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Decadal increases in carbon uptake offset by respiratory losses across northern permafrost ecosystems

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Tundra and boreal ecosystems encompass the northern circumpolar permafrost region and are experiencing rapid environmental change with important implications for the global carbon (C) budget. We analysed multi-decadal time series containing 302 annual estimates of carbon dioxide (CO_2) flux across 70 permafrost and non-permafrost ecosystems, and 672 estimates of summer CO_2 flux across 181 ecosystems. We find an increase in the annual CO_2 sink across non-permafrost ecosystems but not permafrost ecosystems, despite similar increases in summer uptake. Thus, recent non-growing-season CO_2 losses have substantially impacted the CO_2 balance of permafrost ecosystems. Furthermore, analysis of interannual variability reveals warmer summers amplify the C cycle (increase productivity and respiration) at putatively nitrogen-limited sites and at sites less reliant on summer precipitation for water use. Our findings suggest that water and nutrient availability will be important predictors of the C-cycle response of these ecosystems to future warming.

High-latitude ecosystems store nearly half the terrestrial C stocks[1]. The northern circumpolar permafrost region, which includes most of the tundra biome and a large fraction of the boreal forest biome[2], represents only 15% of the Earth's soil area but stores approximately one-third (approximately 1,460–1,600 Pg) of global soil organic C[3–5]. Permafrost ecosystems are currently warming three to four times faster than the global mean[6,7], making this critical soil C pool increasingly vulnerable to decomposition. Although increased plant C uptake may offset some portion of soil C losses, the climate impact of CO_2 and methane (CH_4) C emissions from the permafrost region over the next century will likely be comparable to a high-emissions nation[3]. However, these permafrost C losses are not accounted for in the emissions targets set forth in the Paris accord[8]. Evidence from remote sensing and modelling efforts suggest that both gross primary productivity (GPP)[9–13] and ecosystem respiration (R_{eco})[9–12] are increasing across high latitudes; however, the magnitude of this C-cycle amplification and its effect on decadal trends in the net ecosystem exchange (NEE; the relatively small difference between GPP and R_{eco}) of CO_2 with the atmosphere remain highly uncertain[3,5,14–16].

Previous ground-based syntheses of decadal changes in NEE in permafrost ecosystems were limited by a scarcity of year-round (annual) measurements, leading to contradictory conclusions[9,17]. Between 1990 and 2009, annual NEE measurements binned by decade suggested that tundra ecosystems were becoming an increasing CO_2 sink (accumulating ecosystem C over time)[17]. However, a separate analysis of the same time period based on the difference between trends of growing-season and non-growing-season NEE suggested that upland tundra ecosystems were becoming an increasing CO_2 source (losing ecosystem C over time)[9]. Since the publication of these time series studies, the number of sites directly measuring non-growing-season NEE (via eddy covariance or chambers) has more than doubled, capturing critical autumn, winter and springtime dynamics[18]. These more recent ground-based estimates suggest that non-growing-season CO_2 losses are currently higher than process model estimates of growing-season CO_2 uptake and are expected to increase in coming decades[19]. However, estimates of recent decadal NEE trends vary considerably depending on the modelling approach, especially in the permafrost zone[20–22]. Thus, a comprehensive time

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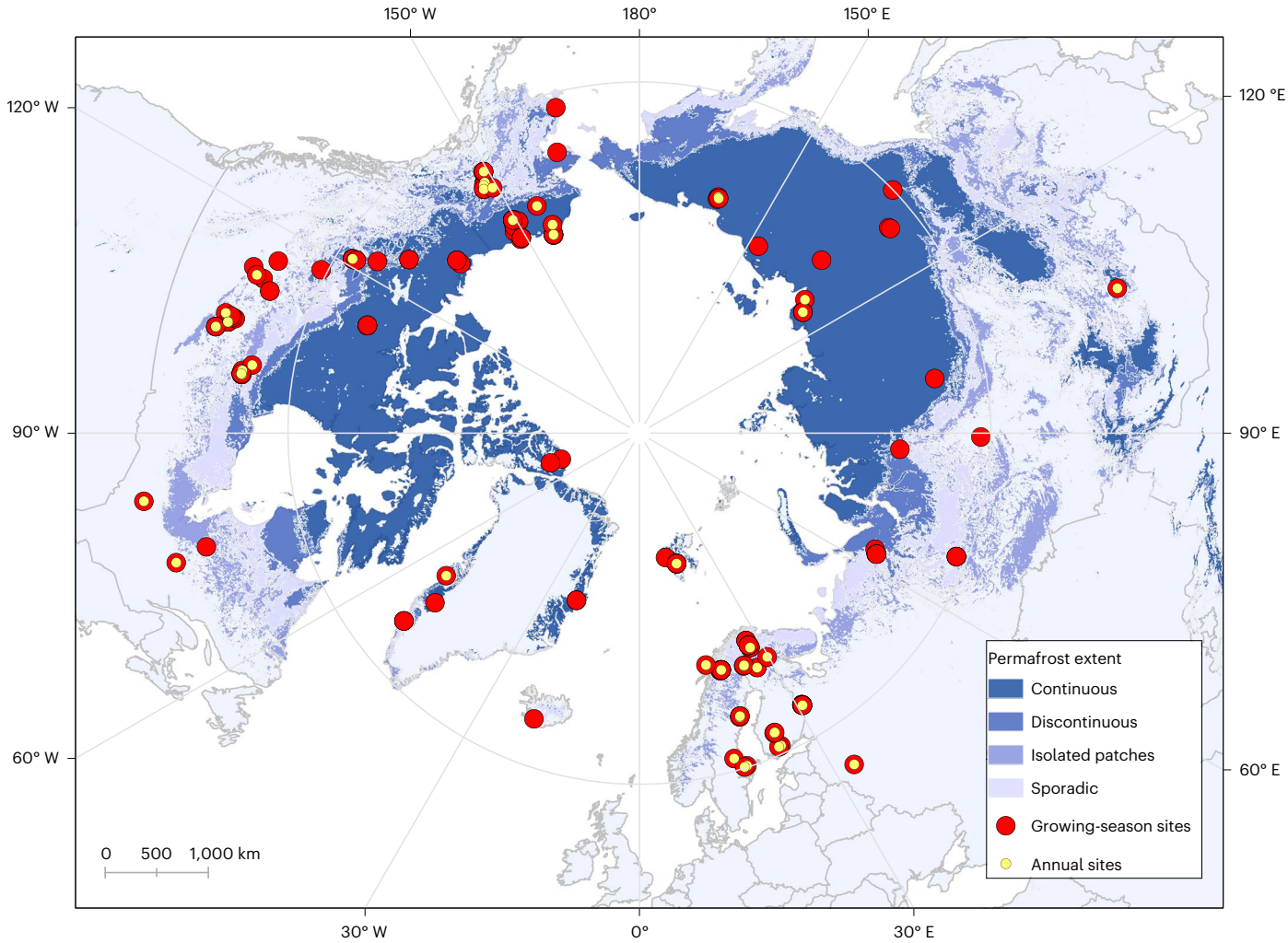

Fig. 1 | Distribution of sites containing summer (June–August) and annual CO_2 flux measurements across tundra and boreal forest ecosystems. Figure reproduced with permission from ref. 51, Elsevier.

series analysis of ground-based, annual measurements is needed to help constrain recent trajectories in the CO_2 balance of ecosystems across this rapidly warming region.

Although climate warming is probably contributing to an amplification of the annual C cycle of northern ecosystems, field-based observations of the C-cycle response to interannual temperature anomalies remain empirically unexplored. Direct temperature limitation of plant and microbial metabolism is well documented globally[23,24] and is exacerbated under high-latitude growing-season conditions[23,25–27]. However, evidence from warming experiments reveals that the responses of GPP and R_{eco} to temperature are rarely of equal magnitude, resulting in variable effects of temperature on NEE across ecosystems[28–31]. This is partially because GPP and R_{eco} are constrained by additional resources that limit plant and microbial processes and mediate their temperature response[32–34]. Water and nitrogen (N) availability are expected to limit both productivity and decomposition in ecosystems as temperature and CO_2 concentrations continue to rise[26,34–38], collectively influencing the NEE response to temperature[34]. Consequently, the magnitude of the GPP and R_{eco} response to temperature is expected to vary with the local resource limitations of plant and microbial communities, resulting in differential impacts on net CO_2 balance across sites[34]. Thus, an empirical understanding of how resource availability dictates the temperature response of NEE across ecosystems will be critical to constraining future projections under warming[34,39–44].

Here we present a comprehensive time series analysis of CO_2 flux observations across ecosystems within the tundra and boreal biomes, including the first analysis of full-year (annual) NEE observations. Our objectives were to (1) describe differences in decadal trends of NEE, GPP and R_{eco} between permafrost and non-permafrost ecosystems at the growing season and annual scale; and (2) determine how ecosystem-level factors such as permafrost presence, biome type, water balance and N availability affect the interannual C-cycle response to temperature across these ecosystems.

Long-term trends in C fluxes

We analysed decadal trends and drivers of interannual variability based on available data containing 6,741 monthly fluxes from 349 sites (1989–2022), 672 summer growing-season fluxes (June, July and August) from 181 sites (1992–2022) and 302 annual fluxes across 70 sites (1995–2022) (Fig. 1 and Supplementary Fig. 1). Most of these data are included in the ABCflux dataset[45], with some additional aggregate estimates from other sites (Methods and Supplementary Tables 1 and 2). To explore decadal trends in aggregate CO_2 fluxes over time, we fit a series of linear mixed-effects models with year as a fixed effect, an autoregressive correlation structure (corCAR1), and random slopes and intercepts for each site[9,46].

During the 92 day summer (June–August), we found strong evidence for increased net CO_2 uptake (decreasing NEE) across the time series. Notably, the observed change in summer NEE was

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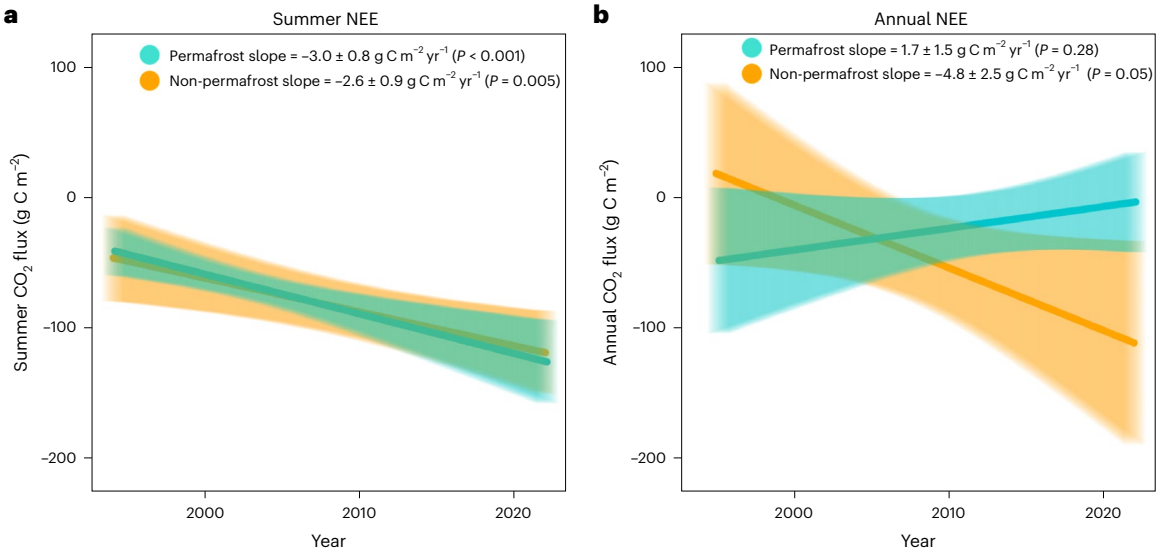

Fig. 2 | Slopes from linear mixed-effects models showing decadal changes in summer and annual NEE across high-latitude ecosystems. Slopes are reported ±s.e., with error bands on the lines representing 95% confidence intervals. **a**, During the summer (June–August), permafrost and non-permafrost ecosystems show similar decreases in NEE (increased land C uptake). **b**, Annual trends diverge, with non-permafrost sites showing a statistically significant decrease in NEE (greater C uptake) and permafrost sites trending towards increasing NEE (greater C losses) through time.

similar between ecosystems with permafrost (−3.0 ± 0.8 g C m^{-2} yr^{-1}, conditional R^2 ($R^2_{cond.}$) = 0.75, P < 0.001; Fig. 2a) and those without (−2.6 ± 0.9 g C m^{-2} yr^{-1}, $R^2_{cond.}$ = 0.79, P = 0.005; Fig. 2a). However, the presence of permafrost led to a strong divergence in the annual (12 month) trends. Across non-permafrost ecosystems, the annual net CO_2 sink increased more than that in the summer alone, with annual NEE decreasing at a rate of −4.8 ± 2.4 g C m^{-2} yr^{-1} ($R^2_{cond.}$ = 0.79, P = 0.05; Fig. 2b). In contrast, we did not detect a statistically significant trend in annual NEE across permafrost ecosystems, although the overall slope was positive (decreasing CO_2 sink, 1.7 ± 1.5 g C m^{-2} yr^{-1}, P = 0.28; Fig. 2b). This positive trend was statistically significant across North American permafrost sites (3.7 ± 1.7 g C m^{-2} yr^{-1}, $R^2_{cond.}$ = 0.46, P < 0.05; Supplementary Table 4), which encompassed 82% of our annual permafrost observations. These diverging annual trends highlight large differences in the trajectories of non-summer (September–May) CO_2 losses, which are offsetting increased summer gains in permafrost ecosystems but not non-permafrost ecosystems.

Decadal trends in both GPP and R_{eco} revealed clear amplification of the annual C cycle across permafrost ecosystems, with non-significant trends observed in the same direction but with greater variability across non-permafrost ecosystems (Fig. 3). In permafrost ecosystems, R_{eco} increased at a rate of 3.1 ± 1.1 g C m^{-2} yr^{-1} ($R^2_{cond.}$ = 0.83, P = 0.005; Fig. 3b) during the summer and at a rate of 6.1 ± 3.2 g C m^{-2} yr^{-1} ($R^2_{cond.}$ = 0.81, P = 0.06; Fig. 3d) annually, suggesting that half the R_{eco} increases in these ecosystems occurred during non-summer months (September–May). Carbon uptake also increased in permafrost ecosystems, with summer GPP decreasing at a rate of −6.8 ± 2.1 g C m^{-2} yr^{-1} (negative scale, decreasing GPP denotes increasing land uptake; $R^2_{cond.}$ = 0.77, P = 0.001; Fig. 3a) and annual GPP decreasing at a similar rate of −6.3 ± 2.9 g C m^{-2} yr^{-1} ($R^2_{cond.}$ = 0.89, P = 0.03; Fig. 3c). Thus, greater increases in productivity than respiration led to an increased summer CO_2 sink in permafrost ecosystems (Fig. 2a), supporting the idea that increasing non-summer R_{eco} is responsible for shifting permafrost systems towards an annual CO_2 source[19,47] (Fig. 2b). Conversely, we found less evidence for a consistent amplification of GPP or R_{eco} across non-permafrost ecosystems (Fig. 3), despite net increases in summer and annual CO_2 uptake (decreasing NEE; Fig. 2). Interestingly, this suggests that rates of GPP are increasing relative to R_{eco} in non-permafrost sites where both fluxes are increasing, but also that the ratio of GPP to R_{eco} may be increasing in sites where both fluxes are declining or remaining relatively stable though time.

An analysis of monthly flux trends revealed further evidence that permafrost ecosystems are experiencing greater amplification of the CO_2 cycle than non-permafrost ecosystems (Fig. 4 and Supplementary Table 6). Generally, NEE during summer months (June–August) trended towards greater CO_2 uptake (negative NEE slopes), with greater CO_2 release (positive NEE slopes) in the autumn and early winter (Fig. 4a). We found much stronger evidence for increased GPP and R_{eco} across permafrost ecosystems (Fig. 4b,c), consistent with the greater amplification we observed in summer and annual fluxes. September GPP gains in permafrost ecosystems suggest a lengthening growing season (Fig. 4b) but this increased late-growing-season CO_2 uptake was accompanied by increased respiratory CO_2 losses (Fig. 4c), leading to little change in September NEE (Fig. 4a). Critically, increases in R_{eco} in permafrost ecosystems extended into early winter (October–December; Fig. 4c), suggesting that deeper summer thaw is enhancing soil decomposition after plants become dormant and offsetting summer GPP gains[19,20,47,48] (Figs. 2 and 4a).

Drivers of temperature effects on summer C flux

To assess how interannual variation in summer air temperature influenced summer CO_2 exchange across sites, we used a meta-regression approach to characterize how environmental factors affect the relationship between temperature and CO_2 fluxes. This analysis was independent of our time series analysis and instead focused directly on environmental controls over the relationship between temperature and C cycling. For each site with ≥5 years of data (Supplementary Fig. 1 and Supplementary Table 7), we calculated standardized slopes describing the relationship between temperature anomaly and CO_2 flux anomaly during the summer (June–August). We then used these temperature–flux slopes as dependent variables in separate variance-weighted regressions, with permafrost presence, biome type and soil C:N ratio as categorical predictors (Methods). To assess the effect of summer water availability across sites, we calculated an index of summer water use as the difference in millimetres between the 30 year mean summer actual evapotranspiration (AET_{summer}) and mean summer annual precipitation (MAP_{summer}) and used it as a predictor variable. Here, sites with positive values are less reliant on precipitation for their summer water

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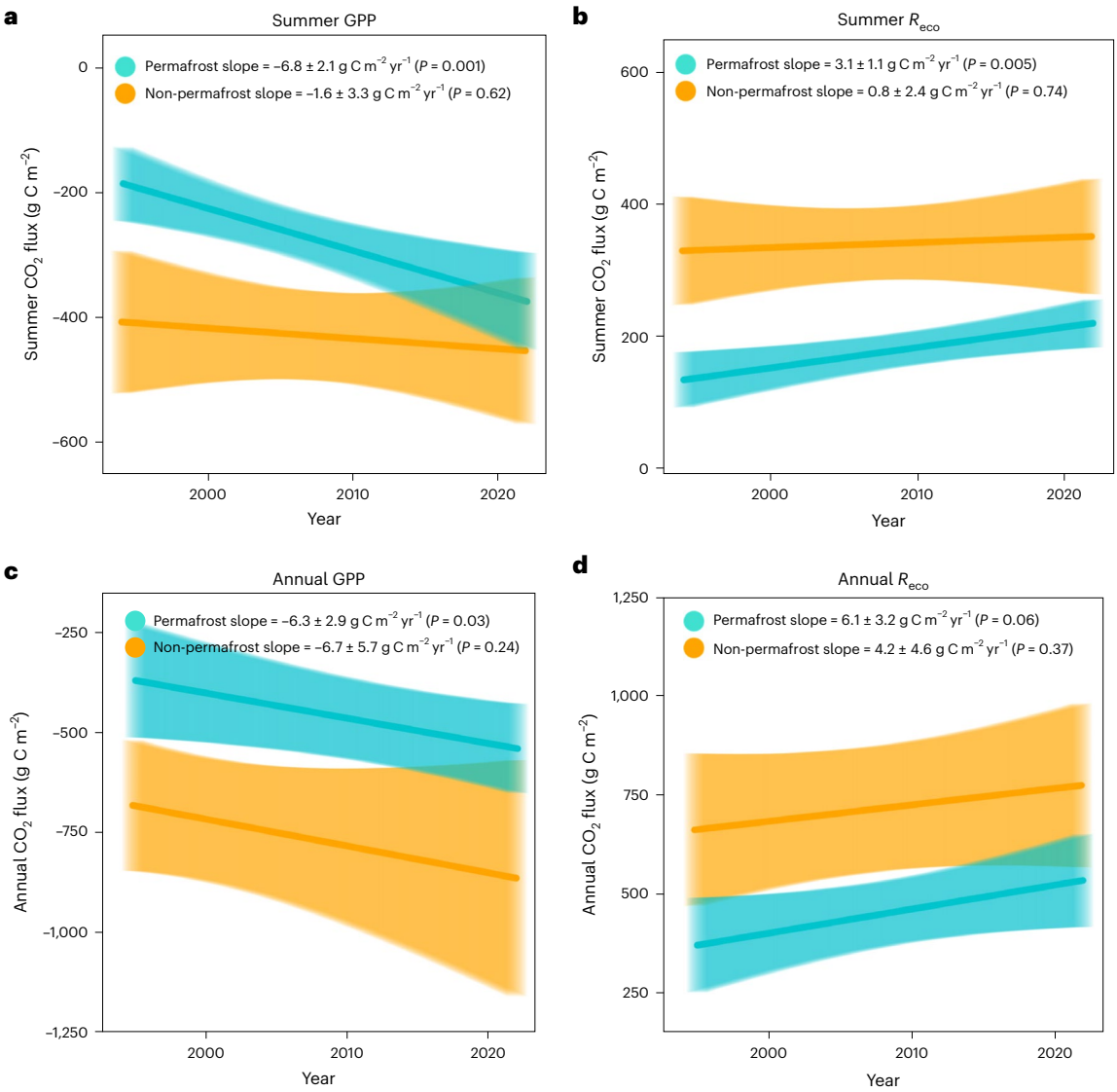

Fig. 3 | Decadal trends of summer annual GPP and R_{eco}. Slopes are reported ±s.e., with error bands on lines representing 95% confidence intervals. **a**,**b**, Rates of summer (June–August) GPP (**a**) and R_{eco} (**b**) increased significantly and at a much greater rate in permafrost sites (green) than non-permafrost sites (orange), highlighting a greater amplification of the C cycle over time in these ecosystems. **c**,**d**, Estimates of annual GPP (**c**) and R_{eco} (**d**) show similar trends but with greater uncertainty due to a lower number of annual observations.

use, probably due to the presence of a high water table and subsidies from snow-melt. Climate variables and soil C:N ratio were derived using the TerraClimate[49] and SoilGrids[50] datasets. Site-based permafrost presence was confirmed by site investigators or based on the TTOP model[51,52] when site-based information was unavailable.

We did not find strong evidence that the temperature response of NEE differed between permafrost and non-permafrost ecosystems ($P = 0.14$) but non-permafrost ecosystems had a more consistently positive relationship between NEE and air temperature anomaly (lower-than-average CO_2 uptake in warmer-than-average summers; $P = 0.08$; Fig. 5a, top). Similarly, we did not find strong evidence that the temperature response of NEE differed by biome ($P = 0.15$; Fig. 5a, middle) but boreal forest ecosystems tended to have a positive relationship between NEE and summer temperatures (decreased summer CO_2 sink in warmer years; $P = 0.10$; Fig. 5a, middle), whereas tundra ecosystems showed both positive and negative relationships. In contrast, the effects of temperature on GPP and R_{eco} were more uniform regardless of permafrost presence or biome. Warmer summers consistently led to both higher plant CO_2 uptake (GPP negative scale, $P = 0.04$ across all sites; Fig. 5b, top and middle) and respiratory CO_2 losses ($P < 0.001$ across all sites; Fig. 5c, top and middle). Thus, warmer years consistently amplified the summer C cycle (GPP and R_{eco}) but the combined effect of this amplification on CO_2 balance (NEE) was more variable across ecosystems.

Although warmer summers tended to have both higher GPP and R_{eco}, soil C:N ratio (calculated on a mass basis) emerged as a dominant constraint over this temperature amplification of the summer C cycle. This finding was present when the C:N ratio was used as a categorical (Fig. 5b,c, bottom) and as a continuous predictor variable (Extended Data Fig. 1 and Methods). In putatively N-poor ecosystems (C:N ratio > 15 in surface soils, below which microbial N-use efficiency has been shown to drop precipitously[53]), warmer growing seasons led to higher GPP (increased CO_2 uptake, GPP negative scale; Fig. 5b, bottom) and R_{eco} (increased CO_2 losses; Fig. 5c, bottom). Interestingly, these relationships were opposite in more N-rich sites, where both GPP and R_{eco} tended to be lower than average during warmer years (Fig. 5b,c, bottom). Although relationships of fluxes with temperature were not consistently negative across all N-rich ecosystems ($P = 0.08$

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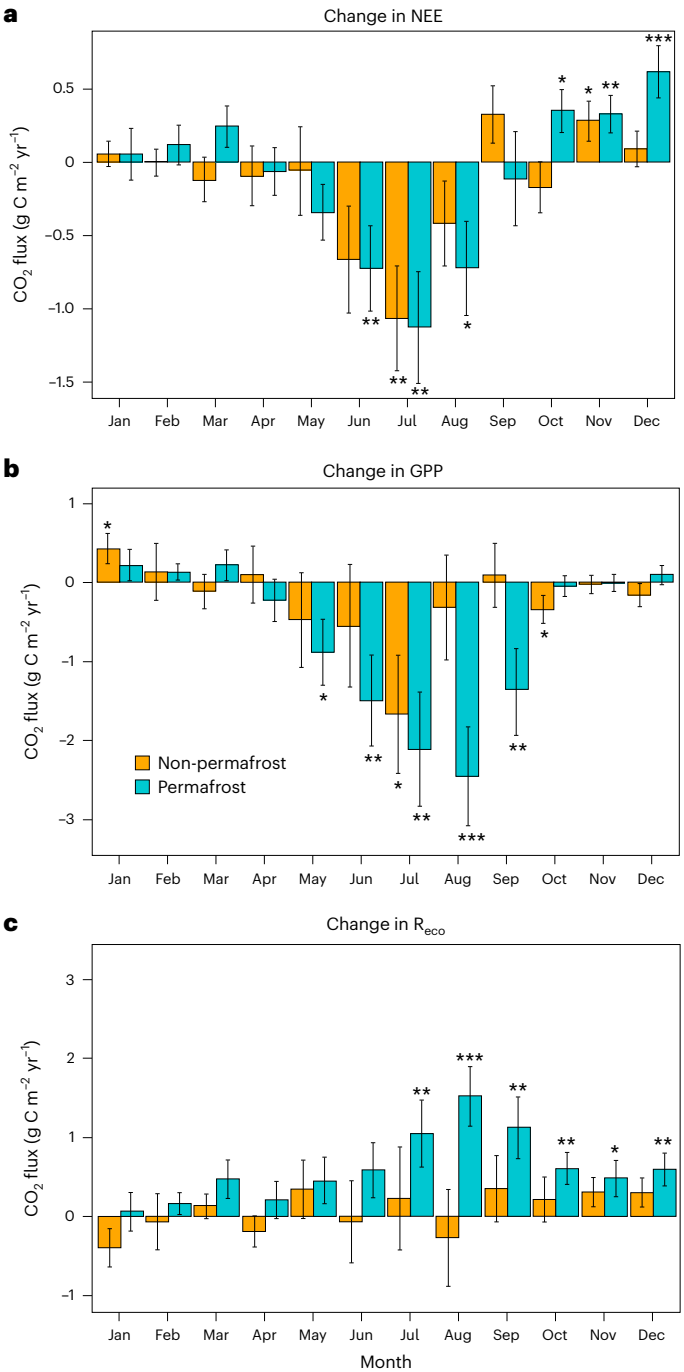

Fig. 4 | Decadal changes in NEE, GPP and R_{eco} by month. a–**c**, The monthly CO_2 flux changes in NEE (**a**), GPP (**b**) and R_{eco} (**c**) are shown. The *y* axis reflects the slope of change over time based on linear mixed-effects models with a random effect for site. Positive slope values indicate increasing NEE over time (decreasing net CO_2 uptake) and negative slope values indicate decreasing NEE over time (increasing net CO_2 uptake). Negative GPP slopes represent increasing productivity (CO_2 uptake), and positive R_{eco} slopes represent increasing respiratory losses to the atmosphere. Error bars reflect the s.e. for each slope. Asterisks denote statistical significance of the slopes not adjusted for multiple comparisons; $^*P \le 0.05$, $^{**}P \le 0.01$, $^{***}P \le 0.001$. Model parameters can be found in Supplementary Table 6.

for GPP, $P = 0.28$ for R_{eco}), they differed strongly from the uniformly positive temperature responses observed across more N-limited ecosystems ($P < 0.001$ for both GPP and R_{eco}). Interestingly, although soil C:N ratio strongly affected the magnitude and direction of the GPP and R_{eco} response to warmer summers, it did not consistently predict the response of net C balance (NEE).

Beyond soil N availability, we found evidence that water availability also controlled the C-cycle response to temperature across ecosystems. In many permafrost ecosystems, water is perched near the soil surface on the thaw front, which prevents downward drainage, providing a source of near-surface summer water beyond rainfall. Ecosystems that regularly used water in excess of summer precipitation (long-term mean AET_{summer} was greater than MAP_{summer}) showed higher-than-average GPP ($R^2 = 0.09$, $P = 0.05$; Fig. 6b) and R_{eco} ($R^2 = 0.16$, $P = 0.008$; Fig. 6c) during warm years. As the mean and interannual variability of summer GPP at most sites (mean = −356 g C m^{-2} yr^{-1}, s.d. = 71 g C m^{-2} yr^{-1}) was greater than R_{eco} (mean= 269 g C m^{-2} yr^{-1}, s.d. = 51 g C m^{-2} yr^{-1}), the similar relative temperature sensitivity of these processes also resulted in some evidence for higher-than-average CO_2 uptake (lower NEE) in warm years at sites that were less reliant on summer precipitation for water use ($R^2 = 0.07$, $P = 0.07$; Fig. 6a). Both MAP_{summer} and AET_{summer} were individually correlated with a positive NEE response to temperature (higher-than-average NEE in warm years; Extended Data Fig. 2) across ecosystems but did not consistently affect GPP or R_{eco}.

Historically, high-latitude ecosystems have served as net annual C sinks for millennia[54–56]. We found strong evidence that net summer CO_2 uptake has increased across these ecosystems in recent decades, with similar trends in permafrost and non-permafrost ecosystems. However, trends in non-summer months led to a strong divergence in the annual CO_2 budgets of these ecosystems (Fig. 2b). In non-permafrost ecosystems, the annual net CO_2 sink increased more than during the summer alone, suggesting that longer growing seasons are increasing annual plant uptake relative to respiration. By contrast, non-summer respiratory losses negated summer gains in permafrost ecosystems, leading to no detectable increase in the annual CO_2 sink (Figs. 2 and 3). Previous ground-based syntheses have suggested that permafrost ecosystems may have represented a net CO_2 source in recent decades[9,19], with non-growing-season CO_2 losses increasing over time[9,19,31], but have been unable to directly detect these changes due to data scarcity. Our analysis of an expanded dataset suggests that permafrost ecosystems may have remained neutral or a small net CO_2 sink in recent decades but provides empirical evidence that increased non-growing-season CO_2 losses have negated increases in summer CO_2 uptake.

Importantly, the site-level observations included in our analysis do not evenly represent the distribution of these ecosystems across high latitudes (Fig. 1), making it important to consider how these results scale globally[18]. Our results regarding permafrost ecosystems are largely driven by North American observations (where the annual sink appears to be decreasing; Supplementary Table 4), whereas the smaller number of annual observations from Eurasian ecosystems (20% of annual NEE observations; Supplementary Table 2) limit the inference regarding past trajectories using data from this region alone. This highlights the urgent need for increased ground-based monitoring of these critical landscapes[18]. By contrast, trends in non-permafrost ecosystems may be more strongly driven by observations from Eurasia[11,21], where trends were more consistent than in North America based on subset analyses (Supplementary Table 4) and both land masses were equally represented (51% North American and 49% Eurasian for annual NEE observations; Supplementary Table 2). The divergent annual NEE trajectories with permafrost presence in our data are largely in line with recent trends produced by satellite-driven, process-based models[21], although they run contrary to those produced by atmospheric inversion models[20]. Cross-validation of our models using a leave-one-out approach (that is, iteratively removing one site at a time and refitting models), and refitting the time series models in a Bayesian framework, suggested that conclusions surrounding changes in NEE were relatively robust but that trends in GPP and R_{eco} were more likely subject to greater biases due to site inclusion (Methods and Supplementary Table 5).

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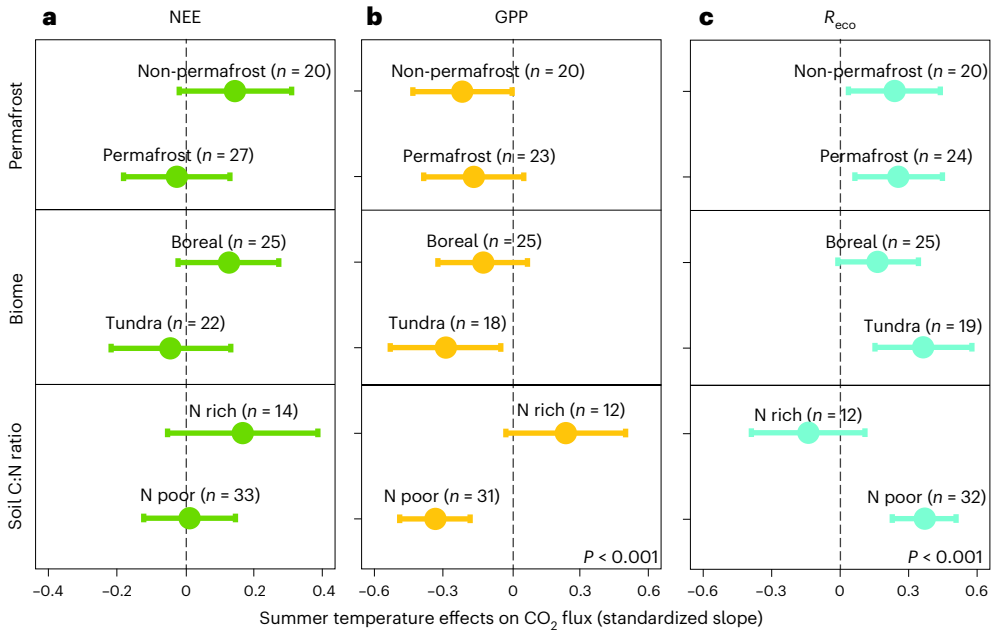

Fig. 5 | Site factors predicting the summer CO_2 flux response to summer air temperature. a–**c**, Results from linear regressions of the effects of ecosystem factors (permafrost presence (top), biome (middle) and soil C:N ratio (bottom)) on the relationship between summer air temperature and summer NEE (**a**), GPP (**b**) and R_{eco} (**c**). Standardized slopes reflect the effect of 1 s.d. (*z*-score) of summer temperature on C flux (also in units of s.d.). Error bars denote 95% confidence intervals, indicating consistent positive or negative relationships when not overlapping with the dashed zero line. Sample sizes (*n* = number of sites) are presented above each bar for each group. On average, both GPP (negative scale; **b**, top) and R_{eco} (**c**, top) increase in warmer years regardless of permafrost presence but markedly less so in N-rich (soil C:N ratio < 15) systems, which have significantly lower rates of both CO_2 uptake and release during warmer years (**b**, bottom; **c**, bottom).

Thus, although this work represents an extensive time series analysis of annual flux measurements from northern ecosystems, it is critical to acknowledge the historical spatial biases present in the dataset.

The interannual NEE trends we observed underscore a rapid amplification of the C cycle in permafrost ecosystems[9–13]. The presence of permafrost contributes to a short window for plant and microbial activity[57], leading to greater sensitivity to global change factors (for example, warming, CO_2 fertilization and nutrient feedbacks). Our time series shows decadal amplification of both summer GPP and R_{eco} across permafrost ecosystems (Figs. 3 and 4), with GPP effects dominating during the summer months and leading to increasing net CO_2 uptake during this time (Fig. 2a). Critically, early winter (October–December) CO_2 losses have also increased markedly in permafrost ecosystems (Fig. 4c), presumably due to warming-induced deepening of the active layer (thawed soil)[58,59], which lengthens the period for microbial decomposition of soil C[60]. Here, increased late-season CO_2 losses offset summer C gains, resulting in little detectable change in the average annual budget across permafrost systems (Fig. 2b), with some indication of a shift towards C neutrality or future net C release. By contrast, decadal trends of increasing GPP and R_{eco} were less consistent (more variable) across non-permafrost ecosystems but their combined changes have resulted in an increased net annual C sink (Fig. 2b).

Summer water use emerged as an important control over the magnitude and direction of the summer C-cycle response to temperature across northern ecosystems[14,61]. Ecosystems that regularly use soil water in excess of summer precipitation (30 year $AET_{summer} > MAP_{summer}$) responded to warmer summers with both higher productivity and respiration, suggesting that plants and microbes may be better able to take advantage of increased temperatures where summertime water subsidies (for example, perched surface water) are more available[29,61,62]. This temperature amplification of GPP and R_{eco} largely cancelled out in these systems, resulting in only a weak trend towards an increased net summer CO_2 sink in warmer years (lower NEE; Fig. 6a). Conversely, sites with higher total MAP_{summer} and AET_{summer} (greater absolute rates of water exchange) showed a significantly reduced summer CO_2 sink (higher NEE) in warm years, despite no consistent effects on the temperature sensitivity of GPP or R_{eco} alone (Supplementary Fig. 2). These higher-precipitation sites were largely non-permafrost landscapes that may lack perched surface water and be more closely tied to timing and availability of summer precipitation, consistent with positive correlations between precipitation and NEE at high latitudes[31]. High-latitude precipitation patterns are expected to change markedly along with temperatures over the next century[63,64]. Our results suggest that the net changes in precipitation versus evapotranspiration, rather than these variables individually, may ultimately determine the GPP and R_{eco} (and together the NEE) response to warmer summer temperatures across these ecosystems. It also highlights C-cycle dynamics in ecosystems that access perched soil water that is likely to change, with access decreasing as permafrost degrades in a warmer world[65].

Our results further point to N limitation as an important control over temperature amplification of the summer C cycle in northern ecosystems, with more N-rich (lower C:N ratio) soils showing a diminished GPP and R_{eco} response to temperature. Soil C:N ratio is the dominant control over the temperature sensitivity of microbial respiration (Q_{10}) globally, with decomposition being more sensitive to temperature in soils with a higher C:N ratio, particularly in permafrost ecosystems[25,66]. This causes N mineralization[67] and productivity[68] to be more temperature sensitive, ultimately leading to a greater temperature response of GPP and R_{eco} in more N-limited soils (Fig. 5b,c, bottom). Conversely, the soil microbial response to temperature is more muted in soils with a lower C:N ratio[25] and plant productivity is more likely to be limited by resources and stressors that are positively, negatively or neutrally related to temperature[61,69–73]. Our findings imply that long-term increases in summer temperatures may lead to an amplification of the C cycle in more N-limited ecosystems. The impacts of warming may be less consistent in more N-rich ecosystems, potentially decelerating the

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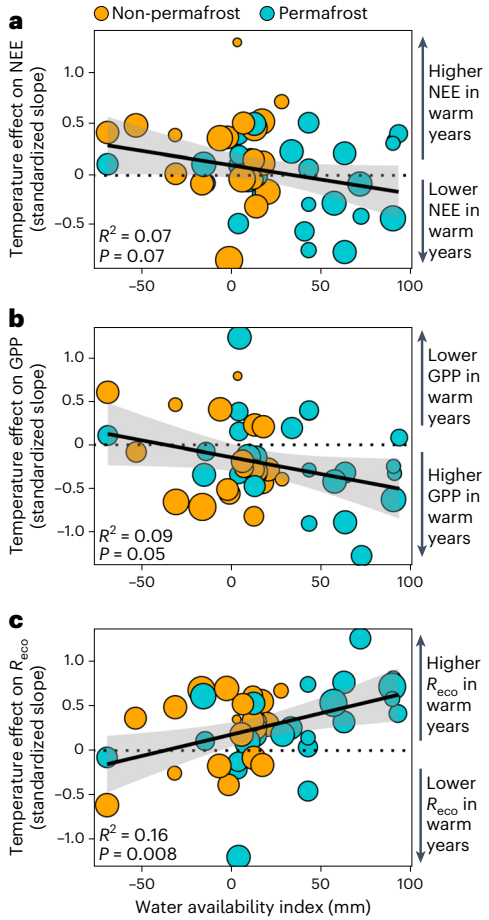

Fig. 6 | Effects of summer water use on summer CO_2 flux response to air temperature. a–**c**, Lines reflect linear regressions of the effects of summer water availability (*x* axis, 30 year mean AET_{summer} minus 30-year MAP_{summer}) on the relationship between summer air temperature and NEE (**a**), GPP (**b**) and R_{eco} (**c**). Standardized slopes reflect the effect of 1 s.d. (*z*-score) of summer temperature on 1 s.d. of summer C flux. Positive *x*-axis values indicate sites where summer water use regularly exceeds precipitation inputs and near-surface soil water may be especially important. Points above the dashed zero line on the *y* axis represent sites where higher-than-average summer temperatures lead to higher-than-average NEE (**a**) and R_{eco} (**c**), or lower-than-average GPP (**b**). Larger points indicate greater confidence in the slope for each site and reflect model weights. Error bands represent 95% confidence intervals.

C cycle in ecosystems where temperature effects are driven by other factors (for example, soil drying and herbivory). Understanding these dynamics will be particularly important in permafrost ecosystems where large (currently unavailable) stocks of N may enter actively cycling N pools with increased thaw[74–77].

In summary, our decadal analysis of annual, ground-based measurements shows significant amplification of the C cycle across permafrost ecosystems. Increased respiration from permafrost soils during the non-growing season is probably causing these ecosystems to become a decreasing CO_2 sink (increasing NEE), despite concurrent increases in summer CO_2 uptake. Conversely, combined changes in GPP and R_{eco} have led to decadal increases in the net CO_2 sink (decreasing NEE) across non-permafrost ecosystems. Critically, temperature increases over the next century will coincide with large regional changes in both precipitation and N availability, particularly in permafrost ecosystems[63,64,74,77]. Our results suggest that although greater N availability may initially increase rates of ecosystem C cycling[78–80], the long-term effects of N enrichment may result in reduced sensitivity of the C cycle (GPP and R_{eco}) to warmer summer temperatures[68,81–83].

Similarly, our results suggest that temperature-induced amplification of summer GPP and R_{eco} will be constrained by water availability, with greater rates of temperature-induced amplification occurring in sites that are less reliant on summer precipitation for water use[61,84]. These findings provide empirical evidence that changing conditions in the permafrost region are affecting the trajectory of annual C dynamics in ecosystems within the tundra and boreal biomes[3,9,15,19] and suggest that local resource availability will constrain the C-cycle response to warming across this region[34,42,61,79].

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-024-02057-4.

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Methods

Data compilation

The majority of the data used in our analysis are published as the ABCflux database, which consists of monthly gap-filled estimates of NEE, GPP and R_{eco}[45]. As the primary objective of this work was to assess long-term trends in annual and summer fluxes, we included published fluxes reported at these timesteps, which were unable to be parsed into monthly timesteps (and therefore not suitable for inclusion in ABCflux). These additional aggregate fluxes were compiled during a working group through the US National Center for Ecological Analysis and Synthesis in 2019. After data cleaning, this resulted in 75 additional summer NEE fluxes across 12 sites, along with 50 and 51 summer fluxes of GPP and R_{eco} across 8 sites. At the annual timestep, this resulted in 29 additional annual NEE fluxes across 4 sites, and 22 annual fluxes of GPP and R_{eco} across 3 sites. Many of these additional aggregate fluxes were included in a recent upscaling study[14]. Finally, more recent monthly observations that were unavailable when ABCflux was published (that is, observations after 30 September 2020) were solicited from site investigators during the Permafrost Carbon Network meeting in December 2021, with data accepted through the end of 2022. This resulted in 275 monthly NEE and GPP (and 299 R_{eco}) estimates not included in ABCflux, with 6 additional ecosystems represented and updated flux estimates for timeseries from 3 sites currently represented in ABCflux.

We calculated summer ecosystem fluxes of NEE, GPP and R_{eco} as the sum of June, July and August for sites with monthly data, without gap-filling (that is, all 3 months were required for inclusion). For summer fluxes incorporated from the literature, we standardized growing-season estimates to 92 days to make them comparable to the summer (June–August) calculated using ABCflux. Similarly, annual fluxes were calculated in ABCflux by summing NEE, GPP and R_{eco} across the 12 month calendar year (that is, January–December). We did not include years with missing months and, in the case of eddy covariance towers, only included annual estimates of GPP and R_{eco} when the site also had a full 12 months of NEE (required for GPP and R_{eco} calculations). The monthly NEE fluxes calculated in the ABCflux database were primarily (79%) measured using the eddy covariance method, with GPP and R_{eco} derived using the night-time partitioning method. ABCflux also includes NEE measured using chamber and diffusion methods (approximately 10–20 chambers per site), which include at least 3 temporal measurements per month for summer months (June–August) and at least 1 temporal replicate during non-summer months. Further details regarding the data coverage, limitations and uncertainties are described in the ABCflux data description[45]. Our final dataset is summarized in Supplementary Tables 1 and 2.

For each site in our analysis, we used the TerraClimate database[49] to provide interannual estimates of summer air temperature (calculated as the 3 month mean of June, July and August) and precipitation and AET (calculated as the sum of June, July and August). We calculated the mean summertime water use for each site as the difference between 30 year mean evapotranspiration and precipitation. Permafrost presence and biome type (tundra or boreal) were reported by investigators or based on literature reports from the site. Sites where permafrost information was unavailable were categorized as permafrost when in the continuous or discontinuous zone based on the Permafrost Extent and Ground Temperature Map[51,52]. Finally, we calculated the soil C:N ratio at each site based on estimates of C and N pools from the SoilGrids 2.0 dataset[50].

Time series analyses of decadal fluxes

An initial Akaike-information-criterion-based assessment of candidate linear mixed-effects models that included time, permafrost, biome and climatic variables (temperature, precipitation and evapotranspiration) revealed the consistent presence of permafrost-by-year interactions across the most parsimonious models (lowest Akaike information criterion). Climate, biome and permafrost presence are inherently correlated across high-latitude ecosystems (the presence of permafrost requires mean annual temperatures <0 °C for a minimum of 2 years) and this dataset was not designed to meaningfully parse these factors. Our primary goal was to assess long-term annual trends in NEE across permafrost ecosystems compared with non-permafrost ecosystems and so we chose a simplified, spatially agnostic approach to detecting change[9]. To test whether C fluxes were increasing through time, we analysed our compiled summer and annual estimates of NEE, GPP and R_{eco} as dependent variables in linear mixed-effects models (fit separately for permafrost and non-permafrost ecosystems), with measurement year as the fixed effect and random slopes and intercepts for each site. We applied an autoregressive variance structure (corCAR1) to all models to account for potential autocorrelation[9]. Model fits were assessed for normality and heteroscedasticity of residuals, with little effect of individual sites driving long-term trends across the dataset (Supplementary Fig. 2). In addition to annual and growing-season changes, we analysed trends in monthly fluxes but were unable to achieve model convergence for many months using our more restrictive model. For consistency, we analysed all monthly trends using a simplified model that included a random intercept (but not slope) for ecosystem and an uncorrelated within-group covariance structure.

Uncertainty and sensitivity analyses of time series models

As the number of sites collecting data has increased since the beginning of our time series, we re-ran our models on a subset of the data to assess the robustness of our findings to temporal biases in data collection. We re-ran the models on the subset of observations from 2003 to present, representing the most recent 20 years of data. This represents 85% and 81% of summer and annual NEE estimates, 87% and 74% of summer and annual GPP, and 85% and 81% of summer and annual R_{eco} estimates, respectively (Supplementary Table 3). Similarly, we subset our data by landmass and re-ran the models separately for North America (including Greenland) and Eurasia (Supplementary Table 4) to assess the effect of broad-scale spatial patterns in data collection on our results. North America (largely Alaska) represents 82% of our annual observations of permafrost NEE (Supplementary Table 2). To further assess the uncertainty in the slope estimates of our full time series models, we refit all models (with an identical random effects and autocorrelation structure) in a Bayesian framework using the brms package in R (Supplementary Table 5). For Bayesian models we assigned the fixed effect parameters from the frequentist model outputs as prior distributions, with relatively uninformative priors for the random effects and covariance parameters (Student's t; degrees of freedom (ν) = 3, location (μ) = 0, scale (σ) = 47) and Lewandowski–Kurowicka–Joe (shape (η) = 1) distributions, respectively), and then ran each time series model 8 separate Markov chain Monte Carlo chains, resulting in 64,000 total samples in the posterior distribution. We further assessed the robustness of the frequentist model findings using leave-one-out cross-validation based on cluster-wise exclusion using the cv package in R[85]. Further descriptions of these analyses accompany the results in Supplementary Tables 3–5. Collectively, these additional analyses point to a greater degree of confidence in NEE time series than in GPP or R_{eco} time series (Supplementary Tables 3–5), perhaps due to the larger sample size for NEE observations (Supplementary Table 2).

Meta-regression of factors influencing summer C flux response to temperature

To assess how ecosystem characteristics affect the summer C-cycle response to temperature, we used a meta-regression approach. For each site in the dataset containing at least 5 years of summer data (June–August, n = 47 for NEE, n = 43 for GPP, n = 44 for R_{eco}; Supplementary Table 6), we calculated standardized slopes for the relationship between summer temperature anomaly (in standard deviations from the 30 year mean) and C flux anomaly (in standard deviations from the interannual mean across available years). We used these

slopes and their associated errors as response variables in a series of variance-weighted regression models (that is, linear models weighted by inverse of site-level standard errors of temperature slopes). Predictor variables included permafrost presence, biome (boreal versus tundra), 30 year mean summer precipitation, 30 year mean AET_{summer}, mean summer water use (evapotranspiration minus precipitation) and soil C:N ratio.

As soil N availability in deeper horizons changes with thaw depth during the summer in permafrost systems, we chose to use the mass-based C:N ratio of surface soil (top 5 cm) as an index of relative plant N limitation across these ecosystems. Unlike climatic factors, which co-vary with ecosystems in this dataset, soil C:N ratio was less consistently related to permafrost or biome type across these sites (Supplementary Table 7). When used as a continuous predictor across ecosystems, we found evidence for soil C:N ratio effects on both GPP and R_{eco} response to temperature (Extended Data Fig. 1). However, the gridded product used to create these soil C:N ratio estimates is subject to considerable uncertainty across sites[50]. Given the relatively small number of observations in our dataset, we chose to bin observations of soil C:N ratio using a threshold of >15 to denote N limitation (Fig. 5). We chose this threshold because it is slightly higher than the average C:N ratio of fungal biomass (approximately 13 on a mass basis[86]), which dominates microbial biomass in high-latitude systems[87], but is still likely a conservative threshold for N limitation as microbial N use efficiency appears to increase with soil C:N ratio up to 20 (ref. 53).

Data availability

Monthly flux data are archived and freely available from the Oak Ridge National Laboratory Distributed Active Archive Center at https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1934. Aggregated fluxes are available with code at Zenodo (https://doi.org/10.5281/zenodo.10987900)[88].

Code availability

Code associated with this work is archived at Zenodo (https://doi.org/10.5281/zenodo.10987900)[88].

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Author contributions

All authors contributed to data collection and curation. C.R.S. conducted the analyses and wrote the first draft of the article with considerable input from E.A.G.S., A.-M.V., S.M.N., B.M.R., M.G. and M. Mauritz All authors contributed to subsequent rounds of article revisions.

Competing interests

The authors declare no competing interests.

Additional information

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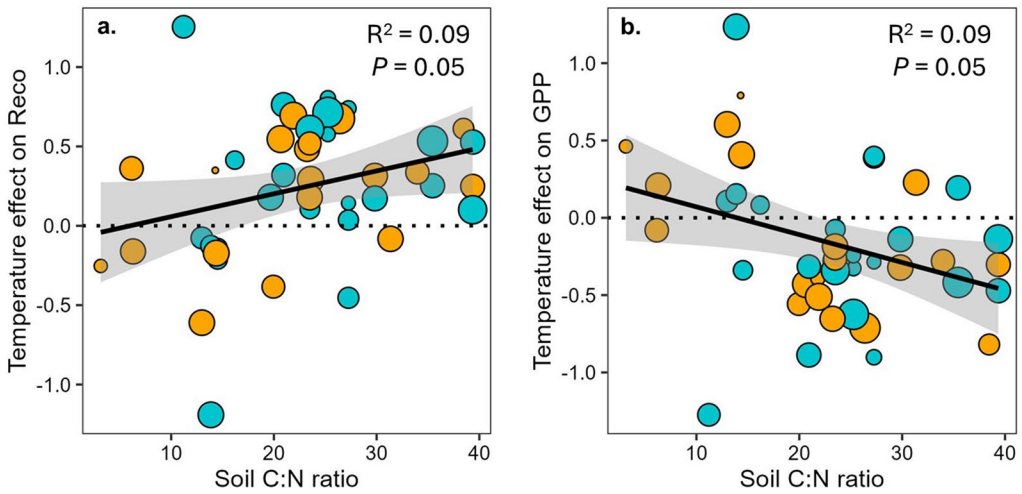

Extended Data Fig. 1 | Soil C:N stoichiometry effects on summer GPP and R_{eco} sensitivity to summer air temperature. Points above the dashed zero line indicate sites where higher than average summer temperatures lead to lower than average GPP (panel a, negative scale, lower plant CO_2 uptake), or higher than average R_{eco} (panel b, positive scale, greater soil CO_2 losses). Larger points indicate greater confidence in the slope for that site and reflect model weights. Orange points denote nonpermafrost sites, while blue points denote permafrost sites. Error bands represent 95% confidence intervals.

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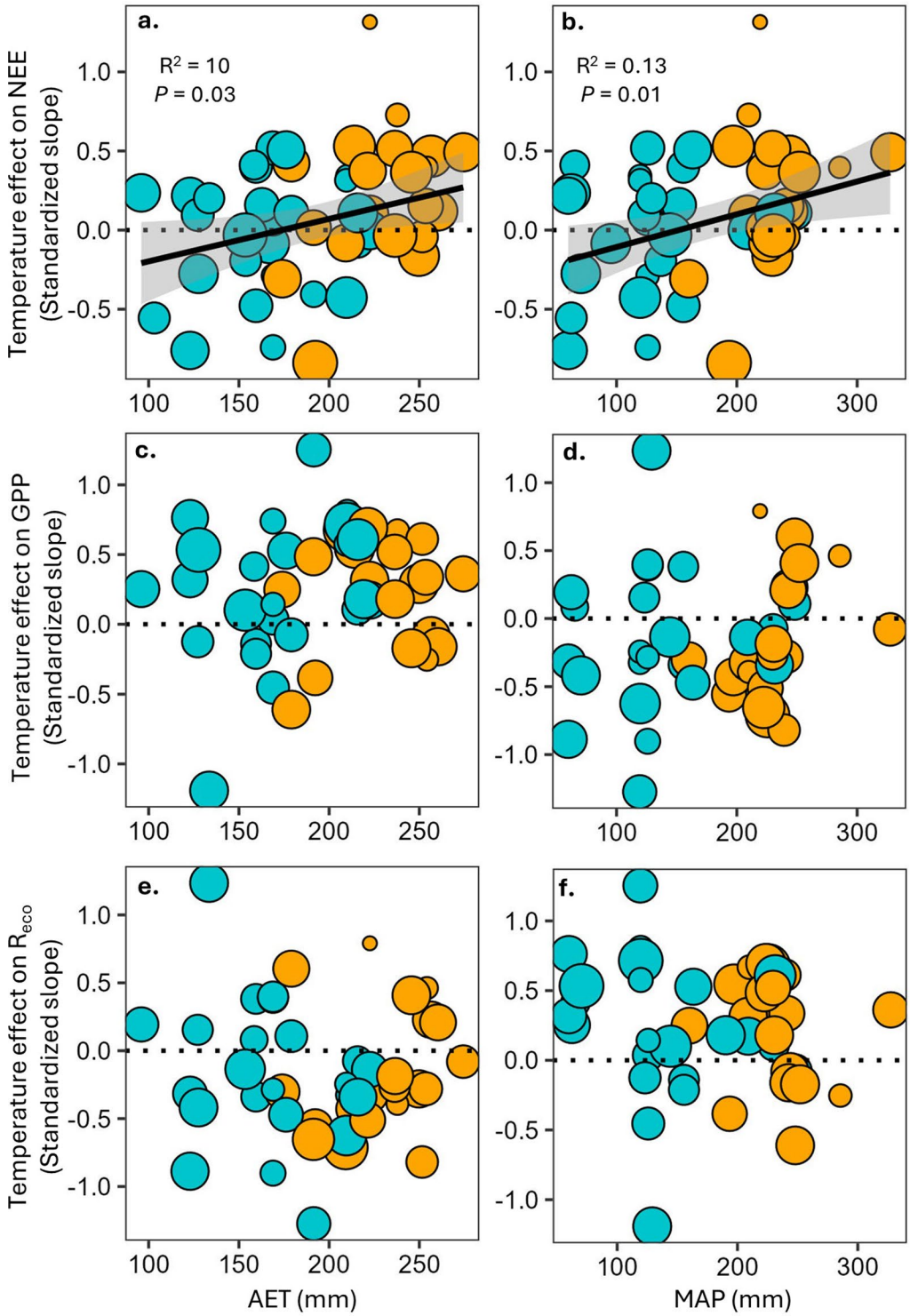

Extended Data Fig. 2 | Sensitivity of summer NEE, GPP, and R_{eco}, to summer air temperature, as a function of mean (30-year) summer precipitation (MAP) and mean summer actual evapotranspiration (AET). Points above the dashed zero line indicate sites where higher than average summer temperatures lead to higher than average NEE (that is lower summer CO_2 uptake; panels a, b) or R_{eco} (panels e, f), and lower than average GPP (panels c, d). Larger points indicate greater confidence in the slope for that site and reflect model weights. Orange points denote nonpermafrost sites, while blue points denote permafrost sites. Error bands represent 95% confidence intervals.