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The changing carbon balance of tundra ecosystems: results from a vertically-resolved peatland biosphere model

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Abstract

An estimated 1700 Pg of carbon is frozen in the Arctic permafrost and the fate of this carbon is unclear because of the complex interaction of biophysical, ecological and biogeochemical processes that govern the Arctic carbon budget. Two key processes determining the region's long-term carbon budget are: (a) carbon uptake through increased plant growth, and (b) carbon release through increased heterotrophic respiration (HR) due to warmer soils. Previous predictions for how these two opposing carbon fluxes may change in the future have varied greatly, indicating that improved understanding of these processes and their feedbacks is critical for advancing our predictive ability for the fate of Arctic peatlands. In this study, we implement and analyze a vertically-resolved model of peatland soil carbon into a cohort-based terrestrial biosphere model to improve our understanding of how on-going changes in climate are altering the Arctic carbon budget. A key feature of the formulation is that accumulation of peat within the soil column modifies its texture, hydraulic conductivity, and thermal conductivity, which, in turn influences resulting rates of HR within the soil column. Analysis of the model at three eddy covariance tower sites in the Alaskan tundra shows that the vertically-resolved soil column formulation accurately captures the zero-curtain phenomenon, in which the temperature of soil layers remain at or near 0 °C during fall freezeback due to the release of latent heat, is critical to capturing observed patterns of wintertime respiration. We find that significant declines in net ecosystem productivity (NEP) occur starting in 2013 and that these declines are driven by increased HR arising from increased precipitation and warming. Sensitivity analyses indicate that the cumulative NEP over the decade responds strongly to the estimated soil carbon stock and more weakly to vegetation abundance at the beginning of the simulation.

1. Introduction

The Arctic is experiencing rapid climate change due to anthropogenic emissions of greenhouse gasses (Cohen *et al* 2014). This rapid warming is thawing permafrost across the Arctic (Jorgenson *et al* 2006, Biskaborn *et al* 2019). It is estimated that

1300–1700 Pg of carbon, or about twice the current atmospheric burden, is stored in Arctic permafrost (Tarnocai *et al* 2009, Hugelius *et al* 2014). As this permafrost thaws, these abundant stocks of carbon are exposed to microbial activity, which releases carbon as carbon dioxide (CO_2) and methane (CH_4) creating a positive feedback that will exacerbate climate change

(McGuire *et al* 2009, Schaefer *et al* 2014, Schuur *et al* 2015).

Whether the Arctic terrestrial biosphere is a net sink or source of carbon to the atmosphere is governed by its net ecosystem productivity (NEP), which reflects the difference of two large offsetting fluxes: the net primary production (NPP) of the vegetation and the heterotrophic respiration (HR) of carbon in the soil and litter. CO_2 measurements from airborne instruments and eddy covariance towers have suggested that Alaska, and especially the Alaskan tundra, is releasing more carbon than in the past (Oechel *et al* 1993, Hinzman *et al* 2005, Commane *et al* 2017). With climate change, the active layer has increased at many sites in the Arctic. Not only is the active layer deepening, but the length of the fall zero-curtain period is increasing, which promotes more HR and carbon loss (Natali *et al* 2015, Euskirchen *et al* 2017). The zero-curtain period occurs when subsurface soil remains at or near 0 °C due to the effect of latent heat during freezing or thawing (Outcalt *et al* 1990). Under the warming climate, freezeback failure is increasing and thawed soil layers that persist through the winter, known as taliks, are forming, which can accelerate permafrost loss and cold season soil respiration (Parazoo *et al* 2018). While winter respiration has been shown to be important to the Arctic carbon budget, until relatively recently year-round flux measurements in tundra ecosystems have not been available (Zimov *et al* 1993, 1996, Euskirchen *et al* 2017). Recent field studies that included year-round measurements have found that significant HR occurs during the fall and winter months when thawed soil layers exist below a frozen surface (Zona *et al* 2016, Commane *et al* 2017). Similarly, carbon dioxide flux measurements across the Arctic indicate high wintertime respiration, that is underpredicted by several terrestrial biosphere models (Natali *et al* 2019). These studies are suggestive of on-going subsurface microbial activity during the zero-curtain period. However, our understanding of the dynamics of HR during the zero-curtain period are currently lacking because current terrestrial biosphere and land surface models being used to predict the Arctic carbon balance poorly represent cold season mechanisms and soil carbon (Alter *et al* 2018, Natali *et al* 2019, Huntzinger *et al* 2020, Tao *et al* 2020, Wang *et al* 2020).

Both soil temperature and moisture affect the rate of HR with warming soil temperatures increasing the rate of HR (Sierra *et al* 2015). Hydrology plays a crucial role in determining whether respiration is aerobic or anaerobic (Bolker *et al* 1998, Lawrence *et al* 2015, Sierra *et al* 2015): aerobic respiration converts soil carbon to CO_2 and is about ten times more efficient at releasing carbon than anaerobic respiration, which produces methane (CH_4). Consequently, permafrost carbon that remains saturated when thawed tends to be preserved (Estop-Aragonés *et al* 2018); however, changes in water table depth by drainage or drought

accelerate carbon loss (Ise *et al* 2008, Euskirchen *et al* 2014).

The interactions between vegetation and the underlying land surface are complex, and thus difficult to represent in terrestrial biosphere models. It is therefore perhaps not surprising that terrestrial biosphere models disagree on the current sign of the Arctic's carbon balance and how it will change in the future (Sistla *et al* 2013, Fisher *et al* 2014, McGuire *et al* 2016, 2018, Schädel *et al* 2018, Virkkala *et al* 2021). There is general consensus that a warming climate in the Arctic will increase gross primary productivity (GPP) and vegetation biomass, thus sequestering atmospheric carbon. There is also consensus that the rate of HR will also increase releasing stored soil carbon that has been accumulating for millennia; potentially offsetting the increase in vegetation biomass. An intercomparison of five terrestrial biosphere models indicate that vegetation biomass over permafrost regions will increase between 0 and 150 Pg by 2300 under the RCP4.5 climate scenario (McGuire *et al* 2018). However, those same simulations showed the soil carbon changing between +70 and −40 Pg due to enhanced respiration. Whether increases in plant growth or soil carbon decay will dominate the future carbon budget is uncertain due to complex environmental sensitivities and responses of vegetation types and ecosystems to climatic change.

In this study, we investigate the dynamics of carbon stocks and carbon dioxide fluxes and the associated biophysical properties of the ecosystem that influence them across three tundra sites at Imnavait Creek, Alaska (AK) using a terrestrial biosphere model that incorporates vertically-resolved soil biophysics and soil biogeochemistry. Reflecting the scope of the current model formulation in this study we only examine impacts on carbon dioxide and not methane production. Our analyses address the following questions: a) To what extent does respiration during the zero-curtain period explain the high rates of observed wintertime respiration? b) How are soil biophysical processes responding to climate variability and changing in Arctic ecosystems? c) What are the leading biophysical drivers of seasonal and interannual variability in the different components of NEP?

2. Materials and methods

2.1. Site description

Observations from three eddy covariance towers located within the continuous permafrost tundra of the Imnavait Creek watershed, Alaska (68 37′N, 149 18′W) were used to evaluate vertically-resolved model formulation. Imnavait Creek is an ideal site for analyzing the patterns and drivers of Arctic carbon dynamics due to the abundance of meteorological, vegetation, and soil measurements available at the site (Kade *et al* 2012, Euskirchen *et al* 2017). The three towers, spaced ∼500 m apart, span a shallow

topographic and associated edaphic gradient from 850 to 900 m with a heath tundra site on the ridge, a tussock tundra site on the slope, and a wet sedge tundra site near Imnavait Creek. The ridgetop has thin, well-drained soil with a shallow (2.3 cm ± 0.3) soil organic matter (SOM) layer, and the organic layer deepens down-slope with 11.7 ± 1.2, and 34 ± 2.6 cm of SOM, respectively, at the tussock, and wet sedge sites (Kade *et al* 2012). Further details of the study site and measurements can be found in (Euskirchen *et al* 2012, 2017, Kade *et al* 2012). During the study period, 2008–2016, the mean annual air temperature measured by the towers was −7.6 °C, and the mean annual precipitation provided by North American Regional Reanalysis across this period was 506 mm (Mesinger *et al* 2006). The site experienced substantial warming over the study period with the annual temperatures in 2014–2016 being 2 °C–3 °C warmer than 2008–2012 at all three tower sites (figure S6 available online at stacks.iop.org/ERL/17/014019/mmedia). This warming occurred predominantly during the winter months. There was also a significant increase in precipitation in 2013 and 2014 with approximately 50% more precipitation during the growing season (figure S6).

2.2. Model description

The simulations in this study were performed using the ecosystem demography model v2.2 (ED2) (Longo *et al* 2019). The ED2 model is a cohort-based terrestrial biosphere model that calculates the fluxes of carbon, energy, and water, all conserved quantities, between the vegetation, soil, and atmosphere (Moorcroft *et al* 2001, Medvigy *et al* 2009). ED2 simulates dynamic vegetation communities and accounts for competition between plant functional types (PFTs) and size, and has been developed and tested across a range of different biomes including boreal, temperate, and tropical forests (Medvigy *et al* 2010, Trugman *et al* 2016, Fisher *et al* 2018). In this study, we introduce a new vertically-resolved treatment of soil carbon processes that is critical for simulating the Arctic ecosystem. We also created new tundra PFTs; deciduous shrubs, evergreen shrubs, and graminoids, based on the prevailing vegetation types found at Imnaviat Creek to parameterize the vegetation formulation for an Arctic setting (see supplementary section S1).

2.3. Vertically-resolved soil biogeochemistry

The new soil biogeochemistry implementation developed in this study consists of a vertically-resolved representation of soil organic carbon (SOC) decomposition and accompanying rates of HR. SOC accumulates in the model from plant litter and is removed through HR based on a simplified version of CENTURY decomposition model in which the SOC within each layer is partitioned into three types; fast, structural, and slow, that respire at different rates

(Bolker *et al* 1998, Longo *et al* 2019). Existing versions of the model use temperature and moisture values from the top 20 cm soil to determine the effects of soil temperature and moisture on the decomposition rates of carbon pools. In the new implementation, the three SOC pools are resolved vertically, and the HR in each discrete soil layer is then determined by the abundances and type of carbon in each layer, and the temperature and moisture conditions in each soil layer following the approach of Ise *et al* (2008). Each type of carbon is assumed to be input at the surface, and each day the depth of the carbon is recalculated based on the total mass of each type of carbon. To calculate the depth of the SOC, we assume a density for each carbon pool; we use average carbon densities of 29.1, 45.9, and 58.7 kgC m^{-3} for fast, structural, and slow carbon pools, respectively based on organic soil densities observed in the Alaskan tundra (Michaelson *et al* 1996, Yi *et al* 2009). A schematic of this model is shown in supplementary figure S3. The temperature and soil moisture sensitivities are plotted in figure S4. The decay rates and parameters relating the temperature and moisture dependencies of decomposition were adjusted based on an offline optimization to minimize the deviations between the simulated and tower NEP (see supplement S2). The optimal temperature in this respiration model is 35° C. The optimal relative moisture content, 0.75, is derived from the optimization.

Soil carbon in the model is dynamic, with carbon added at the top of the soil column and removed at each layer through HR. SOC is redistributed daily with SOC types preferentially moved down based on their density since deeper carbon tends to be denser and more recalcitrant (Yi *et al* 2009). In addition, soil properties, such as thermal conductivity that depend on the soil type, also dynamically change with depth based on soil carbon content. Following the method of Trugman *et al* (2016), the soil type transitions between mineral and organic peat depending on the soil carbon fraction. Ten transitional soil types are represented, whose properties are linearly interpolated between peat and mineral soil types defined in Longo *et al* (2019). The dynamic soil properties affect the profiles of soil temperature and moisture which can feeds back onto the vegetation.

2.4. Model simulation procedure

The simulations at each of the three eddy covariance sites were driven by half-hourly meteorological data, including air temperature, pressure, precipitation, specific humidity, wind speed, and up- and downward short- and long-wave radiation. The simulations were initialized using information on vegetation composition from Kade *et al* (2012) and PFT-level measurements of above ground biomass (AGB) at nearby Toolik Lake for each vegetation community (Shaver and Chapin 1991, Chapin and Shaver 1996). The accompanying size-structure of each PFT

was specified from the output from an equilibrium simulation in which the model was initialized with near bare-ground vegetation state and run for 200 years. To account for the discrepancies between the observed vegetation and the equilibrium simulation, the model was run for nine years using the observed vegetation mass and the simulated equilibrium size structure to allow the energy, carbon, and water fluxes to equilibrate. Total soil carbon at each site was initialized from Euskirchen *et al* (2017) with 17, 16, and 11 kg m^{-2} for the wet sedge, tussock, and heath respectively. The soil carbon was partitioned into the three pools in the following ratios:1, 3, 6 for the fast, structural, and slow carbon based on the equilibrium ratios for peat found using an earlier version of the ecosystem demography model (Ise *et al* 2008). The three carbon pools are defined by their bulk density, decomposition rate, and sources and sinks. Soil temperature was initialized using observations from nearby borehole measurements at 0.34, 0.5, 0.9, and 3 m and soil moisture was initialized with field capacity (Euskirchen *et al* 2017).

In addition to simulations at the three tower sites, we performed a series of sensitivity tests to investigate how the model predictions vary in response to uncertainties regarding the initial soil carbon abundance, initial vegetation abundance, and surface water runoff times. Surface water runoff time, determines timescale at which surface water is reduced by 1/*e*, and is a proxy for slope in the model (Longo *et al* 2019). Runoff affects the water budget by removing surface water not immediately absorbed by the soil after precipitation events. In addition, we quantify the sensitivity of the model predictions to vertically resolving the respiration and allowing the soil texture to be dynamic based on the organic layer thickness (see table S3 and supplementary section S4).

3. Results

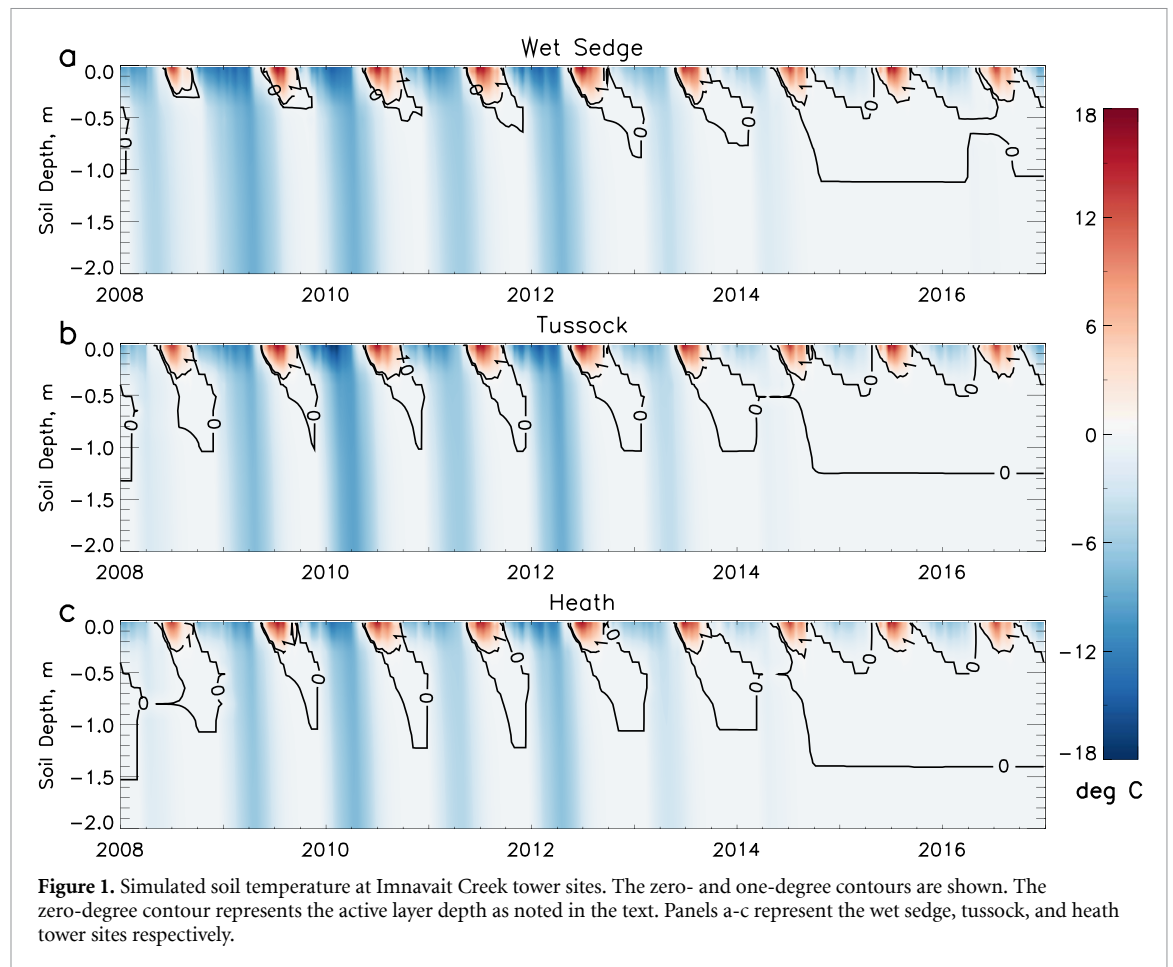### 3.1. Soil temperature, moisture, and the zero-curtain phenomenon

The rate at which SOC is transformed into CO_2 via HR is determined by sub-surface soil moisture and temperature conditions. As figure 1 illustrates, there is a clear warming trend in soil temperatures over the analysis period. During the first five years (2008–2012), a strong seasonal cycle of soil temperature is apparent: surface temperatures are above freezing for a brief three-to-four month period during the summer, followed by strong seasonal cooling over the fall and winter in which cold temperatures (down to -10 °C) permeate to the bottom of the soil column (figure 1). The zero-curtain period is evident in the zero-degree contour line, which indicates thawed soil that persists well into the winter. However, from 2013 to 2016, the duration of the zero-curtain period increases and the magnitude of the seasonal cooling during the fall and winter weakens considerably

(figure 1). For example, at 50 cm depth, the simulated thawed or mixed phase soil increases from about 180 days in 2013 to year-round in 2016 forming a talik. Furthermore, the coldest temperatures at 50 cm depth increase from about -6 °C in 2012 to 0 °C in 2016. This trend is driven both by warming air temperatures (figures S6–S9) and increasing snowpack which insulates the soil from the cold wintertime temperatures (figures S7 and S8). Consequently, the thaw depth (black contour line in figure 1) decreases from approximately 30 cm in 2008–9 to over 110 cm in 2015. This warming trend is corroborated by borehole measurements of soil temperature at Imnavait, which also show a substantial warming trend over this period, particularly during the winter months, consistent with our simulations: the 50 cm borehole minimum winter temperatures increase from -9 °C in 2012 to -3 °C in 2015 (Euskirchen *et al* 2017).

3.2. Impacts of vertically resolving soil decomposition and respiration

Vertically resolving the SOC increases wintertime respiration at depth and decreases wintertime respiration at the surface compared to the original decomposition formulation in which decomposition rates vary in relation to the temperature and moisture conditions in the top 20 cm soil (figure 2). During summer, the vertically-resolved model has increased respiration near the surface and decreased respiration at depth compared to the original formulation (figure 2, compare panels (b) and (d)). Underlying this are large differences in the decomposition factor at depth in the original and vertically-resolved version of the model (figure 2, compare panels (a) and (c)). These translate into modest differences in HR rate (figure 2, panels (b) and (d)) however, because: (a) the deeper slow carbon is more recalcitrant, and thus has a much lower respiration rate; (b), below the organic layer, HR is zero due to the absence of SOC at these depths at the three flux tower sites. The difference in the magnitude and seasonal cycle of HR between the two decomposition formulations increases for soils with deeper organic layers because of the greater contribution from the deep thawed layers (figures S15 and 3(a)).

Model sensitivity tests indicate that the amount, and thus depth, of soil carbon greatly affect the seasonal cycle and magnitude of HR and NEP (figure 3). Simulations initialized with soil carbon abundances from 5 to 135 kgC m^{-2}—reflecting the typical range observed in the North American Arctic (Hugelius *et al* 2014)—indicate that abundant soil carbon leads to more HR and a smaller seasonal amplitude, i.e. relatively more HR during the fall and winter months (figure 3(a)). This altered seasonal amplitude arises because significant amounts of carbon now experience a different pattern of soil temperature and moisture. The pattern of increased fall and wintertime respiration and accompanying reduced seasonal

Figure 1. Simulated soil temperature at Imnavait Creek tower sites. The zero- and one-degree contours are shown. The zero-degree contour represents the active layer depth as noted in the text. Panels a-c represent the wet sedge, tussock, and heath tower sites respectively.

amplitude seen in the vertically-resolved model in essence reflects the seasonal pattern of temperature at depth (figure 1). Furthermore, soil carbon abundance does not greatly affect plant growth, thus the effects on HR are also apparent in NEP (figure 3(b)). Soil carbon abundance has a strong effect on the net carbon flux and can determine the sign of the cumulative NEP, or whether the ecosystem is a net source or sink of carbon.

The decomposition factor in the top 30 cm responds strongly to the seasonal cycle of soil temperatures with notable departures due to changes in soil moisture (figures 4(a)–(c)). At depth, the decomposition factor is relatively high throughout the winter as deeper soil temperatures linger near the freezing point due to the release of latent heat as freezing fronts advance from the surface and permafrost (figure 1). Similarly, HR has a strong seasonal cycle in the top 20 cm; however, despite moderate decomposition factors, there is little HR deeper in the column due to the absence of organic material at these depths (figures 4(d)–(f)).

Soil moisture accounts for more variation than soil temperature in HR across seasons and years, because HR is nonlinearly related to soil moisture—with decomposition rates being highest at a relative soil moisture of 0.75 (figures S4 and S5). Consequently, deviations both below and above this

optimum, due to either drying or saturating of the soil, decrease the rate of decomposition and resulting levels of HR. For example, during the early summer, drying of the soils due to evapotranspiration reduces HR (see days 180–200 in figure 4, panels (d)–(g); see also figures S5 and S11). Consequently, timeseries of total HR at each site show substantial interannual variability (figure 4(g)). For example, during the winter of 2014–2015, HR decreased 85% in the wet sedge, 50% in the tussock, and 38% in the heath compared to the prior winter despite relatively warm winter temperatures due to saturated soils during this period (see figures S5 and S11). The 2014–2015 winter had the highest soil moistures of any year analyzed.

3.3. NEP
The temporal patterns of HR, discussed above, are an important contributor to the temporal trends in NEP at the three sites (figure 5, panels (a), (c), and (e)). As figure 5 illustrates, there is a strong seasonal cycle in the observed NEP with growing season peaks between 0.5 and 1 kgC m^{-2} yr^{-1} and overwinter rates of −0.1 to −0.4 kgC m^{-2} yr^{-1} with the heath having noticeably lower rates of wintertime respiration and the wet sedge having the highest wintertime rates (black lines in panels (a), (c), and (e)). At the wet sedge site (panel (a)), the
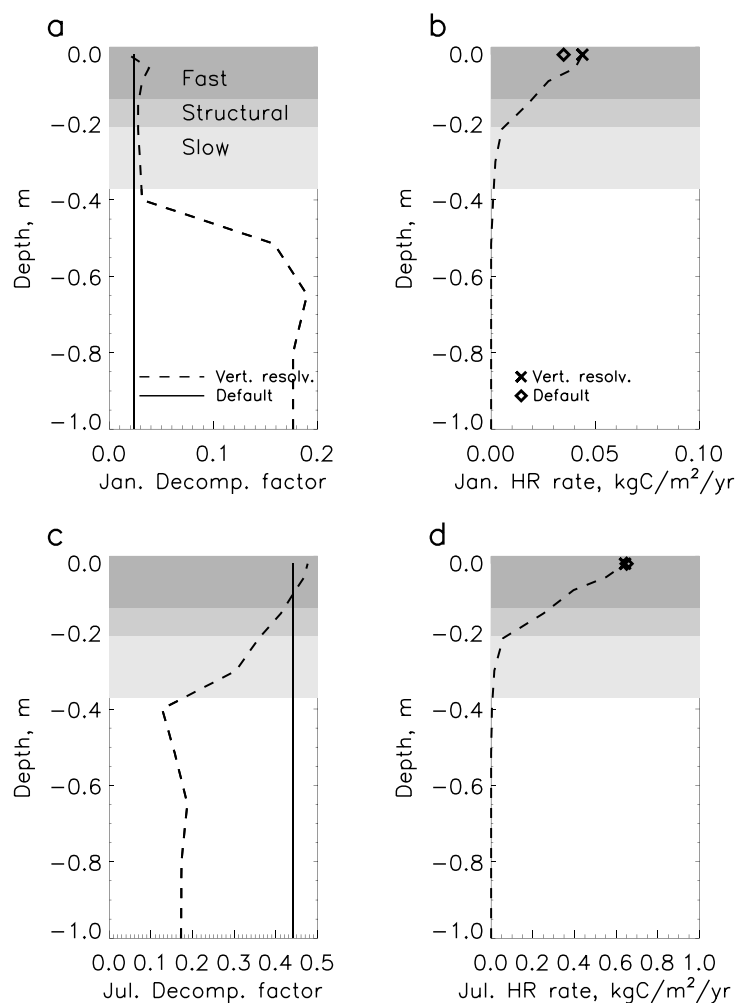
Figure 2. Predicted vertical profiles of January (a), (c) and July (b), (d) mean decomposition factors (a), (b) and mean cumulative heterotrophic respiration rates (c), (d) at the Tussock site in both the default model and the peatlands version with vertically-resolved soil carbon and respiration.
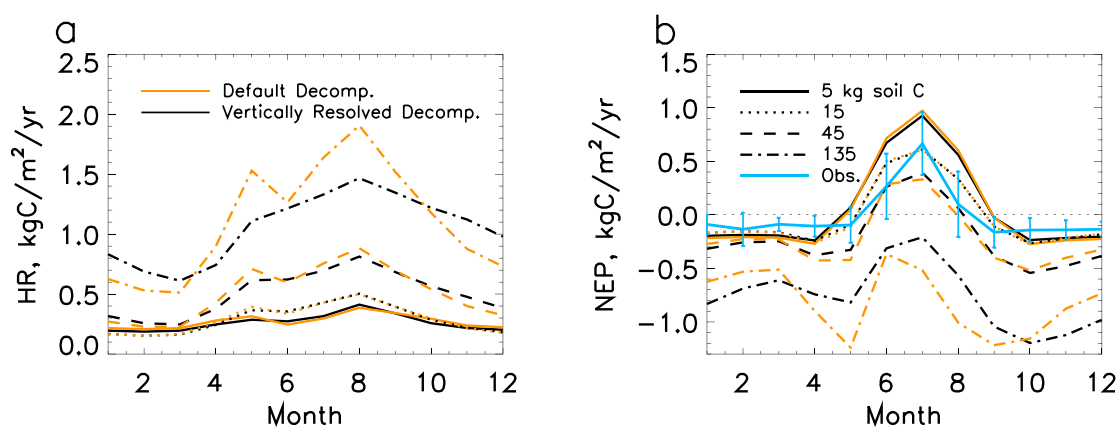

Figure 3. Sensitivity tests of HR and NEP to model formulation (color) and four soil carbon abundances (line style) at the tussock site. (a) The seasonal cycle of HR. (b) The seasonal cycle of NEP compared with eddy covariance tower observations in blue.

model underpredicts the summertime peak NEP by approximately 0.4 kgC m^{-2} yr^{-1} likely due to low simulated primary productivity however, the model predictions are generally within 0.1 kgC m^{-2} yr^{-1} of the observed wintertime fluxes except for the winters of 2012–13 and 2014–15 in which the model predicted too much and too little HR respectively. As discussed above, these wintertime discrepancies were predominantly driven by changes in soil moisture.
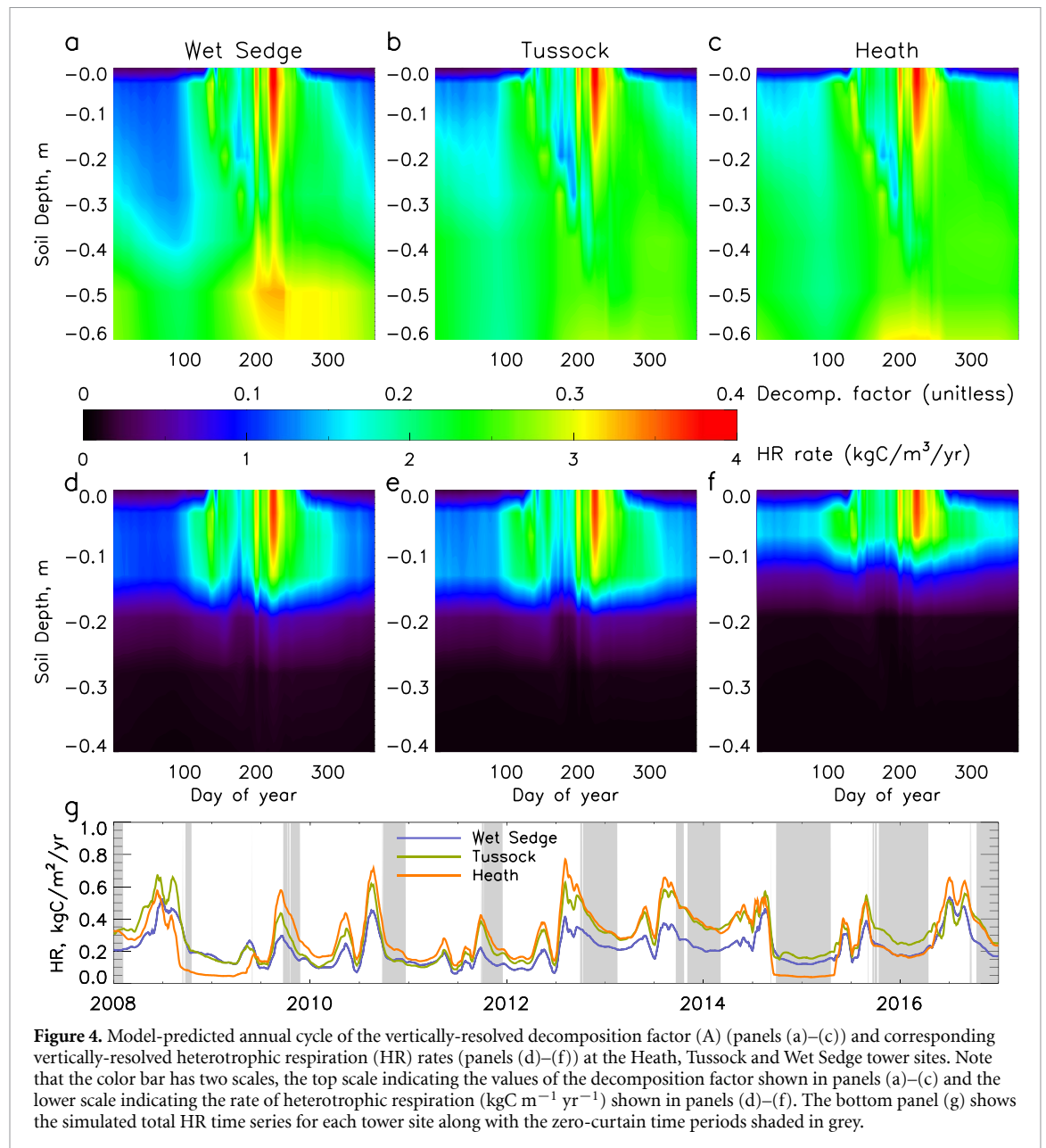
Figure 4. Model-predicted annual cycle of the vertically-resolved decomposition factor (A) (panels (a)–(c)) and corresponding vertically-resolved heterotrophic respiration (HR) rates (panels (d)–(f)) at the Heath, Tussock and Wet Sedge tower sites. Note that the color bar has two scales, the top scale indicating the values of the decomposition factor shown in panels (a)–(c) and the lower scale indicating the rate of heterotrophic respiration (kgC m^{-1} yr^{-1}) shown in panels (d)–(f). The bottom panel (g) shows the simulated total HR time series for each tower site along with the zero-curtain time periods shaded in grey.

At the tussock site (panel (c)), predicted peak growing season NEP was within 0.1 kgC m^{-2} yr^{-1} of the observations except during 2012–13 and 2013–14 when summer maximum NEP was 0.5 kgC m^{-2} yr^{-1} below the observed NEP and wintertime NEP was 0.3 kgC m^{-2} yr^{-1} lower than observations. These discrepancies are due to anomalously high predicted rates of HR during these years as microbial activity responded to warming summer and winter soil temperatures and near-optimal soil moisture (0.75 relative saturation) conditions for decomposition (figures S5 and S11). At the heath site, the model over-predicted both the maximum NEP and the width of the growing season, suggesting an overly-long growing season phenology, potentially related to early off-set and onset of snow cover in the model. Predicted wintertime NEP values are within 0.1 kgC m^{-2} yr^{-1} of the observations with the notable exception of

2012–14, when the model underpredicts wintertime NEP; however, the magnitude of the discrepancy during these years is lower than that seen at the tussock site.

As figure 5 illustrates, the tower measurements (solid black lines in panels (a)–(c)) exhibit a significant gradient in cumulative NEP across the sites: the heath site is a small net source, the tussock site is relatively neutral, and the wet sedge is a strong net source of carbon to the atmosphere. The model's NEP predictions (orange shading panels (a)–(c)) also vary across the three sites; however in the model predictions the upland heath site is a net carbon sink, the tussock site is a small net source, and the wet sedge site is a large source of carbon to the atmosphere over the observation period.

There is an inflection point in the predicted cumulative NEP at all sites after 2013. At the tussock
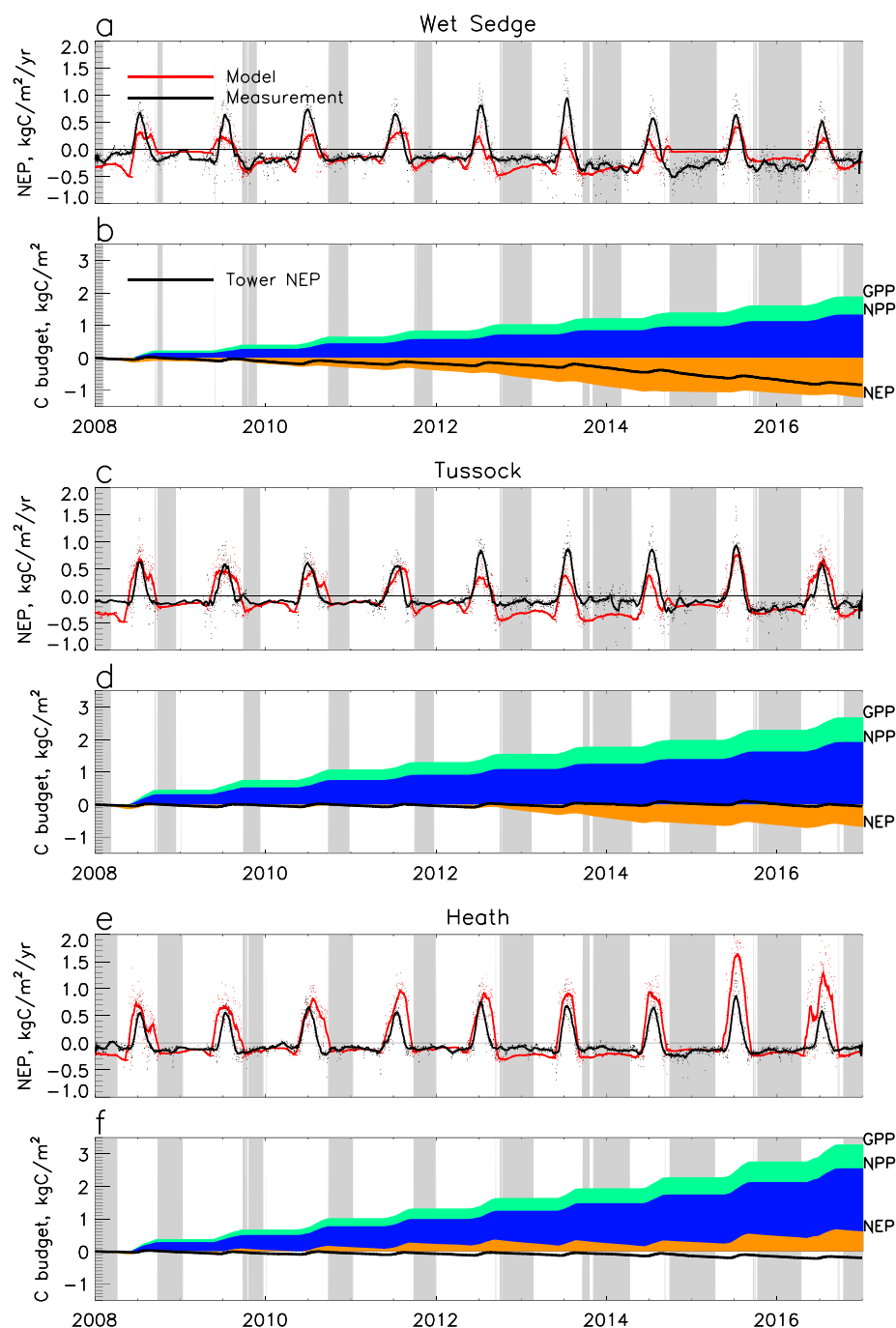
Figure 5. Model and eddy covariance tower measurements of the NEP at each tower site (panels (a), (c), (e)). Daily observations and simulations are smoothed by 30 days. The grey shading indicates the zero-curtain time period. The cumulative carbon budget at each tower site over the study period is shown in panels (b), (d), and (f). The top of the green shading corresponds to the cumulative GPP, while the top of the blue shading corresponds to the cumulative NPP. The green shaded region indicates the cumulative autotrophic respiration, while the orange shading indicates the total change in ecosystem carbon over this period. The eddy covariance tower cumulative NEP is the solid black line. Positive values indicate a flux ((a), (c), (e)) or CO_2 sink ((b), (d), (f)) into the vegetation and soil, while negative values indicate a flux ((a), (c), (e)) or source ((b), (d), (f)) of CO_2 to the atmosphere.

and wet sedge sites, warmer and wetter conditions (see panels (a) and (b) in figures S10 and S11) increase HR substantially, resulting in increased carbon losses at these two sites as indicated by the declines in the orange curves in panels (b) and (d) of figure 5. In contrast, the heath site transitions from being a net carbon sink to a weak carbon source in 2013 and 2014 as indicated by the slight dip in orange curve in panel (f) of figure 5 during this period, before returning

to a net carbon sink in 2015 and 2016. Examination of the effect of underlying temperature and moisture conditions on decomposition rates (figure S5) indicate that is due to relatively warm soil temperatures and soil moisture values reaching near optimal values for decomposition during this period.

Despite the close proximity of the three sites, there is distinct variability in their NEP and net carbon budget over this time period (figure 5). The variability

in net ecosystem carbon change spans zero, with the heath site a carbon sink, the tussock site near neutral, and the wet sedge site a net carbon source (figure 5). A series of sensitivity tests exploring the key biological and physical differences between these sites (vegetation abundance, surface water runoff time, and soil carbon abundance) indicate that the abundance of soil carbon is the largest driver of the response of the NEP to climate due to increased HR (figures 3(a) and (b), figures S14, S17(a)–(d)).

The second largest driver of NEP variability between the study sites is the initialized vegetation abundance. However, the sensitivity of NEP to initial vegetation was weak compared to initial soil carbon (see figures S17 (i)–(l)). GPP varies significantly between the sites, with the differences predominantly driven by differences in initial soil carbon and vegetation communities (figure S12). Metrics of vegetation productivity and abundance (GPP, AGB and leaf are index) were predicted to increase across all sites over this time period as temperatures warm (see supplement S5, figure S19). Most of the increases in plant productivity come from enhanced shrub growth (figure S19). This pattern is consistent with observed 'Arctic greening' trends (Forbes *et al* 2010, Myers-Smith *et al* 2015, Martin *et al* 2017); however, other factors such as changes in snow cover, standing water, cloud cover can also cause changes in vegetation indices (Myers-Smith *et al* 2020).

4. Discussion

4.1. Zero-curtain carbon emissions

Complex biophysical interactions between soil temperature, soil moisture and HR are a key control on the net carbon flux of tundra ecosystems. Our simulations indicate a thawed layer persists in the soil below a frozen surface for months into the fall and winter (figure 1), consistent with nearby borehole measurements (Euskirchen *et al* 2017). The active layer depth increased and the duration of the zero-curtain period extended between 2008 and 2017 due to warming air and soil temperatures over this time period. Given current climate trends in the Arctic region (Cohen *et al* 2014), we expect continued increases in the duration of the zero-curtain period as the climate warms and snow cover is reduced in the future (Collins *et al* 2013). A warming soil column could lead to more CO_2 emissions further enhancing rates of Arctic warming.

While soil temperatures tend to show relatively stable seasonal patterns (figure 1), soil moisture is typically more variable on short and long timescales (figure S11). For example, snowmelt and associated wetting of the soil can lead to rapid changes in the rates of HR in our simulations, which can increase the rate of HR in dry conditions or greatly reduce the rate of HR if the soils become saturated (figure S5). Deviations from the optimum moisture, both

wetting and drying, can decrease the rate of HR. This complex relationship between HR and soil moisture can confuse attempts to attribute changes in the NEP, which are often attributed to temperature alone (e.g. Nottingham *et al* 2020).

The seasonality and type of precipitation are also important drivers of the Arctic carbon budget. Wintertime snow increases HR as deep snowpack acts as an insulator to cold wintertime temperatures (Liston and Elder 2006, Morgner *et al* 2010) and may reduce productivity by reducing the growing season (Galvagno *et al* 2013, Bieniek *et al* 2015, Scholz *et al* 2018), such as in the spring of 2014 and 2015 in our simulations (Figures S6–S9). These processes shift the carbon balance towards a net source to the atmosphere. This finding is consistent with a study of heath tundra in Greenland, which found that winter precipitation is correlated with HR and negatively correlated with GPP (Zhang *et al* 2018). More growing season precipitation may increase vegetation growth, however, this depends on the rate at which evapotranspiration and temperature increase (Wania *et al* 2009, Collins *et al* 2013). Increased precipitation could also increase soil moisture potentially inhibiting HR and CO_2 release (Chivers *et al* 2009, Zona *et al* 2009). Both of these processes would shift the carbon balance of the land and biosphere towards a net sink. Future increases in precipitation associated with global warming have an uncertain effect on the carbon budget due to these complex processes.

Translating soil temperature and moisture into realistic rates of HR requires vertically resolving soil carbon abundance and decomposition. The vertical structure of soil temperature and moisture determine the decomposition rate that acts on the vertical profile of soil carbon to determine the HR (figure 2). During the zero-curtain period, e.g. January (figure 2(b)), the rate of HR is higher using vertically-resolved soil dynamics. Capturing zero-curtain emissions arising from a subsurface thawed layer is important for correctly simulating the seasonal cycle and amplitude of NEP (Zona *et al* 2016, Commane *et al* 2017, Euskirchen *et al* 2017). The wintertime decomposition rate is much higher at depth, which translates into higher wintertime HR where soil carbon was present (figure 4). Due to the shallow organic layer depth, this effect was relatively modest in the tundra sites we simulated; however, sensitivity tests indicate that soils with deeper organic layers, such as can be found in boreal peatlands, had much higher wintertime respiration (see figures 3(a) and S15, panels (a)–(d)). Increasing rates of wintertime HR are consistent with recent observational studies in the Arctic (Natali *et al* 2019, Hashemi *et al* 2021).

Another important process affecting the dynamics of the Arctic carbon cycle is cryoturbation: the physical mixing of material in the soil column as a result of freeze/thaw processes. This process tends to vertically transport carbon deeper into the soil,

omitting it may concentrate soil carbon near the surface altering rates of HR and the resulting carbon budget (Koven *et al* 2009). As seen in figure 2, carbon at the tussock site is confined to the top 40 cm of soil, which is within the seasonal active layer. Carbon transported deeper into the soil column would decompose more slowly thereby lowering the total annual HR, and also reducing the seasonal amplitude of HR because decomposition at depth extends into the fall and winter (figures 3 and 4). The effects of cryoturbation were not explicitly included in this study because rates of vertical mixing arising from cryoturbation are poorly constrained and spatially variable (Koven *et al* 2013). However, this is an avenue for future development that may improve the model representation of subsurface carbon abundance.

4.2. Carbon budget

Previous studies have concluded that GPP dominates the variability in the growing season carbon budget (Shaver *et al* 2007, López-Blanco *et al* 2017, Schädel *et al* 2018). Simple models that only include LAI, light, and temperature can explain much of the NEP variability across tundra sites (Shaver *et al* 2007, Loranty *et al* 2011). However, these studies do not consider soil carbon variability as a predictive factor, and recent year-round measurements are challenging the notion that GPP is the primary control on annual NEP, i.e. whether the Arctic ecosystems are a net source or sink of carbon to the atmosphere (Euskirchen *et al* 2014, 2017, Zona *et al* 2016). GPP may be the largest source of interannual variability in areas of low soil carbon such as some upland tundra ecosystems. However, much of the Arctic has large stores of soil carbon (Crowther *et al* 2019), and in these areas the large soil carbon reservoir means that there is far larger potential for large changes in rates of HR. Small changes in the rate of respiration, due to a warming climate for example, applied to a large reservoir of carbon can greatly affect the net carbon flux. Both observations and model predictions show increases in wintertime respiration during the latter half of the study period (2013 onwards), without corresponding increases in NPP (Euskirchen *et al* 2017). We find that changes in HR predominantly determined whether an ecosystem was a net source or sink of carbon during this period (figure 5), and sensitivity tests illustrate that the leading driver of variation in HR and NEP between the tower sites is the soil carbon abundance (figures 3, S14–S17).

The relationship between soil carbon abundance and net CO_2 flux is often not emphasized in local scale studies; however, it is an underlying assumption in papers discussing long-term carbon release from permafrost loss (Schaefer *et al* 2014, Koven *et al* 2015, Schuur *et al* 2015, McGuire *et al* 2018, Wieder *et al* 2019). A recent statistical upscaling of net CO_2 fluxes across the panarctic found that SOC is the most important variable for predicting annual

NEE (Virkkala *et al* 2021). We also find that the soil carbon abundance influences GPP (and NEP) through hydraulic feedbacks; in particular, the simulated over-productivity of the heath site (figure 5) results, at least in part, from differences in the hydraulic properties between organic and mineral soils. Reflecting observations, the heath site was initialized with approximately 30% less soil carbon, and our simulations show that springtime stomatal opening is substantially enhanced in soils with shallower organic layers that results in higher GPP (figures S12 and S13 panels (a) and (d)).

More generally our findings suggest that more accurate quantification of spatial variation in belowground carbon stocks will be critical for improving predictions of how the carbon budgets of the Arctic ecosystems are responding to ongoing changes in temperature and precipitation. As illustrated in figure 3, the amount of soil carbon initialized in this study greatly affects the net CO_2 fluxes. The model sensitivity to the soil carbon stock is not surprising, as it is a first order term in the equation for HR (EQ S6). Model assumptions about soil carbon can determine whether the model predicts a net source or sink in the future (Wieder *et al* 2019); however, current models largely fail to reproduce observed values of soil carbon abundances (Huntzinger *et al* 2020). We circumvent this problem by initializing the model with observed soil carbon abundances. Patterns of interannual variability in the carbon budget are predicted to vary spatially, and differences in soil carbon stocks—rather than differences in vegetation—may be the leading driver of spatial variation across tundra landscapes (figure S17). This largely depends on the relative magnitude of the heterogeneity in soil carbon and vegetation abundance.

In summary, we find that tundra ecosystems that are both net carbon sinks (heath) and sources (tussock and wet sedge) to the atmosphere are strongly sensitive to changes in temperature and precipitation, and the magnitude of the net CO_2 flux increases with temperature. The effects of changes in precipitation on the tundra carbon budget are more complex however, and depend on both the season and form (rain vs. snow) of precipitation, and the existing moisture conditions of the soil. Between 2008 and 2017, we see a transition from a net CO_2 sink to a source in ecosystems with deeper organic soil layers during warmer and wetter years. This change is driven by a longer zero-curtain period and deeper active layer resulting in increased HR. Our results suggest that as the climate warms and wets in the future, the active layer will deepen and the zero-curtain period will extend, enabling more wintertime respiration (McGuire *et al* 2018, Natali *et al* 2019). As a consequence, ecosystems with shallower organic soils may continue to be net sinks while ecosystems with deep, organic rich soils may become carbon sources to the atmosphere.

Data availability statement

No new data were created or analysed in this study.

Acknowledgments

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References

Alter R E, Douglas H C, Winter J M and Eltahir E A B 2018 Twentieth century regional climate change during the summer in the central United States attributed to agricultural intensification *Geophys. Res. Lett.* **45** 1586–94

Bieniek P A *et al* 2015 Climate drivers linked to changing seasonality of Alaska coastal tundra vegetation productivity *Earth Interact.* **19** 1–29

Biskaborn B K *et al* 2019 Permafrost is warming at a global scale *Nat. Commun.* **10** 264

Bolker B M, Pacala S W and Parton W J 1998 Linear analysis of soil decomposition: insights from the century model *Ecol. Appl.* **8** 425–39

Chapin F S and Shaver G R 1996 Physiological and growth responses of Arctic plants to a field experiment simulating climatic change *Ecology* **77** 822–40

Chivers M R, Turetsky M R, Waddington J M, Harden J W and McGuire A D 2009 Effects of experimental water table and temperature manipulations on ecosystem CO_2 fluxes in an Alaskan rich fen *Ecosystems* **12** 1329–42

Cohen J *et al* 2014 Recent Arctic amplification and extreme mid-latitude weather *Nat. Geosci.* **7** 627–37

Collins M *et al* 2013 Long-term climate change: projections, commitments and irreversibility *Climate Change 2013 - The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* ed T F Stocker, D Qin, G-K Plattner, M M B Tignor, S K Allen, J Boschung, A Nauels, Y Xia, V Bex and P M Midgley (Intergovernmental Panel on Climate Change, Cambridge University Press) pp 1029–136

Commane R *et al* 2017 Carbon dioxide sources from Alaska driven by increasing early winter respiration from Arctic tundra *Proc. Natl Acad. Sci. USA* **114** 5361–6

Crowther T W, van Den Hoogen J, Wan J, Mayes M A, Keiser A D, Mo L, Averill C and Maynard D S 2019 The global soil community and its influence on biogeochemistry *Science* **365** eaav0550

Estop-Aragonés C, Czimczik C I, Heffernan L, Gibson C, Walker J C, Xu X and Olefeldt D 2018 Respiration of aged soil carbon during fall in permafrost peatlands enhanced by active layer deepening following wildfire but limited following thermokarst *Environ. Res. Lett.* **13** 085002

Euskirchen E S, Bret-Harte M S, Scott G J, Edgar C and Shaver G R 2012 Seasonal patterns of carbon dioxide and water fluxes in three representative tundra ecosystems in northern Alaska *Ecosphere* **3** art4

Euskirchen E S, Bret-Harte M S, Shaver G R, Edgar C W and Romanovsky V E 2017 Long-term release of carbon dioxide from Arctic tundra ecosystems in Alaska *Ecosystems* **20** 960–74

Euskirchen E S, Edgar C W, Turetsky M R, Waldrop M P and Harden J W 2014 Differential response of carbon fluxes to climate in three peatland ecosystems that vary in the presence and stability of permafrost: carbon fluxes and permafrost thaw *J. Geophys. Res. Biogeosci.* **119** 1576–95

Fisher J B *et al* 2014 Carbon cycle uncertainty in the Alaskan Arctic *Biogeosci. Discuss.* **11** 4271–88

Fisher R A *et al* 2018 Vegetation demographics in earth system models: a review of progress and priorities *Glob. Change Biol.* **24** 35–54

Forbes B C, Fauria M M and Zetterberg P 2010 Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows *Glob. Change Biol.* **16** 1542–54

Galvagno M *et al* 2013 Phenology and carbon dioxide source/sink strength of a subalpine grassland in response to an exceptionally short snow season *Environ. Res. Lett.* **8** 025008

Hashemi J, Zona D, Arndt K A, Kalhori A and Oechel W C 2021 Seasonality buffers carbon budget variability across heterogeneous landscapes in Alaskan Arctic tundra *Environ. Res. Lett.* **16** 035008

Hinzman L D *et al* 2005 Evidence and implications of recent climate change in Northern Alaska and other Arctic regions *Clim. Change* **72** 251–98

Hugelius G *et al* 2014 Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps *Biogeosciences* **11** 6573–93

Huntzinger D N *et al* 2020 Evaluation of simulated soil carbon dynamics in Arctic-boreal ecosystems *Environ. Res. Lett.* **15** 025005

Ise T, Dunn A L, Wofsy S C and Moorcroft P R 2008 High sensitivity of peat decomposition to climate change through water-table feedback *Nat. Geosci.* **1** 763–6

Jorgenson M T, Shur Y L and Pullman E R 2006 Abrupt increase in permafrost degradation in Arctic Alaska *Geophys. Res. Lett.* **33** L02503

Kade A, Bret-Harte M S, Euskirchen E S, Edgar C and Fulweber R A 2012 Upscaling of CO_2 fluxes from heterogeneous tundra plant communities in Arctic Alaska: CO_2 fluxes in Arctic tundra *J. Geophys. Res.* **117** G04007

Koven C D, Lawrence D M and Riley W J 2015 Permafrost carbon—climate feedback is sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics *Proc. Natl Acad. Sci. USA* **112** 3752–7

Koven C D, Riley W J, Subin Z M, Tang J Y, Torn M S, Collins W D, Bonan G B, Lawrence D M and Swenson S C 2013 The effect of vertically resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4 *Biogeosciences* **10** 7109–31

Koven C, Friedlingstein P, Ciais P, Khvorostyanov D, Krinner G and Tarnocai C 2009 On the formation of high-latitude soil carbon stocks: effects of cryoturbation and insulation by organic matter in a land surface model *Geophys. Res. Lett.* **36** L21501

Lawrence D M, Koven C D, Swenson S C, Riley W J and Slater A G 2015 Permafrost thaw and resulting soil moisture changes regulate projected high-latitude CO_2 and CH_4 emissions *Environ. Res. Lett.* **10** 094011

Liston G E and Elder K 2006 A distributed snow-evolution modeling system (snowmodel) *J. Hydrometeorol.* **7** 1259–76

Longo M *et al* 2019 The biophysics, ecology, and biogeochemistry of functionally diverse, vertically- and horizontally-heterogeneous ecosystems: the ecosystem demography model, version 2.2—part 1: model description *Geosci. Model Dev.* **12** 4309–46

López-Blanco E, Lund M, Williams M, Tamstorf M P, Westergaard-Nielsen A, Exbrayat J-F, Hansen B U and Christensen T R 2017 Exchange of CO_2 in Arctic tundra: impacts of meteorological variations and biological disturbance *Biogeosciences* **14** 4467–83

Loranty M M, Goetz S J, Rastetter E B, Rocha A V, Shaver G R, Humphreys E R and Lafleur P M 2011 Scaling an instantaneous model of Tundra NEE to the Arctic landscape *Ecosystems* **14** 76–93

Martin A C, Jeffers E S, Petrokofsky G, Myers-Smith I and Macias-Fauria M 2017 Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach *Environ. Res. Lett.* **12** 085007

McGuire A D *et al* 2016 Variability in the sensitivity among model simulations of permafrost and carbon dynamics in the permafrost region between 1960 and 2009: modeling permafrost carbon dynamics *Glob. Biogeochem. Cycles* **30** 1015–37

McGuire A D *et al* 2018 Dependence of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate change *Proc. Natl Acad. Sci. USA* **115** 3882–7

McGuire A D, Anderson L G, Christensen T R, Dallimore S, Guo L, Hayes D J, Heimann M, Lorenson T D, Macdonald R W and Roulet N 2009 Sensitivity of the carbon cycle in the Arctic to climate change *Ecol. Monogr.* **79** 523–55

Medvigy D, Wofsy S C, Munger J W, Hollinger D Y and Moorcroft P R 2009 Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2 *J. Geophys. Res.* **114** G01002

Medvigy D, Wofsy S C, Munger J W and Moorcroft P R 2010 Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability *Proc. Natl Acad. Sci.* **107** 8275–80

Mesinger F *et al* 2006 North American Regional Reanalysis *Bull. Am. Meteorol. Soc.* **87** 343–60

Michaelson G J, Ping C L and Kimble J M 1996 Carbon storage and distribution in Tundra soils of Arctic Alaska, U.S.A *Arct. Alp. Res.* **28** 414

Moorcroft P R, Hurtt G C and Pacala S W 2001 A method for scaling vegetation dynamics: the ecosystem demography model (ED) *Ecol. Monogr.* **71** 29

Morgner E, Elberling B, Strebel D and Cooper E J 2010 The importance of winter in annual ecosystem respiration in the high Arctic: effects of snow depth in two vegetation types *Polar Res.* **29** 58–74

Myers-Smith I H *et al* 2015 Climate sensitivity of shrub growth across the tundra biome *Nat. Clim. Change* **5** 887–91

Myers-Smith I H *et al* 2020 Complexity revealed in the greening of the Arctic *Nat. Clim. Change* **10** 106–17

Natali S M *et al* 2015 Permafrost thaw and soil moisture driving CO_2 and CH_4 release from upland tundra *J. Geophys. Res. Biogeosci.* **120** 525–37

Natali S M *et al* 2019 Large loss of CO_2 in winter observed across the northern permafrost region *Nat. Clim. Change* **9** 852–7

Nottingham A T, Meir P, Velasquez E and Turner B L 2020 Soil carbon loss by experimental warming in a tropical forest *Nature* **584** 234–7

Oechel W C, Hastings S J, Vourlrtis G, Jenkins M, Riechers G and Grulke N 1993 Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source *Nature* **361** 520–3

Outcalt S I, Nelson F E and Hinkel K M 1990 The zero-curtain effect: heat and mass transfer across an isothermal region in freezing soil *Water Resour. Res.* **26** 1509–16

Parazoo N C, Koven C D, Lawrence D M, Romanovsky V and Miller C E 2018 Detecting the permafrost carbon feedback: talik formation and increased cold-season respiration as precursors to sink-to-source transitions *Cryosphere* **12** 123–44

Schädel C *et al* 2018 Divergent patterns of experimental and model-derived permafrost ecosystem carbon dynamics in response to Arctic warming *Environ. Res. Lett.* **13** 105002

Schaefer K, Lantuit H, Romanovsky V E, Schuur E A G and Witt R 2014 The impact of the permafrost carbon feedback on global climate *Environ. Res. Lett.* **9** 085003

Scholz K, Hammerle A, Hiltbrunner E and Wohlfahrt G 2018 Analyzing the effects of growing season length on the net ecosystem production of an Alpine grassland using model–data fusion *Ecosystems* **21** 982–99

Schuur E A G *et al* 2015 Climate change and the permafrost carbon feedback *Nature* **520** 171–9

Shaver G R and Chapin F S 1991 Production: biomass relationships and element cycling in contrasting Arctic vegetation types *Ecol. Monogr.* **61** 1–31

Shaver G R, Street L E, Rastetter E B, Van Wijk M T and Williams M 2007 Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in alaska and sweden *J. Ecol.* **95** 802–17

Sierra C A, Trumbore S E, Davidson E A, Vicca S and Janssens I 2015 Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture *J. Adv. Model. Earth Syst.* **7** 335–56

Sistla S A, Moore J C, Simpson R T, Gough L, Shaver G R and Schimel J P 2013 Long-term warming restructures Arctic tundra without changing net soil carbon storage *Nature* **497** 615–8

Tao J, Zhu Q, Riley W J and Neumann R B 2020 Improved ELMv1-ECA simulations of zero-curtain periods andCold-season CH_4 and CO_2 emissions at Alaskan Arctic tundra Sites (frozen ground/biogeochemistry/biology) (available at: https://tc.copernicus.org/preprints/tc-2020-262/)

Tarnocai C, Canadell J G, Schuur E A G, Kuhry P, Mazhitova G and Zimov S 2009 Soil organic carbon pools in the northern circumpolar permafrost region: SOIL ORGANIC CARBON POOLS *Glob. Biogeochem. Cycles* **23** GB2023

Trugman A T, Fenton N J, Bergeron Y, Xu X, Welp L R and Medvigy D 2016 Climate, soil organic layer, and nitrogen jointly drive forest development after fire in the North American boreal zone: CLIMATE AND SOIL DRIVE BOREAL CARBON *J. Adv. Model. Earth Syst.* **8** 1180–209

Virkkala A *et al* 2021 Statistical upscaling of ecosystem CO_2 fluxes across the terrestrial tundra and boreal domain: regional patterns and uncertainties *Glob. Change Biol.* **27** 4040–59

Wang J A, Sulla-Menashe D, Woodcock C E, Sonnentag O, Keeling R F and Friedl M A 2020 Extensive land cover change across Arctic–boreal Northwestern North America from disturbance and climate forcing *Glob. Change Biol.* **26** 807–22

Wania R, Ross I and Prentice I C 2009 Integrating peatlands and permafrost into a dynamic global vegetation model: 1. Evaluation and sensitivity of physical land surface processes: peatlands and permafrost in LPJ, 1 *Glob. Biogeochem. Cycles* **23** GB3014

Wieder W R, Sulman B N, Hartman M D, Koven C D and Bradford M A 2019 Arctic soil governs whether climate change drives global losses or gains in soil carbon *Geophys. Res. Lett.* **46** 14486–95

Yi S, Manies K, Harden J and McGuire A D 2009 Characteristics of organic soil in black spruce forests: implications for the application of land surface and ecosystem models in cold regions *Geophys. Res. Lett.* **36** L05501

Zhang W, Jansson P-E, Schurgers G, Hollesen J, Lund M, Abermann J and Elberling B 2018 Process-oriented modeling of a high Arctic tundra ecosystem: long-term carbon budget and ecosystem responses to interannual variations of climate *J. Geophys. Res. Biogeosci.* **123** 1178–96

Zimov S A, Davidov S P, Voropaev Y V, Prosiannikov S F, Semiletov I P, Chapin M C and Chapin F S 1996 Siberian

CO_2 efflux in winter as a CO_2 source and cause of seasonality in atmospheric CO_2 *Clim. Change* **33** 111–20

Zimov S A, Zimova G M, Daviodov S P, Daviodova A I, Voropaev Y V, Voropaeva Z V, Prosiannikov S F, Prosiannikova O V, Semiletova I V and Semiletov I P 1993 Winter biotic activity and production of CO_2 in Siberian soils: a factor in the greenhouse effect *J. Geophys. Res.* **98** 5017–23

Zona D *et al* 2016 Cold season emissions dominate the Arctic tundra methane budget *Proc. Natl Acad. Sci. USA* **113** 40–45

Zona D, Oechel W C, Kochendorfer J, Paw U K T, Salyuk A N, Olivas P C, Oberbauer S F and Lipson D A 2009 Methane fluxes during the initiation of a large-scale water table manipulation experiment in the Alaskan Arctic tundra: WATER TABLE IMPACTS ON METHANE FLUXES *Glob. Biogeochem. Cycles* **23** GB2013