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# Warming effects on arctic tundra biogeochemistry are limited but habitat-dependent: a meta-analysis

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**Citation:** Pold, G., N. Baillargeon, A. Lepe, E. B. Rastetter, and S. A. Sistla. 2021. Warming effects on arctic tundra biogeochemistry are limited but habitat-dependent: a meta-analysis. Ecosphere 12(10):e03777. 10.1002/ecs2.3777

**Abstract.** Arctic tundra consists of diverse habitats that differ in dominant vegetation, soil moisture regimes, and relative importance of organic vs. inorganic nutrient cycling. The Arctic is also the most rapidly warming global area, with winter warming dominating. This warming is expected to have dramatic effects on tundra carbon and nutrient dynamics. We completed a meta-analysis of 166 experimental warming study papers to evaluate the hypotheses that warming changes tundra biogeochemical cycles in a habitat- and seasonally specific manner and that the carbon (C), nitrogen (N), and phosphorus (P) cycles will be differentially accelerated, leading to decoupling of elemental cycles. We found that nutrient availability and plant leaf stoichiometry responses to experimental warming were variable and overall weak, but that both gross primary productivity and the plant C pool tended to increase with growing season warming. The effects of winter warming on C fluxes did not extend into the growing season. Overall, although warming led to more consistent increases in C fluxes compared to N or P fluxes, evidence for decoupling of biogeochemical cycles is weak and any effect appears limited to heath habitats. However, data on many habitats are too sparse to be able to generalize how warming might decouple biogeochemical cycles, and too few year-round warming studies exist to ascertain whether the season under which warming occurs alters how ecosystems respond to warming. Coordinated field campaigns are necessary to more robustly document tundra habitat-specific responses to realistic climate warming scenarios in order to better understand the mechanisms driving this heterogeneity and identify the tundra habitats, communities, and soil pools most susceptible to warming.

**Key words:** Arctic; biogeochemistry; climate change; experimental warming; meta-analysis; stoichiometry; tundra.

**Received** 30 March 2021; accepted 7 April 2021. Corresponding Editor: Debra P. C. Peters.

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## INTRODUCTION

The Arctic is warming at an unprecedented rate (Cohen et al. 2014). Projecting how this rapid warming is affecting tundra carbon (C) cycling and the mechanisms underlying this change is significant because of the vast quantities of soil C protected by low temperatures in the Arctic (Tarnocai et al. 2009). Dozens of arctic experimental warming studies have been established with the objective of projecting how plants, microbes, and biogeochemical processes respond to rapid Arctic warming, providing essential data for ground-truthing high-latitude C cycling models (Sistla et al. 2014). This has led to a flurry of meta-analyses focusing on specific components of the Arctic warming response ranging from primary productivity to nitrogen (N) cycling dynamics (Henry and Molau 1997, Arft et al. 1999, Dormann and Woodin 2002, Walker et al. 2006, Bouskill et al. 2014, Salazar et al. 2020). However, these meta-analyses have neglected to consider how different tundra plant–environment trait combinations ("habitats") or the season of warming perturbation might influence these responses.

The Arctic is a highly seasonal system broadly characterized by a brief summer growing season followed by a sustained cold period that encompasses early snow and cold periods in fall, extremely cold periods of fully frozen active layer (the seasonally thawed soil component), and a spring thaw period (Olsson et al. 2003). However, arctic climate warming is not uniform across seasons, with winter warming exceeding summer warming by at least a factor of four (Bintanja and van der Linden 2013). Summer air warming, however, appears particularly important for arctic greening (Berner et al. 2020), and warming-driven shrub expansion might also indirectly increase wintertime temperatures by trapping more snow and creating a deeper, more insulating snow bed (Loranty and Goetz 2012). On the other hand, reduced or delayed snowpack formation might leave soils more susceptible to rapid freezing in fall (Sistla et al. 2019). Concurrently, summer and winter are dominated by distinct biogeochemical cycling processes (Buckeridge et al. 2013, Sistla and Schimel 2013, McLaren et al. 2017), so the effect of climate change on arctic C fluxes is likely to depend on both the intensity and timing of warming (Sistla et al. 2014).

The majority of C in arctic tundra is stored as soil organic matter (SOM) (Schuur et al. 2018), which decomposes slowly because low temperatures limit microbial activity (Tarnocai et al. 2009). Nonetheless, decomposers remain active even in deeply frozen soils (McMahon et al. 2011), and small changes in temperature can drastically increase soil microbial respiration as soil thaws (Mikan et al. 2002). Increased decomposition rates with warming might also stimulate net depolymerization and/or mineralization of N- and P-rich compounds to plant- and microbially available forms. Similarly, the extension of the seasonally thawed active layer into what was previously permafrost increases the size of the total nutrient pool available to plants (Salmon et al. 2016). Because arctic primary producers are limited by N and/or P in addition to temperature (DeMarco et al. 2014), this increased nutrient availability might stimulate plant growth. However, numerous other factors such as competition with microbial decomposers (Sistla et al. 2014), seasonal leaching (Treat et al. 2016), and changes in plant community composition might modulate this response (Wahren et al. 2005, Borner et al. 2008), making the overall effects of warming on nutrient supply unclear.

Further, warming can "decouple" arctic tundra habitat element cycling if it differentially accelerates the C, N, and P cycles, reducing their interdependence. For instance, reduced N availability relative to C availability could increase microbial N use efficiency (Mooshammer et al. 2014) or lower C use efficiency (Manzoni et al. 2010), which would alter the rate at which litter C is converted to SOM, and organic N is converted to mineral N. Alternatively, in tundra systems where microbes are primarily N-limited but plants are P-limited or N and P co-limited, increased N availability alone might lead to a net loss SOM, but increased N and P availability together might cause increased ecosystem C storage (Street et al. 2018). Therefore, variation in the relative strength of these warming responses or in the identity of limiting nutrients across habitat types might lead to tundra habitat specific decoupling of the C, N, and P cycles.

Although the tundra biome is generically defined by cold temperatures, permafrost, low precipitation, and an absence of trees, it consists of a wide variety of different habitat types that might respond differently to ongoing climate warming. Arctic soils are highly variable in their texture, pH, and organic matter content, which in turn lead to variation in moisture content, soil redox state, and nutrient availability. The vegetation cover is also variable in space, ranging from sparse, such as in polar deserts, to dense, such as in the tussock tundra, and from predominantly non-vascular, such as in lichenous polar semi-deserts, to dominated by vascular plants such as in erect shrub tundra (Walker et al. 2005). Each of these plant communities is broadly associated with different rates of biogeochemical cycling (Shaver and Chapin 1991), and these cycles are likely to be regulated by different factors across habitats (Sistla et al. 2019). For instance, soil redox state, which is significantly affected by warming as permafrost thaws, is an important control on P availability in wet tundra soils with a neutral pH, but not in moist acidic tundra (Emerson et al. 2015, Herndon et al. 2019). Biological relationships that vary across tundra habitats are also likely to strongly influence net response to warming. For example, N fixation might contribute more to the N economies of sparsely vegetated polar semi-desert compared to shrub tundra (Stewart et al. 2011), where N mineralization is high and plant–mycorrhizal interactions favor organic N uptake by plants (Clemmensen et al. 2008). As such, habitat types are likely to be differentially sensitive to global change factors such as warming. However, habitat-specific predictions of biogeochemical responses to climate warming remain sparse.

A growing number of studies that have synthesized plant and soil responses to experimental warming suggest that warming can accelerate rates of biogeochemical cycling and enhance plant growth, but effects are heterogeneous (Dormann and Woodin 2002, Bouskill et al. 2014, Bjorkman et al. 2020, Salazar et al. 2020). This disparity may reflect variations among arctic tundra habitat types and/or depending on the season in which warming treatment is applied. To better understand how habitat and season of warming affects arctic terrestrial ecosystems, we completed a meta-analysis testing the effects of experimental warming on the biomass, C, N, and P contents of soil, plants, and microbes, plant and microbial community structure, and on ecosystem C fluxes across the Arctic.

We hypothesize that warming will accelerate biogeochemical cycling rates asymmetrically, leading to shifts in plant, soil, and microbial stoichiometry in a habitat-specific manner. Specifically, we predict that (1) warming will increase both soil nutrient availability and the nutrient concentrations of plants and soil microbes; (2) microbes will become more nutrient enriched compared to plants (leaves) because of the ability of the community to shift dynamically in the former; (3) deciduous shrubs will become enriched in nutrients compared to sedges because remote sensing data indicate shrubs specifically have increased with summer warming in some areas of the Arctic in recent decades; and (4) inorganic P availability will show stronger habitat specificity in its warming response as compared to N availability, because of the greater relative importance of soil mineralogy and abiotic factors for the P compared to N (Herndon et al. 2019).

## METHODS

### *Literature review*

We used Web of Science and Google Scholar to identify papers under the terms "arctic experimental warming," "high latitude experimental warming," "tundra experimental warming," "arctic warming," "high latitude warming," "arctic experiment warming," "high latitude experiment warming," "tundra experiment warming," and "tundra warming." The search was completed in October 2019 and repeated on 15 April 2020 to identify additional papers. An additional 12 papers known to us to be missing from our search were also included. This led to a total of 377 unique papers. We ultimately ended up with 164 papers in our quantitative analysis by excluding: 86 papers unrelated to tundra, 48 meta-analyses and modeling papers without original field data, 66 papers that did not include variables of interest (defined below), 12 qualitative data only papers, and one paper where data were clearly represented incorrectly.

### *Data collection*

We extracted the mean, standard error (SE), and number of field replicates for the following variables: plant and microbial biomass; microbial biomass C, N, and P (MBC, MBN, and MBP) and their elemental ratios; soil N and P; soil C and organic matter stocks ("SOM stocks"); soil C and organic matter by mass ("mass percent SOM"); soil dissolved organic C (DOC), dissolved organic N (DON), $NH_4^+$, $NO_3^-$, and $PO_4^{3-}$; rate of N and P mineralization; plant part and whole plant community biomass C, N, and P; plant and microbial community structure; extracellular enzyme activity and gas fluxes. C fluxes (i.e., net ecosystem exchange, gross primary productivity, net primary productivity, and soil respiration) included both instantaneous and time-integrated values. C fluxes were separated into measurements taken during (or designed to emulate) some or all of the growing season (snow-free season), the non-growing season, or the annual flux. We only used flux measurements taken during the growing season (typically defined by authors as when the ground was snow-free) in our analysis because of limited data availability outside this period.

Data were extracted from values in tables or public data repositories if available and from figures using DataThief (v. 1.7 January 2015, Tummers 2006) or WebPlotDigitizer (v. 4.2, Marin et al. 2017). We collected data both from studies where only temperature manipulations were applied, and where both warming and long-term nutrient or litter addition were applied. However, we only included unfertilized plot data in our final analysis. We grouped papers by field experiment and removed duplicate data for the same duration of a warming experiment presented in different papers. We considered experiments where different levels or seasons of warming were applied to different plots at the same site to be separate experiments for the purpose of our analysis but included site ID as a random effect in our models.

When error bars were absent or too small to extract from figures, we emailed authors to request raw data. For two papers where the SE was smaller than symbols and we were either unable to contact the authors or the authors denied our request for SE, we conservatively estimated standard error as half the symbol in the corresponding figure. When SE was reported as zero in a table, we set it to 1% of the mean so that effect sizes were defined. When an error was not presented as SE, standard deviation (SD), or variance, we used the methods of (Wan et al. 2014) to estimate standard error. All SE measurements were subsequently converted into SD using the equation $\mathrm{SD} = \mathrm{SE} * \mathrm{sqrt}(n)$ where n is the sample size. We excluded 185 sets of measurements for studies where the SE could not be obtained through any of these avenues. Additional data on the latitude and longitude of sites, mean annual precipitation, temperature, and tundra habitat type were collected from papers when available, or otherwise from papers describing the same experimental site.

We calculated composite variables for several responses. When both total dissolved N and inorganic N were reported, but organic N was not, we subtracted the latter from the former to estimate DON. Likewise, when data were reported at a finer scale than that used in our analysis, we summed the values to the scale of interest. For instance, when coarse roots and rhizomes were reported separately from fine roots or for different depths and we wanted total living belowground biomass (Grogan and Chapin 2000, Rinnan et al. 2007*b*, 2008, Zamin et al. 2014, Ravn et al. 2017), or when organic soil C stock was reported separately from mineral soil C stock (Rinnan et al. 2008, Sistla et al. 2013, Christiansen et al. 2018, Semenchuk et al. 2019). When above and belowground biomass were reported in different units and needed to be added to estimate total biomass (Monteux et al. 2018, Jung et al. 2020), we assumed a bulk density of 1g $\mathrm{cm}^{-3}$ unless otherwise reported. We weighted root mass by depth interval sampled and summed the values across all depths. Errors for all summed values were propagated using the equation $\sqrt[2]{\mathrm{sd}_1^2 + \mathrm{sd}_2^2 + \ldots \mathrm{sd}_n^2}$. If both C and SOM were reported for stocks and/or concentrations of organic matter in soil, we calculated the mean effect size and used this to calculate the cross-study effect size. Finally, if C and/or N and/or *P* values for biomass were reported but the C:N:P ratios were not, we calculated them and used the following formula to estimate standard error: $\sqrt[2]{(x_1)^2 + (x_2)^2}$, where $x$ is sd/mean.

*Habitat classification.—*We first grouped papers into experimental warming studies based on the coordinates, site description, and reported timing of warming treatment initiation. We then used all habitat descriptions for a given warming experiment to generate the best estimate of the habitat, using both vegetation and moisture to drive our decisions. We defined heaths as locations where prostrate shrubs dominate the overstory. Dry heaths (ex. "fellfields" at Abisko) were defined as sites where prostrate shrubs dominated in rockier, drier locations with patchy vegetation, and a patchy or absent organic horizon. As such, dry heaths were differentiated from heaths by coarse-textured substrate and patchy or absent organic soil leading to low soil moisture during summer, rather than necessarily by low mean annual precipitation. Dry heaths were combined with dry tundra sites dominated by non-vascular vegetation for our analysis. Sites dominated by erect, tall deciduous shrubs were classified as shrub tundra. We defined moist tundra sites dominated by herbaceous species as tussock tundra where *Eriophorum* dominated and pooled all other moist tundra sites into a moist non-tussock tundra category that included both acidic and non-acidic sites. Sites where the water table was above the surface of the soil for at least part of the growing season and vegetation was dominated by graminoids were designated as wet sedge sites and were pooled with wet, peat-rich *Sphagnum* dominated bog sites for our analysis. Sometimes our habitat classifications contrasted with those provided by authors of the paper, paralleling inconsistencies in habitat classification within the field (Walker et al. 2005), but our approach enabled the consistent classification within and among sites necessary for our analysis. We recognize that our classification is not universal and have provided the full data set in Data S1 for anyone wishing to complete a re-analysis within their preferred habitat categorization framework.

*Classifying season of warming.*—Data were grouped by timing of warming into four categories based on when the manipulation was applied as described by authors: “growing season” (warming applied during spring/summer, summer, spring/summer/fall, and summer/fall; $n = 92$ experiments), “winter” (fall/winter, winter, and winter/spring; $n = 30$ experiments), year-round warming (sites with both snow fences in winter and greenhouses or open top chambers in summer or spring/summer; $n = 10$ experiments), and incubations (ex situ experiments; $n = 23$ experiments). We considered snow fences to increase snow depth, fleece, heaters, and heating cables to cause winter warming and did not consider sites where open top chambers or greenhouse frames were left in place over winter to receive winter warming, with two exceptions. These two exceptions were where chambers were explicitly used to increase winter warming by accumulating snow at an Abisko bog site (Hicks Pries et al. 2015), and where increased winter snow accumulation was noted using ITEX chambers at the Alexandra Fjord heath site (Marion et al. 1997).

### Data analysis

Plant and microbial community response to warming was analyzed using both quantitative (for alpha diversity) and qualitative (for beta diversity and community composition) metrics. All quantitative data analysis was completed in R version 3.6.1 (R Core Team 2019). We calculated warming effect size for each date that measurements were taken using the escalc() function in the metafor package (Viechtbauer 2010). A value of 0.00001 was added when the mean was zero. Our effect size metric was Glass’s Delta (Glass’s$_\Delta$ = $(x_t - x_c)/\mathrm{sd}_c$; Glass 1976), which uses the standard deviation of the control rather than the pooled standard deviation. This metric is preferable when estimates of treatment and control means have widely different errors associated with them, as was frequently the case for the soil nutrient and plant biomass data. We used the final datapoint collected for each variable in our analysis, except for total biomass in one instance where we were unable to clarify with the authors why the reported values were approximately three times lower than expected for the site. When a variable of interest was represented by multiple measurement times in the final year of the experiment, we calculated the meta-analytical mean of the effect sizes for each individual timepoint. Thus, a single value represented one year at a given warming experiment.

We completed quantitative hypothesis testing using the rma.mv() function in metafor, which fits a linear mixed-effects model to estimate an effect size for all variables where there are data available for two or more studies. We evaluated the effect of warming separately for each aggregated habitat and season of warming. Because some warming studies had multiple levels (i.e., high vs. low) or seasons (i.e., summer only or summer + spring) of warming embedded in them, we built models without random effects and compared them to models where site ID was included as a random effect. Habitat was included as a random effect when looking for a warming effect across all habitat types combined. For variables such as leaf stoichiometric ratio where values were reported for multiple species per site, and the same species might appear across sites, we also used study ID as the random effect. We considered a significant warming effect to occur when the $P$ value (following a $Z$-distribution) was $\leq 0.05$. All data collected for this meta-analysis, scripts, and final aggregated effect sizes used in our analyses (including non-final timepoints) are available in Data S1.

## RESULTS

### *Data type summary*

We collected a total of 5860 data points from 155 experiments, which yielded 3345 data points after aggregating the data by experiment, response variable, and year. A total of 2635 of these could be considered "final" time points, or the last year of data published for a given variable that appeared in our study. The data were not equally distributed across the Arctic, with the majority of measurements coming from Alaska and Scandinavia (Fig. 1). Most measurements were taken in areas likely to have discontinuous permafrost based on their mean annual temperatures (Appendix S1: Fig. S1; Smith and Riseborough 2002). Nine experiments occurred in bioclimate zone B (Northern Arctic Tundra), 31 in C (Middle-southern Arctic Tundra), 19 in D (North-Middle Sub-Arctic Tundra), 73 in E (Southern Sub-Arctic Tundra), and 46 occurred outside Walker et al.'s (2005) classification system. Where degree of warming was reported, experimental warming raised air temperatures by 0–7.96°C (median = 2), and soil temperatures by −1.8 to 7°C (median = 1). There was no relationship between mean annual temperature and degree of soil or air warming accomplished (Pearson correlation $\leq 0.2$ and $P \geq 0.1$ in both instances). Sites with growing season only warming were overrepresented in our data set, accounting for 1644 of the 2655 final data points (versus 554 and 240 data points for winter and year-round warming, respectively) and 89 of the 155 warming experiments ultimately included in our quantitative analysis (versus 30 and 10 for winter and year-round warming). This limited and imbalanced data availability restricted our ability to evaluate how the timing of warming and habitat type influenced experimental warming response.

### *Plant and soil nutrient response*

Warming did not increase soil nutrient availability across habitat types overall. Soil nutrient concentration increased only in heath habitats under growing season or lab-based warming (Fig. 2; Appendix S1: Fig. S2). Rates of N and P net mineralization were not detectably affected by warming (Appendix S1: Fig. S3). Both winter and growing-season warming decreased community-level leaf C:N ratio across all habitats (Fig. 3), and leaf C:N tended to be similarly affected across habitats and timings of warming. Forbs/herbs (primarily from wet sedge/bog sites in this instance; Appendix S1: Fig. S4) had higher C:N ratios under growing season and year-round warming (Fig. 3), while there was no change in the C:N ratio of sedges in the same community. N:P ratio of leaves was unaffected by warming across all plant functional types.

### *Microbial warming response*

Microbial biomass stoichiometry was evaluated in only a few studies ($n = 11$). Growing season warming reduced the C:P ratios for the two heath studies that reported microbial stoichiometry and tended to reduce both the C:P and N:P ratios across all habitat types combined (Appendix S1: Fig. S5). This nutrient enrichment was not underlain by a consistent increase in the mass percent P or decrease in C or N in biomass, and warming did not increase microbial biomass (Fig. 4). Field-based studies of extracellular enzyme activity were mostly limited to tussock tundra and dry tundra/heath habitats; strong changes in total potential activity were not observed (Appendix S1: Fig. S6A), although there was a tendency toward an increase in oxidative (ligninolytic) enzyme activity. Likewise, the ratio of enzyme activities responsible for accessing sources of C, N, and P was overall unaffected by experimental warming (Appendix S1: Fig. S6B). Heath soils incubated under higher temperatures in the lab tended to have increased potential hydrolytic C-degrading extracellular enzyme activity and decreased hydrolytic N-degrading activity (Appendix S1: Fig. S2), which led to higher C:N and C:P extracellular enzyme activities but a lower N:P activity.

### *Ecosystem C stocks and fluxes*

Considering all habitat types together, growing season warming does not detectably impact the mass percent of SOM (Fig. 5A) or its total stock through the whole sampled soil column (Fig. 5B). However, growing season warming increased organic SOM stocks in shrub tundra sites. Winter warming (deepened snow) reduced mineral soil % C and whole sampled soil column C stocks but did not affect C stocks or % C of organic soil.

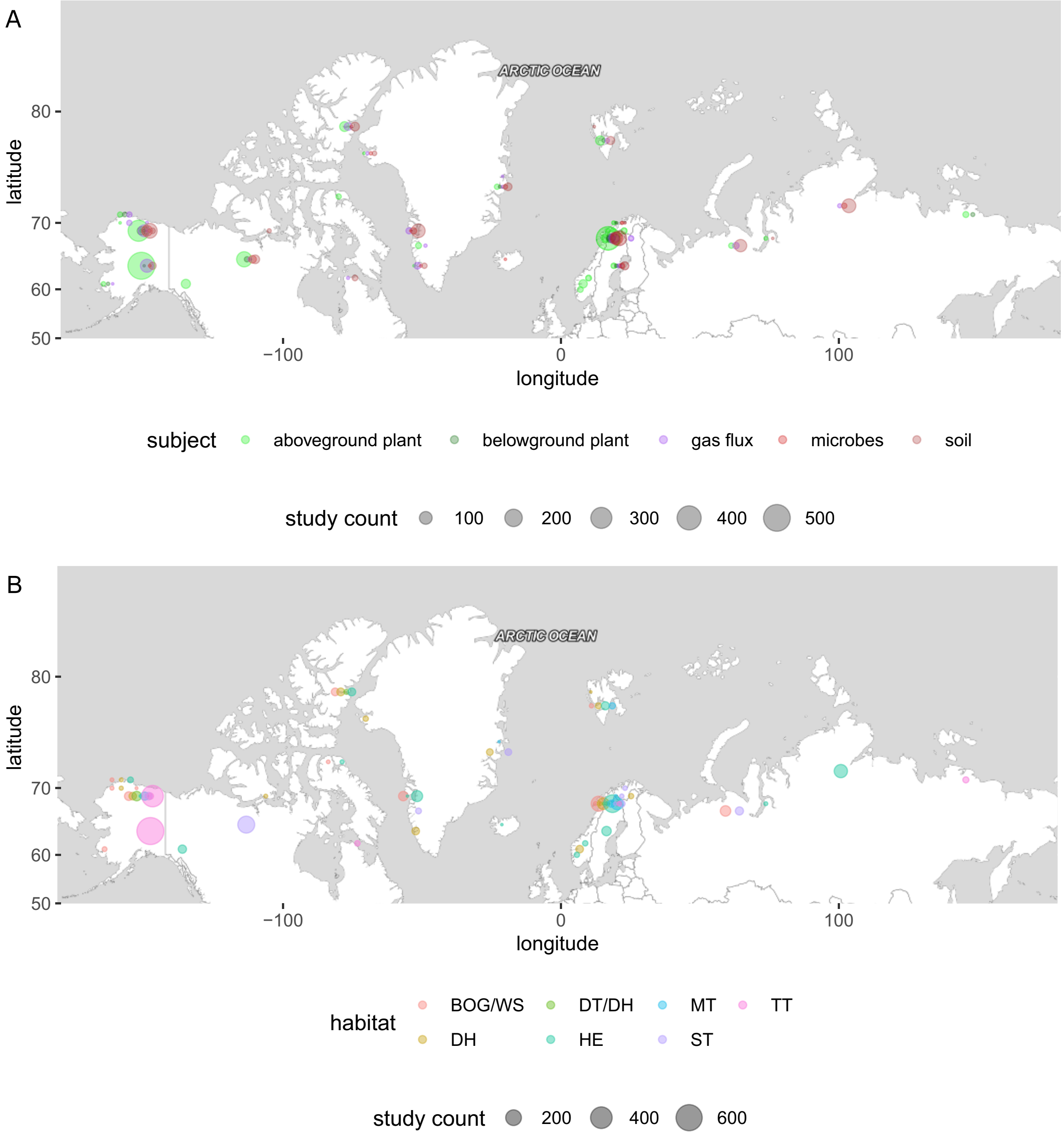

Fig. 1. Map of studies used in this meta-analysis. Each point represents one geographic location (to the nearest degree), where the size represents the number of years of data from that experiment. In (A), the color denotes the component of the ecosystem measured. In (B), the color denotes the habitat type sampled. Points are horizontally jittered for ease of viewing. Habitat-type abbreviations are as follows: TT: tussock tundra; ST: erect shrub tundra; MNTT: moist herbaceous non-tussock tundra; HE: heath; DT/DH: dry tundra/dry heath; BOG/WS: bog/wet sedge.

Experimental growing season warming tended to increase plant biomass; this effect differed between above and belowground biomass across habitat types (Fig. 4; Appendix S1: Fig. S7). These differences are associated with an interaction between habitat type and biomass responses of plant functional types to warming (Appendix S1: Fig. S8). For instance, growing season

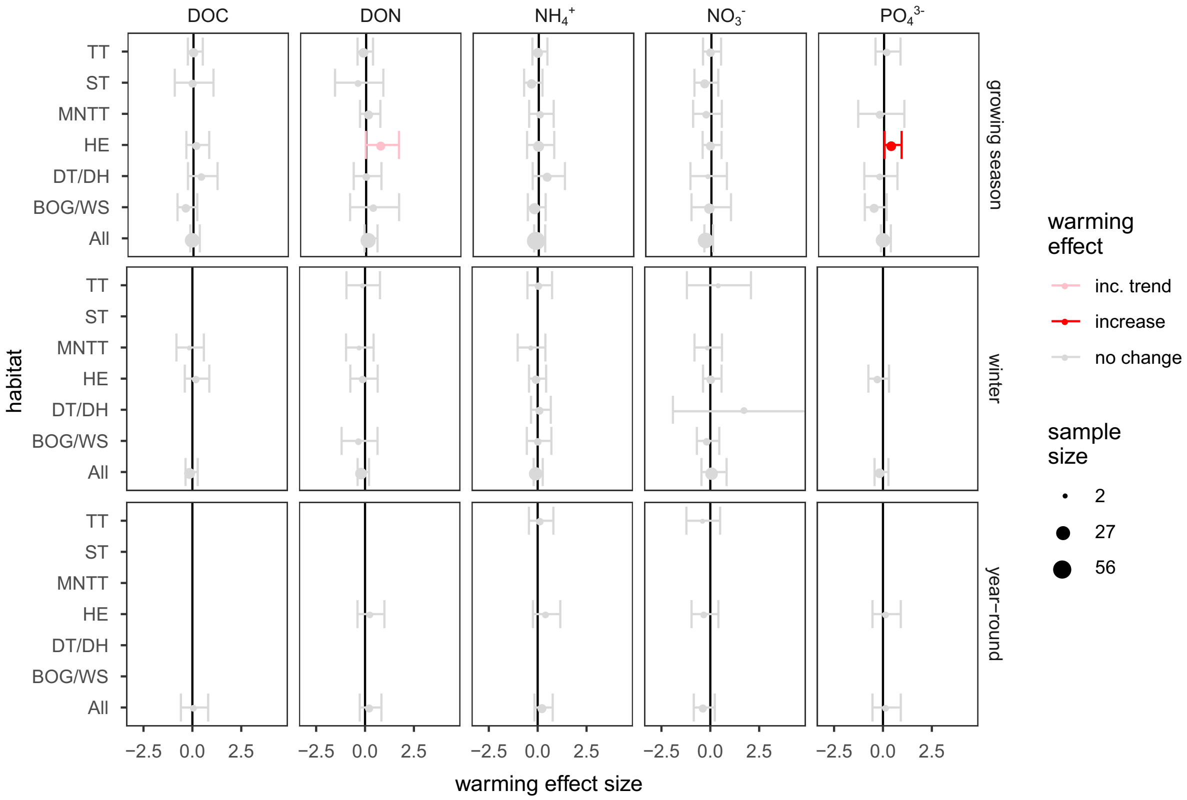

Fig. 2. Warming effect on soluble soil nutrients when warming is applied across different seasons (facet rows) and habitat types (rows). Points are larger when there are more data for a value and are colored according to the $P$ value of the $Z$ statistic (red: $P < 0.05$; pink: $P < 0.1$; gray $P > 0.1$). The error bars denote the upper and lower bounds of the confidence intervals on the meta-analysis mean and extend beyond the plot in some cases. Habitat-type abbreviations are as follows: TT: tussock tundra; ST: erect shrub tundra; MNTT: moist herbaceous non-tussock tundra; HE: heath; DT/DH: dry tundra/dry heath; BOG/WS: bog/wet sedge; all: all habitat types combined.

warming reduced biomass of mosses and lichens at moist non-shrubby tundra sites but tended to increase it in heath and bog/wet sedge sites. Data on plant biomass responses to winter or year-round warming were sparse, but similarly indicated either no warming effect or an increase in biomass (Appendix S1: Fig. S7), except for aboveground heath biomass, which was reduced by winter warming. This reduction in heath biomass under winter warming is attributed to decreases in deciduous shrubs rather than its namesake evergreen heath shrub species (Appendix S1: Fig. S8).

C flux responses to warming were highly variable (Fig. 6). Notably, the effects of winter-only warming on C fluxes did not extend beyond the period of active warming to impact growing season C fluxes; there was insufficient winter flux data to conduct a standalone winter response. Plant gross primary productivity was increased by growing season and year-round warming, while soil respiration and net ecosystem exchange were unaffected by experimental warming overall.

### *Plant and microbial community structure*

Growing season warming reduced fungal diversity (Shannon's H or Rényi's entropy) on average but did not impact bacterial diversity (Appendix S1: Fig. S9). Litter fungal communities from a moist heath habitat (Christiansen et al. 2017), and total (Geml et al. 2015),

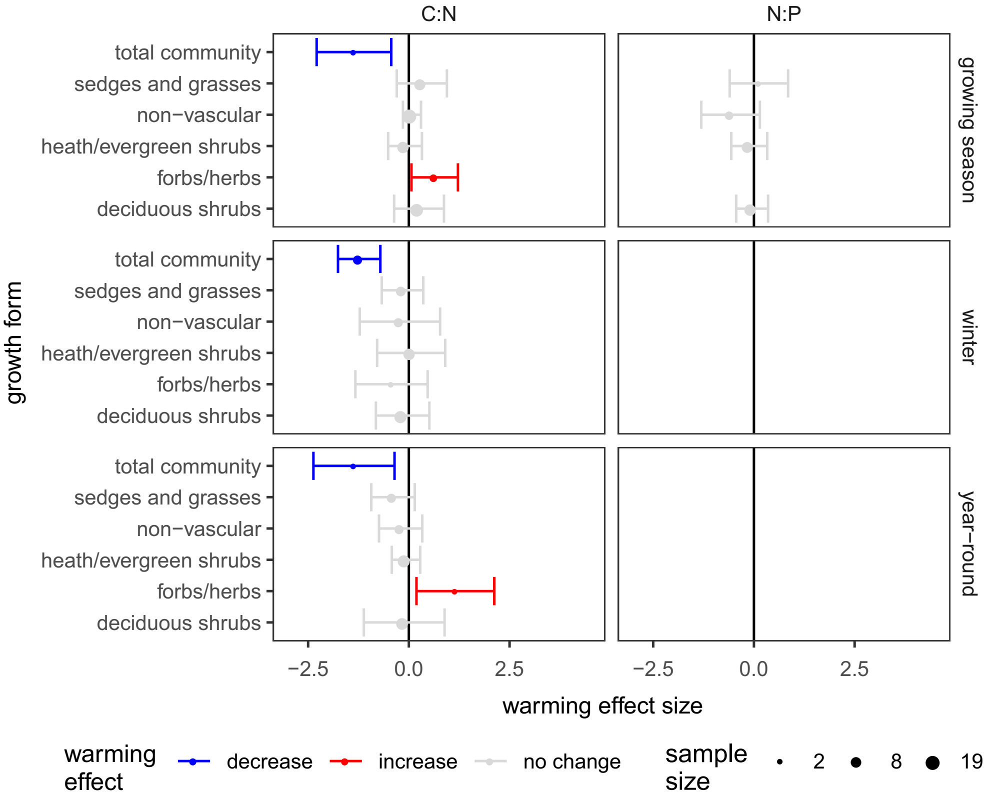

Fig. 3. Warming effect on plant stoichiometry when warming is applied across different seasons and plant functional types. Points are larger when there are more data for a value and are colored according to the direction of the warming effect and $P$ value of the $Z$ statistic (red and blue: $P < 0.05$; gray: $P > 0.1$). The error bars denote the upper and lower bounds of the confidence intervals on the meta-analysis mean. C:N: carbon:nitrogen ratio; N:P nitrogen:phosphorus ratio.

Ascomycete (Semenova et al. 2015), and ectomycorrhizal communities (Morgado et al. 2015) from a tussock tundra habitat responded to experimental warming more strongly than did communities at adjacent dry sites, independent of the season of warming. Notably, there was insufficient data to examine whether microbial diversity responded differently to winter vs. growing season warming.

Experimental warming generally—but not uniformly—led to increasing shrub dominance. In 15 of 51 studies where plant community structure was reported across a range of warming seasons and habitat types, no change in aboveground plant community composition was reported (although six of these experiments were co-located in a bog habitat at Abisko; Keuper et al. 2011). Graminoids (including sedges) increased in relative biomass with winter warming in bog (Monteux et al. 2018) and with growing season warming in heath (Gornall et al. 2009). Shrub functional type was the most responsive to warming, with evergreen (Wahren et al. 2005, Molau 2010, Zamin et al. 2014, Little et al. 2015, Christiansen et al. 2018) and deciduous shrubs (Chapin et al. 1995, Borner et al. 2008, Sorensen et al. 2008, Ylanne et al. 2015) increasing in relative abundance in a variety of habitats.

### *Heterogeneity in effect sizes*

Sample means were heterogeneous among studies, and the $Q$-test for heterogeneity indicated that there are likely additional factors explaining variation in effect sizes not captured in our models (Data S1). This heterogeneity was true even for well-defined ecosystems and

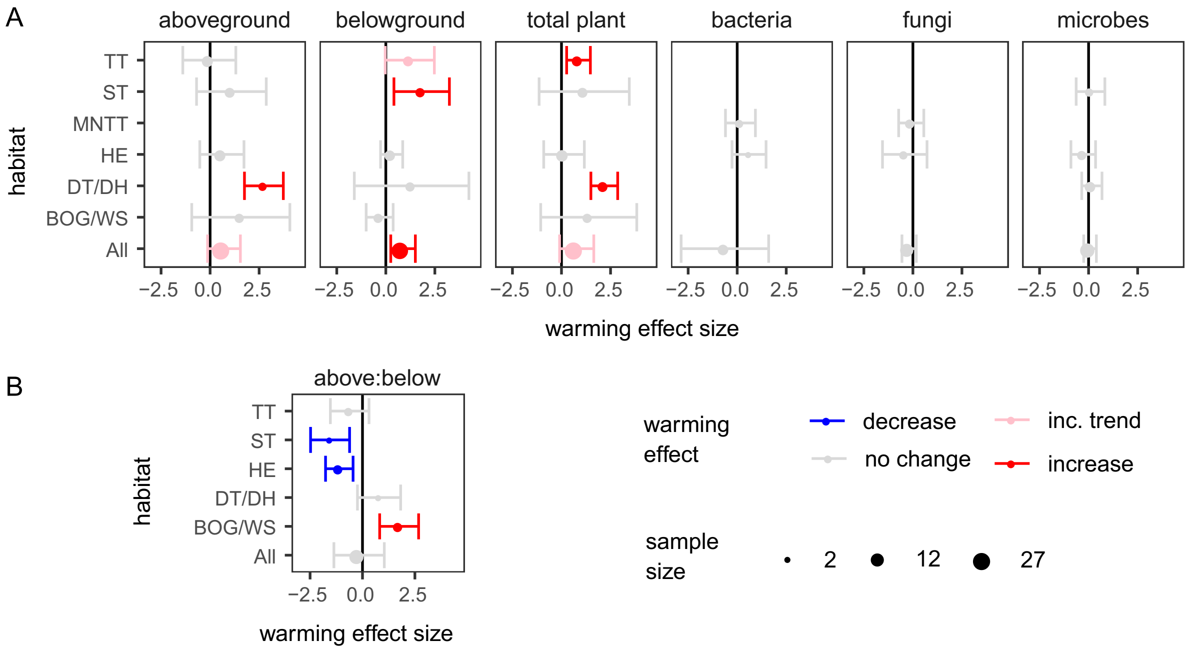

Fig. 4. Warming effect on plant and microbial biomass (A) and above:belowground biomass ratios (B) when warming is applied during the growing season; other seasons are in Appendix S1: Fig. S7. If no community-level biomass was reported but the values for dominant community members were, we summed the biomass for all the plant species presented. Points are larger when there are more data for a value and are colored according to the $P$ value of the $Z$ statistic (red and blue: $P < 0.05$; pink and light blue: $P < 0.1$; gray: $P > 0.1$). The error bars denote the upper and lower bounds of the confidence intervals on the meta-analysis mean. Habitat-type abbreviations are as follows: TT: tussock tundra; ST: erect shrub tundra; MNTT: moist herbaceous non-tussock tundra; HE: heath; DT/DH: dry tundra/dry heath; BOG/WS: bog/wet sedge; All: all habitat types combined.

response variables such as total aboveground plant biomass in tussock tundra but was particularly true for variables known to vary seasonally or spatially and that were measured over a range of frequencies. For example, microbial stoichiometry, soil nutrient pools and fluxes, and C fluxes were measured at a single timepoint in some studies (e.g., Zamin et al. 2014), but at multiple times in others (e.g., Buckeridge and Grogan 2008, Ylanne et al. 2020), such that distinct transitional time points in the active layer thaw process might be captured in different studies.

## DISCUSSION

Despite the importance of nutrient availability in regulating ecosystem response to warming (Sistla et al. 2014, Pearce et al. 2015), and the differences in regulators of nutrient availability across habitat types (Herndon et al. 2019), there is no cohesive understanding of which habitats are likely to be susceptible to element-cycle decoupling under climate change. In this synthesis, we evaluated how the C, N, and P cycles differed in their responses to warming depending on the season of warming and habitat type.

### *Warming does not consistently disrupt biogeochemical cycles*

We found limited support for our hypothesis that warming drives the asymmetric acceleration of biogeochemical cycling in tundra systems. Elemental cycle decoupling can occur if the availability of a nutrient increases compared to another, disrupting co-limitation or co-regulation of nutrient cycles and resulting in limitation by only those factors not stimulated by warming. Warming only changed soil nutrient concentrations under a few scenarios. However, this does not preclude changes in plant nutrient availability because

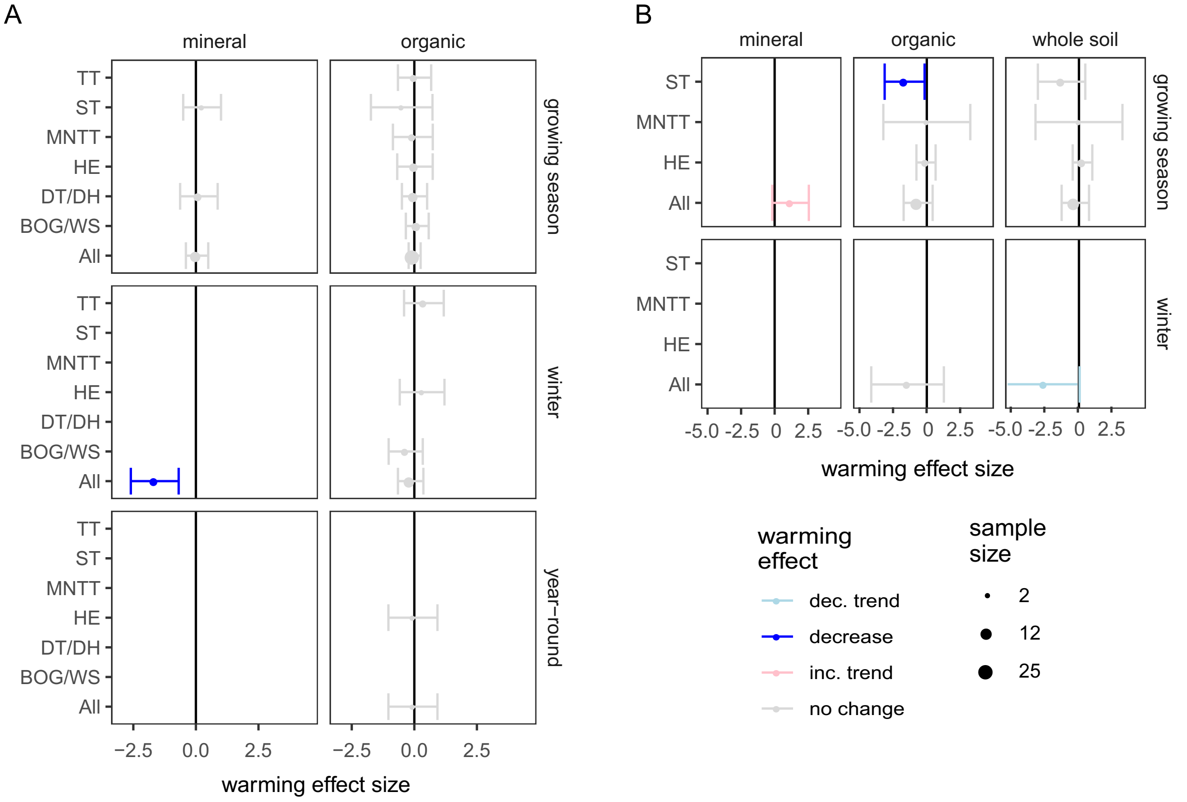

Fig. 5. Warming effect on percent soil C or organic matter (A) or total soil C stock (B) when warming is applied across different seasons and habitat types. Points are larger when there are more data for a value and are colored according to the *P* value of the *Z* statistic (blue: $P < 0.05$; pink and light blue: $P < 0.1$; gray: $P > 0.1$). The error bars denote the upper and lower bounds of the confidence intervals on the meta-analysis mean and are smaller than the symbol size in some cases. Habitat type abbreviations are as follows: TT: tussock tundra; ST: erect shrub tundra; MNTT: moist herbaceous non-tussock tundra; HE: heath; DT/DH: dry tundra/dry heath; BOG/WS: bog/wet sedge; All: all habitat types combined.

active layer soil nutrient concentrations are highly variable over short periods (Buckeridge et al. 2010, McLaren et al. 2017) and soil nutrient sampling does not necessarily coincide with periods of greatest plant demand and/or competitive success with microbes (Jonasson and Chapin 1991). Indeed, microbially available P appears to have become more available relative to C and N under warming because microbial biomass became enriched in P.

Therefore, variable (but occasionally strong) impacts of warming on organism C: nutrient ratio and total biomass detected in this meta-analysis are likely more reliable metrics of how nutrient availability changes with warming than measurements of the pools themselves. Growing season warming decreased the total community leaf C:N but increased forb and herb leaf C:N (Fig. 3). Increased plant nutrient access could be a function of increased soil nutrient concentrations, thaw depth (Salmon et al. 2016), greater investment in the acquisition of nutrients through increased root biomass (Yan et al. 2020), and/or tighter coupling between mineralization and uptake of nutrients through association with a mycorrhizal network (Clemmensen et al. 2006). However, we did not find consistent evidence for any of these mechanisms. One reason may be that this emphasis on leaf stoichiometry neglects how increased investment in high C:N ratio tissues (wood) can allow habitats to store more C without apparent nutrient limitation; unfortunately, complete community biomass stoichiometry responses to warming are

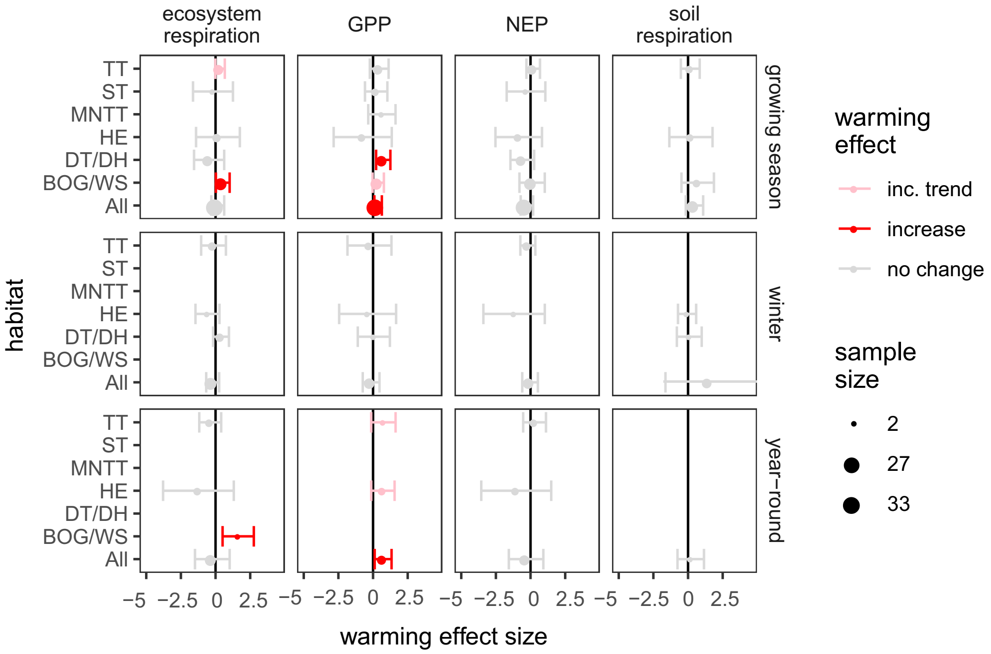

Fig. 6. Effect of warming on C fluxes measured during the growing season. Points are larger when there are more data for a value and are colored according to the *P* value of the *Z* statistic (red and blue: $P < 0.05$; pink: $P < 0.1$; gray: $P > 0.1$). The error bars denote the upper and lower bounds of the confidence intervals on the meta-analysis mean. Habitat-type abbreviations are as follows: TT: tussock tundra; ST: erect shrub tundra; MNTT: moist herbaceous non-tussock tundra; HE: heath; DT/DH: dry tundra/dry heath; BOG/WS: bog/wet sedge; All: all habitat types combined. GPP = gross primary productivity or gross ecosystem productivity, and NEP = net ecosystem productivity.

poorly documented. Thus, identifying the scale at which changes in leaf stoichiometry are indicative of larger changes in ecosystem stoichiometric imbalance, including changes in microbial stoichiometry, is critical to projecting future element balance in a warming Arctic.

Tundra soil microbes are particularly C-limited in winter, causing net N mineralization during this time (McMahon and Schimel 2017). Plants do not photosynthesize substantially above their compensation point under deep snow (Starr and Oberbauer 2003), but microbial respiration increases exponentially as soil temperatures increase (Mikan et al. 2002). This pattern implies that microbes should become more C-limited and mineralize more N under winter warming (Sullivan et al. 2020), providing greater N for plant uptake come spring. However, we did not see evidence of increased N availability during the growing season under winter warming (Fig. 2). This muted response could indicate that that any increased N mineralized over winter is leached before plants can take advantage of it, or that, just like C fluxes, measurements taken during the growing season do not capture these N fluxes. High temporal resolution soil nutrient, plant, and microbial stoichiometric ratio data are required to more specifically understand seasonal differences in how warming does or does not decouple elemental cycles (Buckeridge and Grogan 2010, Buckeridge et al. 2010, McLaren et al. 2017).

### *Variation in warming responses among habitats*

Habitat-specific differences in elemental-cycle decoupling were noted, but these effects did not always reflect detectable changes in the elemental balance of pools. For instance, net N mineralization measured during the growing season was unaffected by warming for any habitat type or season of warming, while growing season ecosystem respiration—a metric of C mineralization—increased with growing season and year-round warming in wet habitats (Fig. 6). Warming-driven increased ecosystem respiration in wet tundra habitat suggests that plants and microbes would compete more strongly for nutrients under warming, yet plants allocated more biomass above- rather than below-ground in this habitat (Fig. 4B). On the other hand, heath habitats showed the strongest (albeit still mixed) evidence for disruption; warming increased dissolved soil phosphate concentrations and decreased the C:P ratio of microbial biomass. Based on lab incubations of heath soils, microbial stoichiometric change and increases in soil nutrient concentrations might be linked to increased C-limitation (Čapek et al. 2015). However, because of the patchiness of data for microbial variables in other habitats, we cannot conclude that heath is more susceptible to element-cycle decoupling under warming, or the mechanisms by which habitats might diverge in their sensitivity.

More data were available for non-stoichiometric variables; although many of the responses we examined were unaffected by experimental warming overall, tundra habitats did also show divergent responses to warming. Notably, plant biomass was reallocated belowground without affecting total biomass in shrub habitats, but primarily allocated aboveground in dry tundra (Fig. 4). The increase in biomass dry tundra/dry heath habitats is largely driven by increases in the absolute or relative dominance of evergreen shrubs (Jonasson et al. 1999, Blok et al. 2015), but greater growth across almost all plant functional types explains the increased biomass in moist heath tundra. The generally positive response of the plant community within dry tundra habitats compared to other habitats is surprising given its generally rocky substrate. One possibility is that the evergreen shrubs that dominate these habitats have high nutrient use efficiency compared to other plant communities (Aerts 1990) and so are less dependent on increasing nutrient supply to take advantage of warmer temperatures. The increased belowground plant biomass (Fig. 4A) and reduced SOM stock (Fig. 5B) responses to warming are less surprising for the shrub tundra, given the rapid expansion of shrubs over much of Alaska in recent decades (Tape et al. 2006, Myers-Smith et al. 2020). Nonetheless, our results confirm that ignoring habitat type in tundra meta-analyses might occlude contrasting warming responses (Bouskill et al. 2014).

### *Larger warming responses are detectable for plants compared to microbes*

Plant community structure responded more frequently to experimental warming than microbial community did, and, consistent with previous meta-analyses, generally tended to become more vascular-dominated overall (Cornelissen et al. 2001, Bjorkman et al. 2020). Changes in microbial communities are predicted to occur primarily once vegetation changes (Rinnan et al. 2007*a*) (which would be expected for plant-associated microbes) and that the rate of community change should correlate with turnover rate (in which microbial communities should be more rapidly responsive to warming than longer-living plants; Dukes et al. 2005). Our synthesis of arctic experimental warming studies does not fully support either hypothesis. Microbial community structure can take years to respond to warming (Feng et al. 2020) and in some cases might not change until the vegetation structure changes (Rinnan et al. 2007*a*, Deslippe et al. 2011, Dahl et al. 2017). However, substantial shifts in the composition and functional gene content of the microbial community might occur much more rapidly in deeper soils or at the permafrost thaw front (Xue et al. 2016, Monteux et al. 2018, Johnston et al. 2019) compared to surface soils where warming has yet to fundamentally alter the soil environment (Jung et al. 2020). In either case, microbial community structure measurements were generally taken following a longer duration of warming than were plant community measurements (median 11 yr vs. 8; range 0–21 and 0–25 yr), indicating that the difference in responsiveness does not reflect prematurely sampling microbial community structure. Only two papers specifically assessed plant-associated microbial community structure (Deslippe et al. 2011, Morgado et al. 2015); in both cases, this sampling occurred after the host plant community had been observed to change, making it challenging to assess whether bulk and host-associated microbial communities respond to experimental warming on a similar timeframe.

Microbial community biomass also did not respond to warming to the degree plant communities did. Increased temperatures might cause different members of the microbial community to grow more or less efficiently (Pold et al. 2020), or to turn over more rapidly (Hagerty et al. 2014, Walker et al. 2018), potentially allowing the overall microbial community biomass and respiration to remain unchanged despite the warmer temperatures. If this were the case, then the majority of increases in rates of ecosystem C fluxes under warming (Fig. 6) would be attributable to plants rather than microbes, matching the observation that GPP responded more uniformly to warming than did microbially associated processes.

Arctic microbial responses to warming might also be muted by variation in the assessment and reporting of soil microbial biomass, in terms of both the numerator (ex. chloroform-labile microbial biomass C vs. total lipid P) and the denominator (ex. $g^{-1}$ soil vs. $g^{-1}$ SOM vs. $m^{-2}$). Changes in SOM per gram of soil and of bulk density might further act to occlude a warming response, as might changes in microbial community structure because the fraction of the total microbial biomass C extracted by the method varies according to the composition and physiological status of the community (Jenkinson 1976).

### *Soil organic matter is not uniformly lost*

Soil organic matter did not change overall in response to growing season warming (Fig. 5). Growing season warming increased mineral C stocks in all three studies where stocks were reported separately for this horizon (across heath, shrub, and tussock tundra habitats; Sistla et al. 2013, DeMarco et al. 2014, Ylanne et al. 2015), indicating that at least in some instances loss of OM from the organic horizon might represent differences in how soil horizons are sampled. One purely technical explanation is that warming increases active layer depth (Sistla et al. 2013) and enables a greater depth of soil to be sampled. However, none of these studies included a deeper sampling depth in their SOM stock calculations. Instead, SOM might have been translocated from organic soil into deeper layers through cryoturbation (Chang et al. 2017), greater plant inputs and/or mycorrhizal biomass at depth (Blume-Werry et al. 2019), and/or DOC leaching, causing a homogenization of the C contents across horizons. This finding is consistent with the hypothesis that organic-rich soils could be particularly susceptible to C loss (Crowther et al. 2016).

Our findings demonstrate the importance of simultaneously considering the size of the C stock across the entire active layer, rather than fixed depth sampling or separated by horizons, while acknowledging that different biogeochemical processes are likely to regulate C stocks at different depths (Hicks Pries et al. 2018). Nonetheless, sampling method variability, the relatively low flux to stock ratio of the SOM pool, and high spatial heterogeneity in arctic soil C stocks challenge the ability to detect changes in its size, even with substantial changes in the rates of inputs and/or outputs.

### *Knowledge gaps*

Experimental warming studies are concentrated in sites with growing season warming, even though winter temperatures are increasing faster than summer temperatures (Larsen et al. 2014, Sullivan et al. 2020). A marked paucity of data on the effects of year-round or winter-only warming for a number of biological variables and highly variable temporal scales of assaying response variables limits our ability to infer whether key biogeochemical processes are particularly sensitive to warming in one season or another. In addition, experimental warming is generally small compared to what has already occurred and is expected to occur with climate change (Larsen et al. 2014, Sullivan et al. 2020), particularly for winter warming. Increasing frequency and intensity of extreme climatic events such as fire and midwinter thaw events in northern latitudes (Larsen et al. 2014) are also expected to have a disproportionate impact on biogeochemical cycling. However, these extreme events were considered in only a handful of studies here (Bokhorst et al. 2008, 2010, Beyens et al. 2009). Finally, the coldest and highest Arctic sites are absent from our warming meta-analysis, despite a reasonable density of biogeochemistry observations being made under ambient conditions in this region (Virkkala et al. 2019). Additional focus should be paid to the high Arctic, non-growing season warming responses, and spatial and temporal scales that better capture the habitat and biotic variation characteristic of the Arctic.

## CONCLUSION

Decoupling of elemental cycles is a rarely considered but likely important consequence of climate change (Dijkstra et al. 2012, Mooshammer et al. 2017). Experimental warming rapidly accelerates C cycling—particularly photosynthesis—but has much more mixed impacts on nutrient concentrations, foliage, and microbial stoichiometry. Our synthesis indicates that arctic plant and soil systems likely respond differently to warming in a habitat-specific manner, with the plant response being dominated by shifts in community structure, and the microbial response through changes in community stoichiometry, which could ultimately alter the timing and competition between plants and microbes for nutrient uptake variably across tundra habitats. These findings highlight the need to link temporally robust, intensively studied Arctic systems (e.g., studies set at as major field sites) with spatially extensive, but lower-intensity measurements (e.g., ITEX, satellites) to test hypothesized mechanisms accounting for divergence in element cycling responses to warming across biological systems and habitats.

## ACKNOWLEDGMENTS

The authors wish to acknowledge Kate Buckeridge, Bo Elberling, Stef Bokhorst, Ryan Choi, and Carly Phillips for sharing data required for this analysis, and all authors who posted their raw data in public repositories. Thank you to Michael Johnson and the rest of the NSURP team for organizing the summer program, and to Casey Gibson for discussing statistics. Funding for this project was provided by NSF Signals in the Soil grant number 1841610 to SAS and ER. SAS and ER conceived of and acquired funding for the project. NB completed the literature search. NB and GP extracted and quality-controlled data from papers. SAS supervised data collection and interpretation. GP and SAS developed data analysis plan. GP and AL completed the data analysis. GP and SAS drafted paper. All authors contributed to editing and revising the manuscript.

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## DATA AVAILABILITY

Data and scripts are available in Data S1 and from Figshare: https://figshare.com/s/c8c2eed55ea775901ba4

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3777/full