing season CO₂ uptake supports previous findings of an amplification of tundra carbon uptake in response to regional changes in climate (Oechel *et al.* 2000). We ask whether our inability to detect a significant change in winter CO₂ emissions over the entire time period is due to scarcity of winter observations (Type II error), as opposed to a real lack of response of the winter fluxes to the changes occurring over the last four decades. No matter what the winter temporal trend, the magnitude of C release in the winter made tundra sites, as a whole, annual CO₂ sources from the early-1980s until at least the early 2000s (Fig. 3). Although increases in growing season CO₂ uptake shift tundra towards annual carbon neutrality in the absence of a detectable long-term response, data from the last 7 years suggest that winter CO₂ fluxes are continuing to offset growing season C gains. The importance and ability of offsetting increasing growing uptake by winter emissions has been demonstrated (Oechel *et al.* 1993, 1997, 2000; Welker *et al.* 2000; Belshe *et al.* 2012; Euskirchen *et al.* 2012). Contrary to temporal trends of carbon fluxes, temperature response models predict that winter CO₂ emissions and growing season CO₂ uptake respond similar to increases in temperature. If tundra ecosystems follow observed patterns linked to MAT response (Fig 5), warmer conditions will eventually push CO₂ emissions to exceed uptake and make tundra a CO₂ source on an annual basis, if they are not already doing so. Ultimately more widespread and long-term measurements of both growing season and winter CO₂ flux are needed to definitively resolve the response of tundra carbon cycle to the changes taking place in high-latitude ecosystems.

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AUTHORSHIP

EB collected data from the literature, designed criteria for inclusion of studies, participated in data analysis and modelling and wrote the first draft of the manuscript. BB developed methods and implementation for data analysis and modelling, and contributed to manuscript revisions. ES provided guidance in the initial conception of the study and contributed to manuscript revisions.

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