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RESEARCH ARTICLE

Projected near-future flooding and warming increase graminoid biomass in a high-latitude coastal wetland

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Abstract

1. With rapid climate warming, some coastal high-latitude ecosystems are experiencing more frequent tidal floods. Yet little is known about tundra plant-community responses to flooding, and whether Arctic warming may modulate such responses.
2. In a 2-year, full-factorial field experiment in coastal tundra wetlands of the Yukon-Kuskokwim (Y-K) Delta (western Alaska), we simulated periodic tidal flood events at two severities under both ambient and warmed summer conditions and measured above-ground plant-community responses. Low-severity flooding represented overbank flooding 1 day per month, which is consistent with projections in the next 5 years. High-severity flooding represented a more impactful flooding regime (three consecutive days per month) that is projected to occur in the next 10 years. Our warming treatment (+1°C) also represented a change projected in the next 10 years.
3. Regardless of temperature, high-severity flooding increased graminoid biomass by >45%, in turn increasing live plant-community biomass by >18%. Low-severity flooding had similar, though weaker, effects. Flooding had overall negative effects on both forb and shrub biomass, though shrub responses were weaker. Only during the second summer, warming increased graminoid biomass by 20% and tended to increase shrub biomass, regardless of flooding. Concurrently, warming enhanced standing-dead graminoid biomass by 20%, while high-severity flooding decreased it by 15%. Therefore, wet tundra that was both flooded and warmed had the greatest proportion of graminoids and total live biomass, but standing-dead biomass comparable to that of unmanipulated wet tundra.
4. *Synthesis*. While our manipulations simulated flooding and warming regimes expected in the wetlands of the Y-K Delta over the same, near-future (5-to-10 years) time frame, flooding had stronger effects than warming. What is striking is the rate at which graminoid increases occurred, becoming apparent after only two monthly flood events in the first experimental year. Flooding-induced decreases in standing-dead biomass suggests that the incorporation of dead plant material into the litter layer might be facilitated by tidal floods. These rapid increases in

plant biomass and potentially biomass turnover, especially of graminoids, which are characterized by high-quality litter, may have major implications for carbon and nutrient cycling of more frequently flooded coastal ecosystems in a warmer Arctic.

KEYWORDS
Arctic tundra, climate change, open-top chamber (OTC), plant functional group (PFG), roots, tidal floods, Yukon-Kuskokwim Delta (Alaska)

1 | INTRODUCTION

During the last four decades, coastal high-latitude regions have been experiencing dramatic effects of climate change (IPCC, 2021). Not only has the Arctic warmed approximately four times faster than the rest of the planet, or at a rate of 0.73°C decade^{-1} (Rantanen et al., 2022), but its coastal areas have been threatened by altered flooding regimes (Irrgang et al., 2022). Melting sea- and land-ice and, therefore, relative sea-level rise in tandem with land subsidence (Edwards et al., 2021; Nicholls et al., 2021), increased storminess and associated frequency of storm surges (Sepp & Jaagus, 2011; Vermaire et al., 2013), and the interaction among these forces (IPCC, 2021; Vermaire et al., 2013) are already causing low-lying areas—especially tundra wetlands found in coastal deltaic plains—to experience more frequent tidal floods (IPCC, 2021; Irrgang et al., 2022). Yet to what extent flooding is altering these wetlands and how these alterations compare with the relatively well-studied modifications promoted by elevated temperatures is virtually unknown.

As the Arctic warms, tundra ecosystems are responding through increased plant productivity and biomass (Berner et al., 2020) and changes in community composition (Bjorkman et al., 2020). Some of the most well-documented consequences of higher temperatures include the expansion of shrubs (Mekonnen et al., 2021) and graminoids (Schaefer, 2023), with the predominant trend being area- and context-dependent (Elmendorf et al., 2012). Specifically, shrub expansion predominates in warmer, more productive areas of the sub- and low-Arctic, and notably in wetter habitats. Accordingly, increased shrub abundance and productivity have been observed in relatively productive, fast-warming coastal and near-coastal tundra regions (Berner et al., 2020; Frost et al., 2021). Experimental evidence from a coastal high-latitude wetland in western Alaska also indicates that higher temperatures may be causing a transition from graminoid- to shrub-dominated wetlands (Carlson et al., 2018). Yet, how these warming effects will play out under altered flooding regimes remains to be addressed.

Studies performed in low-latitude wetlands, as well as in riparian plant communities, clearly suggest that more frequent flood events may also have large effects on coastal high-latitude ecosystems. Flooding can influence plant communities through both direct, physical effects and indirect effects mediated by modifications in the abiotic and biotic environments. For example, by depositing sediments on plants (Lowe et al., 2010) and mechanically disturbing the vegetation (Fischer et al., 2021), flooding can directly reduce plant growth, though taller and stiffer plants may be generally less affected (Hanley et al., 2020). Complementarily, by increasing soil nutrient availability (Garssen et al., 2017; Wright et al., 2015) and favouring a small number of plant species often found in regularly flooded areas, including graminoids (Campbell et al., 2016; Insausti et al., 1999), flooding can increase biomass and decrease species diversity. Therefore, one might expect more frequent tidal floods in high-latitude wetlands of coastal deltaic systems to also promote graminoid abundance at the expenses of less flooding-tolerant plants, including shrubs and forbs. As the relative abundance of fast-growing, nutrient-rich graminoids and forbs versus slow-growing, nutrient-poor shrubs (e.g. Petit Bon et al., 2023; Thomas et al., 2018) governs biomass accrual and litter decomposition (Wookey et al., 2009), understanding how flooding and warming are altering tundra plant-community composition is essential to predict changes in carbon and nutrient cycling. Perhaps nowhere could these alterations be more critical than in wetlands, which only cover 7% of the vegetated Arctic (Walker et al., 2005), but contain large amounts of soil carbon (Nahlik & Fennessy, 2016), with the potential for positive feedback to climate change (Kreplin et al., 2021).

In addition to the effect of flooding alone, another major uncertainty in future of coastal Arctic wetlands is how increasing tidal floods may interact with background warming to shape plant-community composition. Evidence from a 6-year wetland warming experiment in the Yellow River Delta in China suggests that warmer temperatures may reduce ecosystem resistance to flooding (Sun et al., 2022). They found that plant productivity was diminished by an unprecedented (maximum water depth: 72 cm), long-lasting (57 days), natural flood event to a greater extent under warmed than ambient temperatures. Similarly, using grassland mesocosms exposed to three experimental temperature levels, Sánchez-Rodríguez et al. (2019) also showed a simulated 8-week flood event to cause the largest decrease in biomass production at the highest temperatures. Yet, an outstanding question is whether modifications in plant-community biomass and composition elicited by more frequent, shorter-lasting, tidal flood events in temperature-limited, high-latitude ecosystems will be amplified or diminished by warming?

The Yukon-Kuskokwim (Y-K) Delta, located between the Yukon and Kuskokwim Rivers in western Alaska, is one of the largest high-latitude riverine deltas in North America (~129,500 km^2). The area is warming rapidly (SNAP, 2020) and is characterized by a low coast-inland elevational gradient of ~2 m within 10 km of the coast (Jorgenson & Ely, 2001), rendering it exceptionally vulnerable to current flood events and projected increases in their frequency and intensity (Sweet et al., 2022; Terenzi et al., 2014). In one of the few studies addressing vegetation responses to tidal inundation at high latitudes, Person and Ruess (2003) flooded three different plant communities and showed that tidal floods can rapidly increase graminoid biomass and decrease shrub biomass in the Y-K Delta, though responses were limited to the community experiencing the lowest frequency and intensity of natural flooding. Importantly, their experiment was conducted in the outer coastal zone, where the salinity of tidal water is high (total dissolved solids [TDS]: ~28 $g L^{-1}$; Person & Ruess, 2003). Thus, plant-community responses detected there, as well as following saline incursions driven by extraordinary storm surges (Lantz et al., 2015), might not necessarily mirror responses to periodic, greater high-tide water input in freshwater-to-oligohaline (TDS: ~0–6 $g L^{-1}$) wetlands dominating the more extensive, inner part of coastal deltaic systems.

In this study, we asked how more frequent tidal flood events and elevated temperatures might be affecting the plant community in freshwater-to-oligohaline coastal tundra wetlands. Over 2 years, we simulated periodic summer flooding at two severities and increased summer temperatures in a full-factorial field experiment in the coastal Y-K Delta, and measured alterations in root productivity and plant-community biomass and composition. We simulated low-severity and high-severity flooding, as well as warming, to mimic changes projected for these freshwater-to-oligohaline wetland ecosystems in the next 5-to-10 years. Hence, the short-term responses quantified here are indicative of near-future changes happening in the Y-K Delta. We hypothesized flooding (i) to have overall positive effects on graminoid biomass and negative effects on shrub biomass (e.g. Person & Ruess, 2003). Therefore, we expected small net changes in plant-community biomass under flooding. Conversely, we hypothesized warming (ii) to increase plant-community biomass, with shrubs showing the greatest responses (e.g., Elmendorf et al., 2012). Finally, we expected (iii) the combined effects of these climate-change drivers to also differ between shrubs and graminoids, with flooding dampening the positive responses of shrubs to warming and having little effects on warming responses of graminoids (cf. Sun et al., 2022).

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out during the summers of 2022 and 2023 in the Yukon Delta National Wildlife Refuge (Figure 1a), which encompasses ~75,000 km^2 of low-Arctic tundra lowlands (i.e. wetlands) and uplands (Walker et al., 2005) within the Y-K Delta (Alaska). The study site is in the central part of the coastal Y-K Delta (61°26′ N, 165°26′ W), ~19 km inland from the Bering Sea and ~45 river-km upstream of the mouth of the Kashunuk River. The climate is classified as cold oceanic. The average summer (June–August) and winter (January–March) temperatures for the 30-year period 1991–2020 were 12.5 and −12.2°C, respectively, whereas average annual precipitation was 499 mm (rain + snow-water equivalent); data from Bethel weather station, ~200 km from the study site (Palecki et al., 2021).

Unusually high temperatures at the beginning of the 2022 growing season (from late May to mid June) likely caused differences between the two summers, although overall growing season temperatures were similar (own data; see Section 3). In addition, the onset of the growing season was particularly delayed in 2023, owing to above-average snow accumulation during the 2022/2023 winter (Mudryk et al., 2023).

2.2 | Study design and experimental treatments

Fine-scaled variations in topography, and hence tidal regimes, lead to different ecotypes (sensu Jorgenson, 2000) in the Y-K Delta. The experiment was established in a slightly brackish wet sedge-shrub meadow, an ecotype characterized by a *Carex rariflora-Salix fuscescens* plant association (Jorgenson, 2000; Figure 1b). Covering ~12% of the vegetated area of the central coast of the Y-K Delta (Jorgenson et al., 2018), this widespread ecotype is found on generally inactive floodplain deposits where inundation and sedimentation are historically relatively infrequent. Yet, this ecotype is already experiencing increasing flooding rates, and projections suggest near-future, large shifts in its tidal flood regime (see below for details). Soils are water-saturated, freshwater-to-oligohaline (mean TDS ± standard deviation [SD]: 0.44 ± 0.26 $g L^{-1}$), and neutral to slightly acidic (mean pH: 6.9 ± 0.2), and permafrost is absent; data from five unmanipulated control plots sampled six times during the summer of 2023 (Appendix S1: Data A1; Jorgenson, 2000). Samples collected at the study site in late summer 2022 indicate the following soil chemical composition (mean ± SD): 300 ± 9 $mg g^{-1}$ of total carbon (organic matter: 58 ± 2%), 12.5 ± 0.5 $mg g^{-1}$ of total nitrogen (carbon-to-nitrogen ratio: 24.5 ± 1.4), 9.8 ± 0.5 $\mu g g^{-1}$ of phosphorus, and 60.6 ± 7.3 $\mu g g^{-1}$ of potassium (Ross, 2024).

The plant community is dominated by graminoids. The dominant sedge *C. rariflora* is found with two other sedges (*Eriophorum vaginatum* and *C. lyngbyei*) and several grasses (e.g. *Calamagrostis canadensis*, *C. deschampsioides*, *Alopecurus alpinus*, *Poa eminens* and *Leymus mollis*). Together with the dominant deciduous dwarf-shrub *S. fuscescens*, deciduous dwarf-shrubs *S. ovalifolia* and *Betula nana* and evergreen dwarf-shrubs *Empetrum nigrum* and *Andromeda polifolia* are also present. The community hosts a high diversity of forbs (e.g. *Potentilla palustris*, *Pedicularis sudetica*, *Polemonium acutiflorum*, *Valeriana capitata* and *Bistorta vivipara*), although their abundance is low. Species nomenclature follows the Flora of Alaska (https://floraofalaska.org/). Across both summers, plant functional group (PFG; sensu Chapin et al., 1996) abundance in the community followed the order: graminoids (55%) > deciduous shrubs (29%) > evergreen shrubs (13%) > forbs (3%); own data collected in early- to mid-August from unmanipulated control plots (see Section 3).

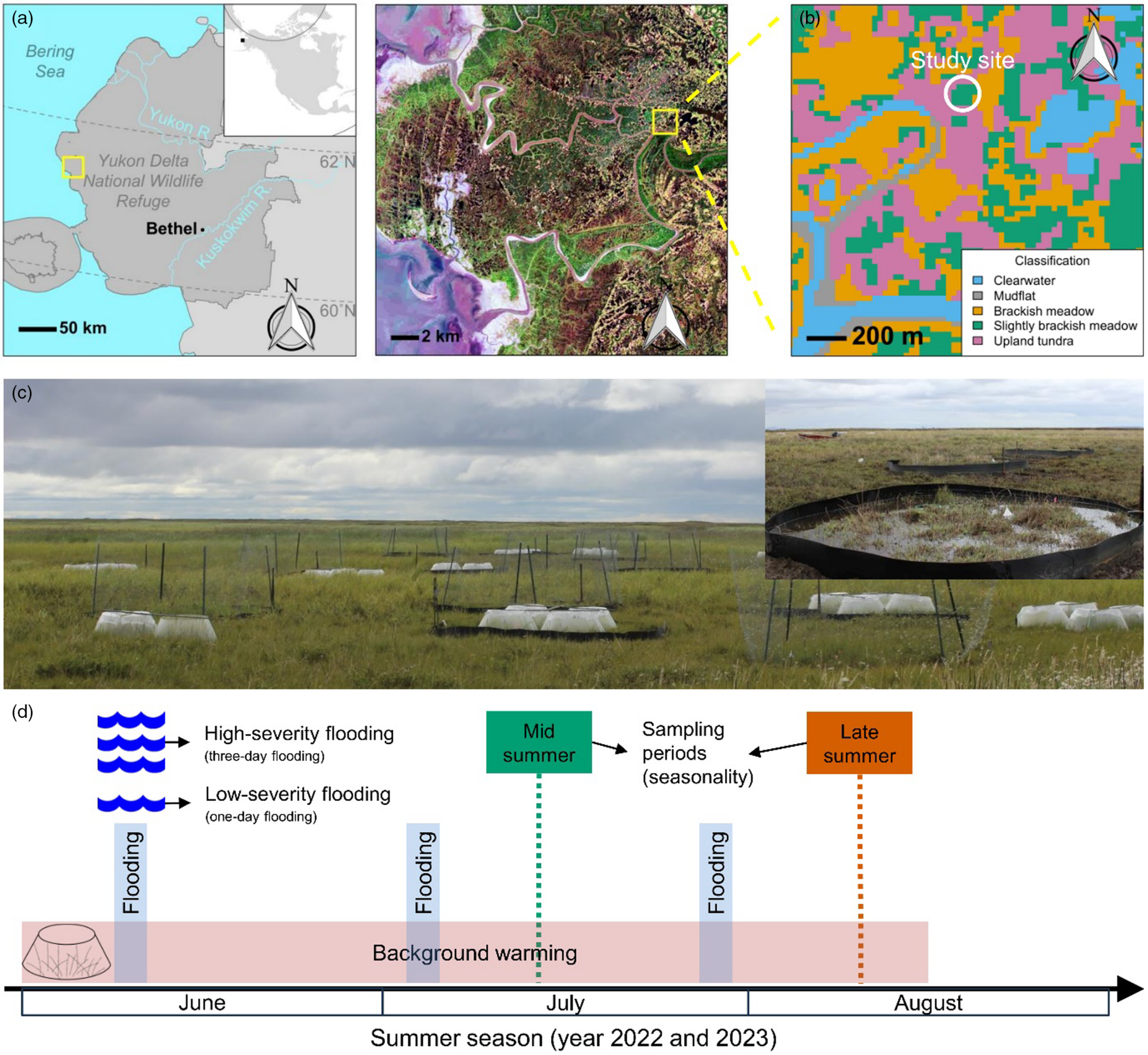

FIGURE 1 Study design and timing of experimental treatments and sampling. (a) Location of the study area. (b) Map of the physiographic features and the mosaic of different ecotypes that characterize the study area. Maps were originated in R ver. 4.3.2 (https://www.r-project.org/) using the package '*basemaps*' (Schwalb-Willmann, 2024), and data were extracted from (a) ESRI 'World Imagery' collection dataset (https://www.esri.com/) and (b) the Alaska Vegetation and Wetland Composite dataset (https://accscatalog.uaa.alaska.edu/). (c) Photographs of the focal slightly brackish wet sedge-shrub meadow (only four experimental blocks are visible) and of a flooded plot (inset). (d) Timing of the experimental treatments for low- and high-severity flooding and summer warming. The dashed lines indicate when sampling for plant-community composition was performed. The *silhouettes* depicting experimental treatments will be consistent throughout the manuscript.

After snowmelt in May 2022, seven blocks (>15 m apart), each comprising six 1.7 m × 1.7 m plots (>2 m apart), were established within the brackish wet sedge-shrub meadow (~170 m × 100 m area), for a total of 42 plots (Figure 1c). Plots within blocks were randomly assigned to a factorial combination of experimental monthly tidal floods (three levels: no-flooding, low-severity flooding, and high-severity flooding) and summer-long warming (two levels: ambient and elevated temperatures). The treatment combination 'no-flooding with ambient temperatures' was the unmanipulated control.

2.2.1 | Flooding treatment

Flooding was conducted by establishing a permanent, semi-circular dam around each of the 28 flooding plots (2.8 m diameter × 36 cm height × 8 mm thick; bamboo polyethylene root barrier), which was used to impound water on the plots (Figure 1c). Dams were larger than plots to reduce edge effects. Dams were inserted into the soil to a depth of 23 cm by excavating trenches using a mini-trencher (Georipper; Makita-powered EK6101), and extended 13 cm above-ground. We installed the dams at the beginning of the experiment (6 June 2022) and kept them in place through regular maintenance until the end of the study (12 August 2023). A water pump (Chemical-resistant Honda WMP20X1) coupled to a system of PVC hoses (5-cm diameter) was used to siphon high-tide water on flooding plots during each flood event using near-surface water of a nearby slough (Appendix S2: Figure A1).

The coastal Y-K Delta is characterized by a mixed semidiurnal tide cycle (an alternation of two high tides and two low tides of different sizes every 24 h) with a maximum tidal range of ~2 m (Huang et al., 2011). Because of tidal cycles combined with meteorological events, our study site currently experiences overbank flooding approximately once per summer. Yet the frequency and intensity of tidal flood events is projected to increase. Our flooding treatment was designed to simulate two different severities of periodic high-tide floods: a low- and a high-severity flooding. The low-severity flooding mimicked overbank flooding 1 day per month, coincident with the monthly highest tide during the summer months. Concurrently, the high-severity flooding represented a more substantially modified flooding regime, where multi-day flooding (three consecutive days) occurs with the monthly highest tides. The three flood events were simulated early- to mid-June, early July, and late July, with 3-to-4 weeks between each event (Figure 1d).

The nearest location at which tide cycles are monitored is Nome (Alaska, ~330 km from the study site). Yet, there is an established linear relationship between tidal stage in Nome and that in the central coast of the Y-K Delta (Terenzi et al., 2014), where our study site is located. Therefore, tidal records from Nome were used to calculate the average difference between the highest tide heights on consecutive days surrounding the highest tide of each summer month. This difference, along with relative sea-level rise projections for the region of Alaska (0.20–0.25 m over 20 years; Sweet et al., 2022), indicates that it will take roughly 5 years before the monthly highest tide results in monthly overbank flooding at our study site, and another 5 years before the site is flooded by the monthly highest high tides on three consecutive days. Therefore, our low- and high-severity flooding are simulating high-tide floods toward the end of the 2020's and in the early 2030's, respectively.

During each flood event, we filled the 28 flooding plots to the height of the dams with high-tide water (rate: ~0.3 $m^3 min^{-1}$; time: 7–10 min), which was then allowed to naturally dissipate out of the plots. Consistent with natural tidal flood events, which inundate soils for up to 4–6 h (The Authors, *personal observation*; Person & Ruess, 2003), water was retained within the lowest microtopography of the plots for a few hours following flooding simulation. Concurrently with each flood event, we measured salinity (TDS: $1.10 \pm 0.34 g L^{-1}$) and pH (7.1 ± 0.3) of flood water, which aligned with salinity ($0.84 \pm 0.75 g L^{-1}$) and pH (7.1 ± 0.3) of high-tide water during the summer; the flooding treatment had negligible impacts on soil salinity and pH (Appendix S1: Data A1). Water chemistry data from rivers in the same region are presented in Appendix S2: Table A1.

2.2.2 | Warming treatment

Summer warming was implemented with a slightly modified version of the ITEX-style (Henry et al., 2022), conical open-top chamber (OTC, Figure 1c; 0.85 m base × 0.50 m top × 0.35 m height, Kalwall Corp., Manchester, New Hampshire, USA). As we were aiming at the highest level of experimental warming, we covered the open-top part of the chambers with transparent plastic sheeting, leaving a 10 cm slit open at the widest part of the chamber opening (for a similar approach, cf. Alatalo et al., 2021 and references therein). The use of OTCs across several Arctic systems has showed an increase in average summer air temperature of ~1.5°C (Elmendorf et al., 2012), though the magnitude of warming can vary greatly among locations (Hollister et al., 2022).

We measured air (+10 cm) and soil (−5 cm) temperatures from the moss/litter surface in all plots every 90 mins during the two growing seasons using temperature loggers (iButtons DS1921G/Z, Maxim Integrated, San Jose, California, USA) with custom-made solar-radiation shields. Across summers, OTCs increased average air temperature by ~1.0°C (see Section 3), which is the temperature increase expected in the Y-K Delta for the period 2030–2039 (SNAP, 2020).

In each warming plot, we used four adjacent OTCs to cover the surface of the plot (cf. Choi et al., 2019). OTCs were put on plots as soon as possible after river break-up, when we could reach our remote study site (beginning of June), and removed in mid-August, when we had to leave the area (Figure 1d).

We investigated whether and how our modified OTCs altered key environmental parameters differently than ITEX-style OTCs (Hollister et al., 2022). We found our modified OTCs to produce twice as high as an increase in summer air temperatures than ITEX-style OTCs at our site. Importantly, our modified OTCs (but also ITEX-style OTCs) did not significantly affect soil moisture, air relative humidity, and free-air CO_2 concentration (Appendix S1: Data A2). Other micro-climatic changes, such as decreased light levels and wind speed, are known to be brought about by OTCs (Bokhorst et al., 2011). Yet, their simple structure facilitates the establishment of warming experiments in remote Arctic sites, such as ours, and therefore the comparison of results obtained therein (Elmendorf et al., 2012). Further, plant-community changes in response to OTC-induced warming have been reported to closely match changes promoted by natural warming (Elmendorf et al., 2015).

To ensure all plots were treated the same with respect to potential disturbance introduced by treatment application, no-flooding plots were also trenched around their perimeter following the methodology applied to flooding plots. As OTCs can operate as herbivore exclosures, we fenced all plots throughout both summers to avoid herbivory as a potential confounding factor. Visual estimates of vegetation cover conducted at the beginning of the experiment (4 June 2022) indicated that there were no significant differences in baseline plant-community composition among plots prior assignment to treatments (Appendix S1: Data A3).

2.3 | Plant community measures

We characterized above-ground plant-community composition using the point intercept frequency methodology (PIM; Bråthen & Hagberg, 2004). In all 42 plots, we established a 0.5 m × 0.5 m permanently demarcated quadrat where PIM was performed twice in both years: mid-summer (early- to mid-July) and late-summer (early- to mid-August). Hence, data from the 2 years inform 1- and 2-year responses to treatments, as well as inter-annual variation in plant-community composition in unmanipulated conditions, whilst within-year data help capture potentially cumulative effects of treatments throughout the growing season.

At each plot and sampling occasion, a 0.5 m × 0.5 m frame with 49 evenly spaced points (density: 196 points m^{-2}), which were made by double-crossing a fine elastic string to give a 90° ground projection, was levelled above the height of the plant canopy (Appendix S2: Figure A1). Below each point, the number of contacts (i.e. intercepts) between the projected line down onto the moss/litter layer and each vascular plant species was counted. We clumped live vascular plant species into four broad PFGs: graminoids, deciduous dwarf-shrubs, evergreen dwarf-shrubs, and forbs (e.g. Chapin et al., 1996; Thomas et al., 2018). Standing-dead graminoids (hereafter dead graminoids), which represent the growth of the past year(s), were also a possible intercept and recorded as a separate PFG. The same observer conducted PIM across the whole experiment.

The number of intercepts for each PFG (live PFGs and hereafter including dead graminoids) was converted into biomass. To achieve this, a total of 23, 25 cm × 25 cm plots were chosen for destructive harvesting within the study area. Plots were selected to show a high variation in above-ground plant biomass and PFG composition. First, we performed PIM at each plot as described above using a 25 cm × 25 cm frame with 49 evenly distributed intercepts (density: 784 points m^{-2}). Then, above-ground vascular plant biomass from each plot was harvested, sorted into PFGs, oven-dried at 60°C until constant mass and weighed. By fitting linear regression models, we calculated the relationship between point intercept data and grams of biomass (dry weight [dw]), separately for each PFG. The R^2 of these PFG-specific models were high ($0.87 > R^2 > 0.93$; Appendix S1: Data A4). The intercept and slope of these models were used to calculate PFG-specific biomass ($g\,m^{-2}$ dw) in our non-destructive experimental plots (cf. Petit Bon et al., 2021; Tuomi et al., 2018).

In 2023, we measured summer root productivity in each plot using six root in-growth cores (4 cm diameter × 7.5 cm length, 2 mm mesh-size; cf. Nadelhoffer et al., 2002), for a total of 252 in-growth cores. In-growth cores were filled with locally collected root-free substrate (soil from low-tide river sloughs), placed in plots on 10 June (>15 cm apart), and retrieved on 12 August (as in Choi et al., 2019). Each in-growth core was washed free of dead leaves and soil, and roots were oven-dried at 60°C until constant mass and weighed. We calculated the average root productivity ($g\,m^{-2}$ $summer^{-1}$ dw) at each plot.

2.4 | Data analysis

All analyses were conducted using the R statistical software ver. 4.3.2 (https://www.r-project.org/) and employed a linear mixed-effects model (LMM) framework. We used the '*lme4*' and '*vegan*' packages (Bates et al., 2015; Oksanen et al., 2020) to fit the models, the '*emmeans*' package (Lenth, 2021) to extract the pairwise comparisons among treatment combinations, and the '*ggplot2*' package (Wickham, 2016) for data visualization.

First, we assessed the effects of flooding (three levels: no-flooding, low-severity flooding, and high-severity flooding) and warming (two levels: ambient and elevated temperatures) on plot air and soil temperatures. We built LMMs separately for the 2 years (2022 and 2023), in which the two treatments and their interaction were set as fixed-effects and block as a random-effect. In these models, we used mean temperature throughout the summer and for the beginning of the growing season (June) as response variables. We obtained these data by calculating mean daily temperatures from our loggers and by averaging these values over the periods of interest.

Then, we examined the effects of our treatments on plant-community biomass. We built LMMs separately for the 2 years, in which flooding, warming and summer period (two levels: mid- and late-summer), as well as all possible two-way interactions, were specified as fixed-effects and block and plot-within-block as random-effects. Plot-within-block was set to account for the repeated sampling in mid- and late-summer across the experiment. Response variables were above-ground biomass of the five PFGs: graminoids, deciduous shrubs, evergreen shrubs, forbs and dead graminoids. As dead graminoids are indicative of the previous year's growth, we present only the data from 2023, which therefore also reflect the effects of the treatments in 2022, the first experimental year. We also built LMMs to assess biomass responses of the whole live plant-community (combined biomass of graminoids, deciduous and evergreen shrubs, and forbs) and of deciduous and evergreen shrubs together. Last, root productivity in 2023 was assessed with a LMM in which flooding, warming, and their interaction were used as fixed-effects and block as a random-effect.

Finally, treatment effects on plant-community composition were assessed in late-summer by permutational multivariate analysis of variance, separately for the 2 years. Here, flooding, warming and their interaction were used as fixed-effects and permutations ($n = 10{,}000$) were restricted within block to account for the spatial structure of the study design. The response variable was the matrix of relative contribution (%) of each PFG to whole plant-community biomass.

When necessary, response variables were either *log*-transformed or *log*-transformed + 1 (when there were values <1) to meet model assumptions, which were validated using standard diagnostic procedures by confirming normality and homogeneity of variances in the residuals and ensuring linearity between observed and fitted values. During this process, 19 outliers (0.91% of all the observations across all fitted models) were detected. As removing these datapoints did not alter biological conclusions, we excluded them to increase the precision of model estimates (Appendix S2: Tables A2–A6).

3 | RESULTS

3.1 | Micro-environment and plant community in unflooded and ambient conditions

Daily mean summer air and soil temperatures in unmanipulated controls were, respectively, 13.0 and 7.0°C (first year of the experiment, 2022) and 12.6 and 8.0°C (second year, 2023) (Figure 2). Temperatures varied between years, with daily mean June air temperature being 1.1°C higher in 2022 than 2023 and June and summer soil temperatures being ~1°C higher in 2023 than 2022 (Appendix S2: Figure A2; Figure 2b).

Control plot above-ground biomass of the whole live plant-community increased from mid- to late-summer by 20% in 2022 (Figure 3a) and by 30% in 2023 (Figure 4a), but PFGs varied in their changes. Plots in late- compared with mid-summer had greater biomass of graminoids (+25% in 2022 and +65% in 2023; Figures 3b and 4b), dwarf-shrubs (+17%, only in 2022; Figure 3c) and forbs (+55%, only in 2023; Figure 4d). Dead graminoid biomass decreased by 20% from mid- to late-summer (Figure 4e). Biomass varied between years, with differences often greater than within-summer seasonal changes. Live plant-community, graminoid, shrub, and forb biomass in 2023 was 35%, 50%, 15% and 70% lower respectively than in 2022.

3.2 | Effects of flooding and warming on the micro-environment

High-severity, but not low-severity, flooding lowered summer and June air temperatures by 0.5°C [$\text{CI}_{95\%}$ 0.8–0.2°C] and 0.6°C [$\text{CI}_{95\%}$ 1.1–0.2°C] respectively in 2022, with weaker effects in 2023 (Figure 2a; Appendix S2: Figure A2). Conversely, both flooding levels raised June soil temperature by ~0.7°C [$\text{CI}_{95\%}$ ~0.1–1.5°C] in 2022 and by ~1.1°C [$\text{CI}_{95\%}$ ~0.1–2.2°C] in 2023, with no effects on summer soil temperature (Appendix S2: Figure A2; Figure 2b). Warming raised summer air temperature by 1.1°C [$\text{CI}_{95\%}$ 0.8–1.4°C] in 2022 and by 0.8°C [$\text{CI}_{95\%}$ 0.5–1.1°C] in 2023 and decreased summer soil temperature by 0.5°C [$\text{CI}_{95\%}$ 0.9–0.1°C] in 2022 and by 0.8°C [$\text{CI}_{95\%}$

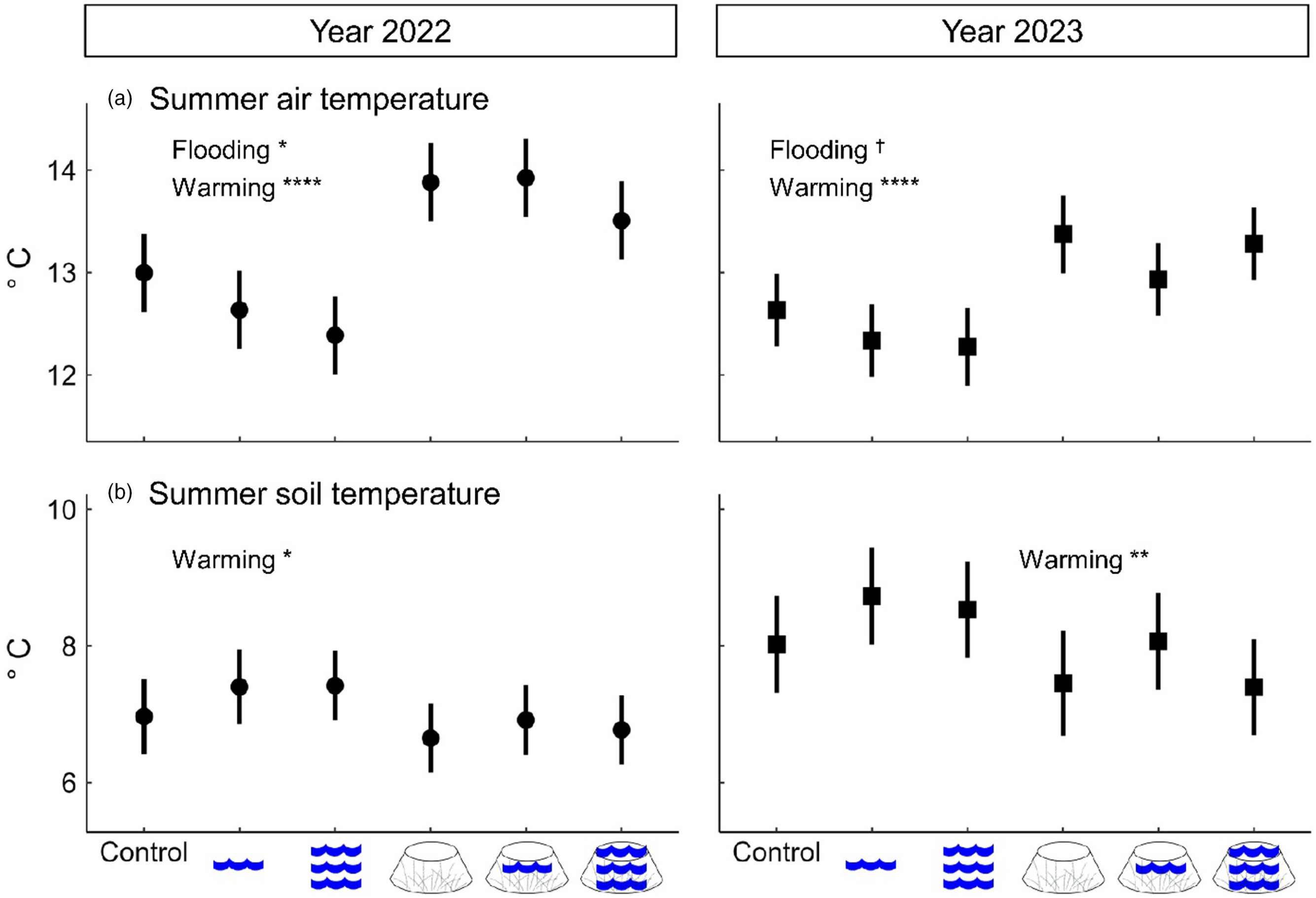

FIGURE 2 Effects of flooding and warming on summer temperatures. Model predictions ±95% confidence intervals for average summer (a) air (+10 cm) and (b) soil (−5 cm) temperatures, separately for the 2 years. Significant and marginally significant effects are shown: $^{\dagger}p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{****}p < 0.0001$. ANOVA results are given in Appendix S2: Table A2.

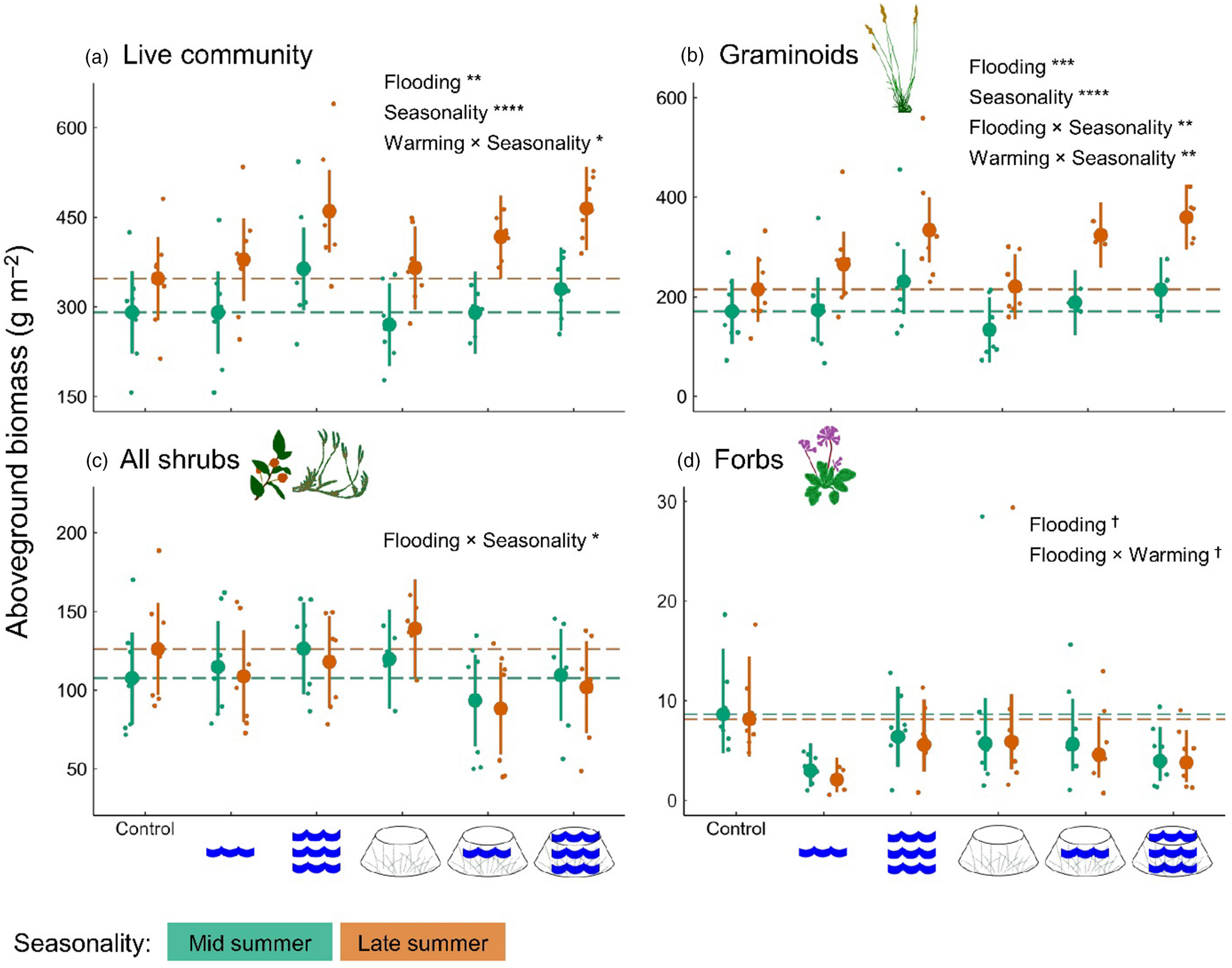

FIGURE 3 Effects of flooding and warming on above-ground plant biomass in summer 2022 (1-year responses). Model predictions ±95% confidence intervals (CIs) for mid-summer and late-summer biomass ($g\,m^{-2}$ dw) of (a) the whole live community, (b) graminoids, (c) shrubs, and (d) forbs. To facilitate the comparison between treatments and unmanipulated control plots, horizontal lines are drawn for the average biomass in controls, separately for mid- and late-summer. Coloured dots in the background show fitted values, which were jittered to enhance readability. Model predictions, their CIs, and fitted values are given on the response scale; note the different scale of *y*-axes. Significant and marginally significant effects are shown: $^{\dagger}p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and $^{****}p < 0.0001$. ANOVA results are given in Appendix S2: Table A3.

1.4–0.2°C] in 2023 (Figure 2a,b), and influenced June temperatures similarly (Appendix S2: Figure A2).

3.3 | Effects of flooding and warming on the plant community

Overall, flooding promoted stronger above-ground biomass responses compared with warming, though responses differed among PFGs. Treatments had generally additive (not interactive) effects and the direction of treatment responses were consistent across years, although their magnitude varied both within (mid vs. late) and between (2022 vs. 2023) summer seasons.

High-severity, but not low-severity, flooding increased live plant-community biomass by 27% [$CI_{95\%}$ 12%–42%] in 2022 and by 18% [$CI_{95\%}$ 5%–32%] in 2023 (Figures 3a and 4a). Warming did not change plant-community biomass in either year, though its positive effect grew stronger throughout the summer of 2022, as indicated by the significant two-way 'warming × seasonality' interaction (hereafter, the presence of interactions is highlighted in figures).

In 2022, high-severity flooding increased the biomass of graminoids by 45% [$CI_{95\%}$ 15%–75%] in mid-summer and by 60% [$CI_{95\%}$ 35%–80%] in late-summer, while low-severity flooding increased it by 35% [$CI_{95\%}$ 15%–55%] in late-summer only (Figure 3b). Despite increasingly positive effects of warming throughout the growing season, warming did not affect graminoid biomass in 2022. In 2023, high-severity flooding increased graminoid biomass by 60% [$CI_{95\%}$ 35%–90%] in mid-summer and by 30% [$CI_{95\%}$ 10%–55%] in late-summer, whereas low-severity flooding increased it by 35%

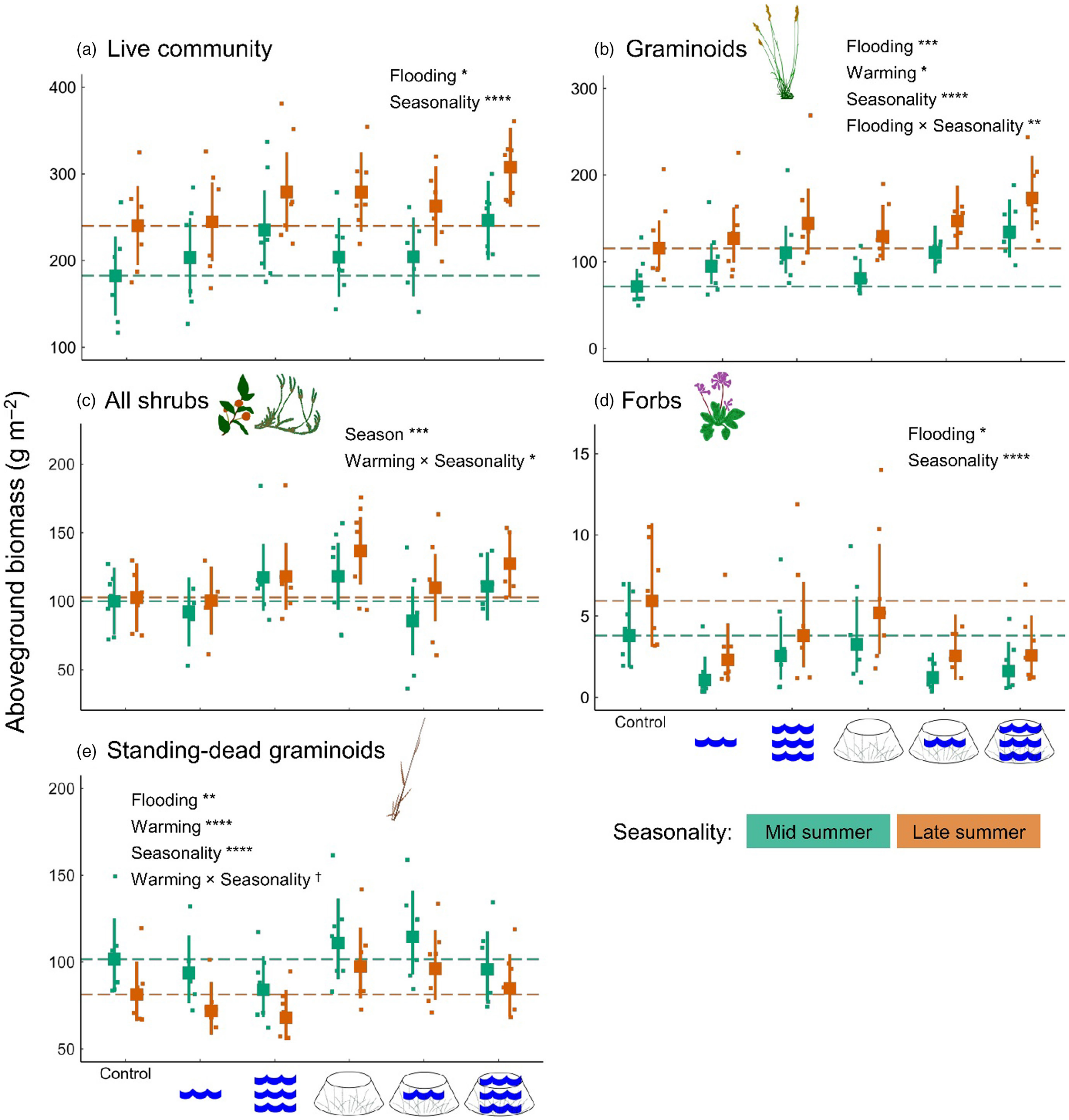

FIGURE 4 Effects of flooding and warming on above-ground plant biomass in summer 2023 (two-year responses). Model predictions ±95% confidence intervals (CIs) for mid-summer and late-summer biomass ($\mathrm{g\,m^{-2}}$ dw) of (a) the whole live community, (b) graminoids, (c) shrubs, (d) forbs, and (e) standing-dead graminoids. To facilitate the comparison between treatments and unmanipulated control plots, horizontal lines are drawn for the average biomass in controls, separately for mid- and late-summer. Coloured dots in the background show fitted values, which were jittered to enhance readability. Model predictions, their CIs, and fitted values are given on the response scale; note the different scale of *y*-axes. Significant and marginally significant effects are shown: $^{\dagger}p<0.1$, $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$, and $^{****}p<0.0001$. ANOVA results are given in Appendix S2: Table A4.

[$\mathrm{CI}_{95\%}$ 15%–60%] in mid-summer only (Figure 4b). In 2023, warming increased overall graminoid biomass by 20% [$\mathrm{CI}_{95\%}$ 5%–35%]. Consequently, wet tundra that was both flooded at high-severity and warmed for 2 years had 90% and 50% higher graminoid biomass in mid- and late-summer, respectively, than unmanipulated wet tundra.

In 2022, low-severity flooding decreased the biomass of all shrubs by 25% [$\mathrm{CI}_{95\%}$ 45%–5%] in late-summer only, while high-severity flooding had no effects, though its negative effect grew stronger during the growing season (Figure 3c). Similar effects of flooding were found on deciduous shrubs only, while evergreen shrub biomass was not altered by either treatment (Appendix S2: Figure A3). In 2023, warming tended to increase shrub biomass by 15% [$CI_{95\%}$ 0%–35%] in late-summer only (Figure 4c), whereas flooding had no effects. When shrubs were separated, neither deciduous nor evergreen shrubs were affected by treatments in 2023 (Appendix S2: Figure A3).

In 2022, low-severity, but not high-severity, flooding decreased the biomass of forbs by 70% [$CI_{95\%}$ >100%–15%] under ambient, but not warmed, conditions (Figure 3d). In 2023, regardless of temperature, low-severity flooding lowered forb biomass by 60% [$CI_{95\%}$ >100%–15%], whilst high-severity flooding marginally lowered it by 45% [$CI_{95\%}$ 90%–0%] (Figure 4d).

High-severity, but not low-severity, flooding decreased the biomass of dead graminoids by 15% [$CI_{95\%}$ 10%–20%]. Conversely, warming raised dead graminoid biomass by 15% [$CI_{95\%}$ 5%–25%] in mid-summer and by 25% [$CI_{95\%}$ 15%–40%] in late-summer (Figure 4e). Consequently, tundra that was both flooded at high-severity and warmed had a dead graminoid biomass that was comparable to that of unmanipulated tundra.

Flooding-induced, but not warming-induced, changes in above-ground biomass translated into differences in plant-community composition (Appendix S2: Figure A4). In 2022, graminoids and shrubs made up respectively ~73% and ~25% of flooded plant communities and 60% and 37% of the unflooded plant community. In 2023, live graminoids and dead graminoids made up respectively 44% and 21% of the plant-community that was flooded at high-severity and 36% and 27% of the unflooded plant-community, with the plant-community that was flooded at low-severity not differing between either of them.

High-severity, but not low-severity, flooding decreased summer root productivity by 35% [$CI_{95\%}$ 60%–5%] in ambient plots. Warming also decreased root productivity by 55% [$CI_{95\%}$ 70%–30%] in unflooded plots. However, when high-severity flooding and warming were combined, root productivity did not differ from unmanipulated conditions (Figure 5).

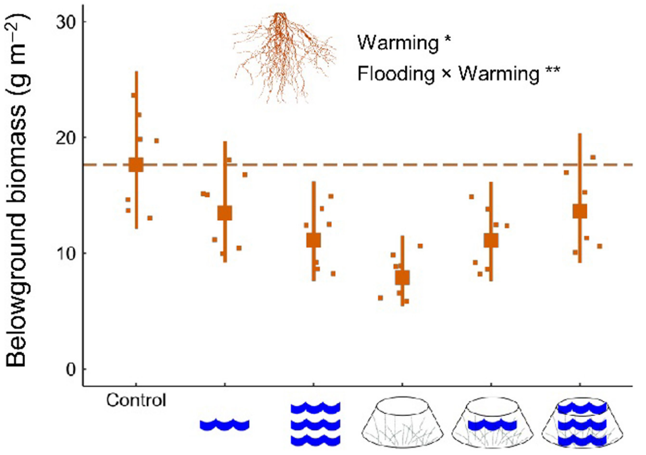

FIGURE 5 Effects of flooding and warming on root biomass productivity in summer 2023. Model predictions and their 95% confidence intervals (CIs) for root production (g m^{-2} dw) during the growing season. To facilitate the comparison between treatments and unmanipulated control plots, a horizontal line is drawn for the average biomass in controls. Coloured dots in the background show fitted values, which were jittered to enhance readability. Model predictions, their CIs, and fitted values are given on the response scale. Significant effects are shown: $*p<0.05$ and $**p<0.01$. ANOVA results are given in Appendix S2: Table A5.

4 | DISCUSSION

We simulated periodic, short-lasting flood events at low- and high-severity, mimicking tidal flood regimes predicted for many low-lying areas of the Y-K Delta in the next ~5 and ~10 years, respectively. We did so in both ambient and warmed wet tundra, to explore whether projected Arctic warming for the next decade may modulate wetland responses to flooding. Regardless of temperature, high-severity flooding greatly increased above-ground biomass of the already dominant graminoids, thereby increasing live plant-community biomass. Low-severity flooding had similar, yet weaker, effects. Concurrently, 2 years of warming also increased graminoid biomass, regardless of flooding. Importantly, while warming increased dead graminoid biomass, high-severity flooding decreased it. These rapid changes in live and dead biomass (Figure 6)—two key ecosystem properties underpinning both carbon and nutrient cycling—are likely to have important implications for ecosystem functioning of more frequently flooded coastal wetland ecosystems in a warmer Arctic.

The experiment examined potential responses of freshwater-to-oligohaline coastal wetlands found in high-latitude deltaic systems (Figure 6a) to increasingly frequent tidal flood events, in both ambient and warmed conditions. An important finding is that, whenever operating together (Figure 6b,c), these two key environmental-change drivers altered plant-community composition in an additive fashion. Most importantly, 2 years of high-severity flooding increased graminoid biomass by ~45%, and this was enhanced by elevated temperatures (+20%). First, this shows that the effect of periodic, short-duration tidal floods dominates over that of summer-long warming, which is particularly relevant because our manipulations simulated flooding and warming regimes expected in the wet sedge-shrub meadows of the Y-K Delta over the same, near-term timeframe. Second, with the most likely future scenario being a more flooded and warmer Y-K Delta, our findings indicate that the concerted effect of these drivers will be to perpetuate a graminoid-dominated vegetation state in these wetlands. This complements results from Carlson et al. (2018), who showed elevated temperatures to favour shrubs over graminoids in a different wetland community found in the outer coastal zone of this same system (~23 km towards the Bering Sea from our study site), highlighting the contextual sensitivity of coastal high-latitude wetland responses to warming (Choi et al., 2022). Further, this pinpoints the crucial role of flooding in structuring these wetlands (cf. Jorgenson & Ely, 2001; Person &

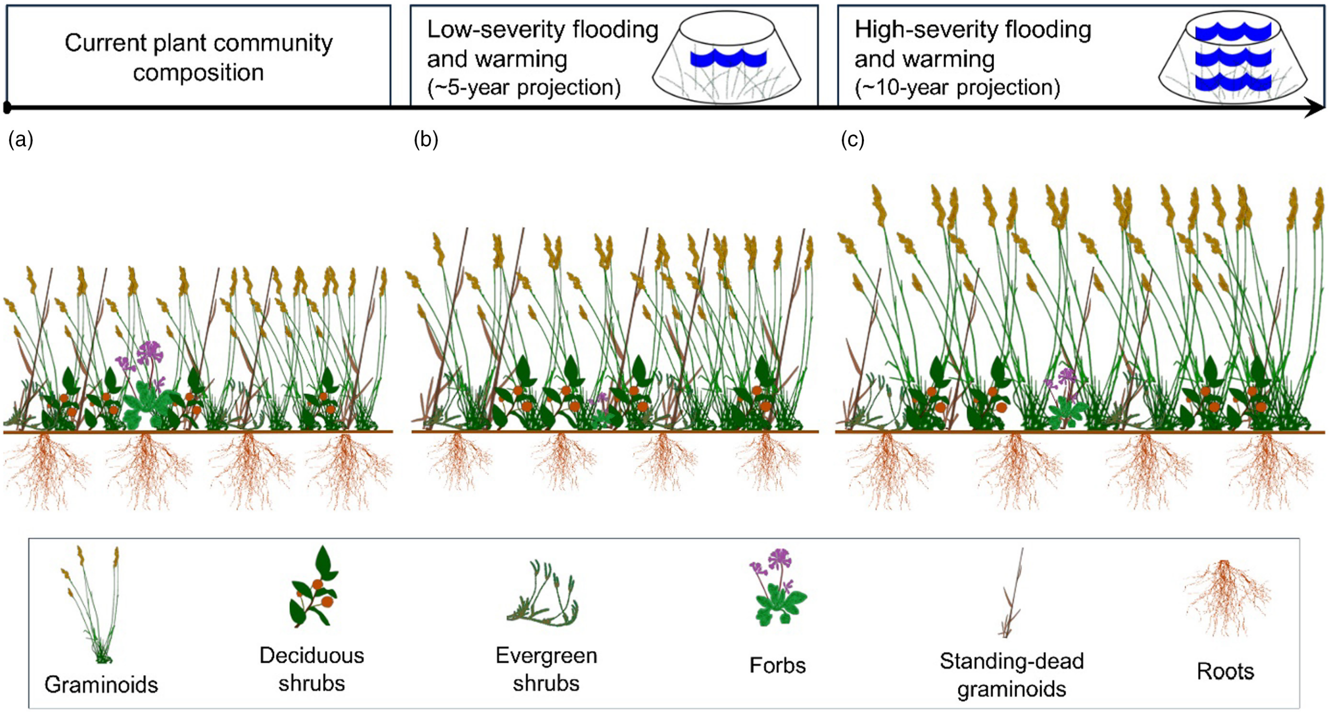

FIGURE 6 Conceptual summary for the combined effect of near-future tidal flooding and warming on plant-community composition of coastal tundra wetlands. (a) Current plant-community composition and biomass and alterations induced by (b) low-severity flooding and warming (scenario expected toward the end of the 2020's) and (c) high-severity flooding and warming (scenario expected in the early 2030's) are shown based on late summer responses to flooding and warming treatments after 2 years. The number of *silhouettes* for each plant functional group (PFG) (e.g., graminoids) used in (a) is proportional to the abundance of that PFG in unflooded and ambient conditions (i.e., unmanipulated control plots). For roots, four *silhouettes* were arbitrarily used. The size of the *silhouettes* for each PFG and roots in (b, c) are scaled proportionally compared to those in (a) based on the observed biomass change. Hence, the e.g., ~50% increase in graminoid biomass promoted by high-severity flooding and warming is shown by ~50% larger graminoid *silhouettes* in (c) compared to (a); see Section 3 for details.

Ruess, 2003), suggesting that considerations on how climate change is altering coastal high-latitude systems must account for concurrent increasing flooding rates.

There are several potential reasons why we found such strong positive graminoid responses to high-tide floods. Flooding increased June soil (−5 cm) temperature by ~0.7–1.1°C and, though not significantly, increased summer soil temperature by ~0.3–0.6°C across both years. Graminoids respond quickly to changes in temperatures, and elevated soil temperature in tundra can rapidly increase their biomass relative to other slower-growing PFGs (Van der Wal & Brooker, 2004; Wang et al., 2017). The increase in air (+10 cm) temperature caused by OTCs also likely promoted the 2-year warming-induced increase in graminoid biomass (Elmendorf et al., 2012). Another, not mutually exclusive, explanation is that soil nutrient (primarily nitrogen and phosphorus) levels increased with flooding (Garssen et al., 2017; but see Toda et al., 2005), potentially increasing plant growth. PFGs with an acquisitive strategy, such as graminoids, generally respond faster to changes in resource availability than PFGs with a more conservative strategy, such as shrubs (Petit Bon et al., 2023; Wang et al., 2017; Wookey et al., 2009), thereby benefitting from enhanced soil nutrient levels more quickly. In line with this, tidal inundation near the coast in this same high-latitude system increased graminoid leaf nitrogen concentration (Person & Ruess, 2003). Enhanced resource availability was also proposed as the mechanism driving increases in grassland (Wright et al., 2015) and riparian plant-community (Garssen et al., 2017) productivity following flooding.

We show that more frequent high-tide floods and, to a lesser extent, warming enhance the biomass of graminoids in this wetland and that, at least for flooding, this increase leads to greater live plant-community biomass. Yet, our findings also point to an interrelated effect, whereby flooding may speed up biomass turnover. In late-summer of the first year of the experiment, there was ~75 and ~130 $\mathrm{g\,m^{-2}}$ more graminoid biomass in low-severity and high-severity flooding plots, respectively, compared with control plots. This presumably translated to greater standing-dead graminoid biomass in flooded tundra at the start of the growing season of the second experimental year. Yet, in late-summer of this second year, there was similar (~90 $\mathrm{g\,m^{-2}}$) and 15 $\mathrm{g\,m^{-2}}$ less dead graminoid biomass in low-severity and high-severity flooding plots respectively compared with controls. Similarly, the 25% increase in late-summer dead graminoid biomass promoted by warming—an expected plant-community response in a warmer Arctic (Elmendorf et al., 2012; Little et al., 2017)—was offset by high-severity flooding. Combined, these results suggest that more frequent tidal floods, plausibly in part through mechanical disturbance from water flow, might increase the input of dead graminoids into the litter-layer subsystem (cf. Wright et al., 2015). Accordingly, vegetation was clearly pushed down in flooding plots, consistent with the effect of natural tidal flood events (M. Petit Bon, *data unpublished* and *personal observation*).

The observation that more frequent high-tide floods consistently produced a large increase in graminoid biomass in both summers is not trivial. Not only was the snowmelt later in 2023, but our plot-level data also indicate that, overall, plants experienced ~1.1°C lower June air temperature in 2023 than 2022. In line with this, graminoid biomass in control plots in 2023 was 50% lower than in 2022, and similar patterns held for other PFGs. Hence, despite large between-summer variability in abiotic conditions dictating large differences in ecosystem properties among growing seasons (this study; Frost et al., 2021; Van der Wal & Stien, 2014), increasing flooding rates will still likely promote greater graminoid and live plant-community biomass in freshwater-to-oligohaline coastal high-latitude wetlands.

Flooding alone reduced forb biomass in both years and weakly reduced shrub biomass in the first year. The very low abundance of forbs (only 3% of the plant-community in control plots), as well as the large confidence intervals around their biomass responses, clearly hint to high uncertainty in the magnitude of their responses. Regardless, storm-driven, saline flood events in the outer coastal zone (Terenzi et al., 2014) are an important driver of forb and shrub biomass reduction in tundra wetlands (Jorgenson et al., 2018; Lantz et al., 2015; Person & Ruess, 2003). Our results indicate that increased flooding in the larger, inner part of coastal deltaic plains, where flood events are inherently less saline, can have similar effects. Greater graminoid biomass, in addition to sequestering larger amounts of nutrients, may have increased shading by promoting denser canopy that overtopped low-laying forb and shrub species (M. Petit Bon, *personal observation*; Elmendorf et al., 2012; Insausti et al., 1999), thus reducing their performance (May et al., 2022). This explanation is supported by the decrease in summer air (+10cm) temperature caused by flooding, suggesting increased graminoid-induced shading near ground. While controlled experiments that can disentangle flooding-induced alterations in both biotic and abiotic environment are needed to tease apart the mechanisms behind differential PFG responses, two considerations emerge from our results. First, in the light of the well-documented positive effect of warming on shrub abundance in relatively productive, fast-warming tundra regions (Carlson et al., 2018; Elmendorf et al., 2012), we show that more frequent high-tide floods could potentially decelerate shrub expansion in coastal low-Arctic wetlands (cf. Person & Ruess, 2003). Second, the observed decrease in forb biomass, combined with the increase of the already dominant graminoids, might indicate a flooding-induced decrease in species diversity and a concurrent increase in biotic homogenization, as shown in other flooding-prone ecosystems (Campbell et al., 2016; Garssen et al., 2017; Insausti et al., 1999).

We found high-severity flooding alone decreased summer root productivity by 35%. Whereas flooding is known to have the potential to decrease root productivity, and hence below-ground biomass (Janousek & Mayo, 2013), such negative effects are often observed when flooding is also negatively affecting above-ground biomass, which was clearly not the case in our study. It is possible that flooding-induced favourable growing conditions for graminoids at least in part reduced their biomass allocation below-ground by fostering above-ground productivity. This could also partially explain the reduction in root productivity caused by warming alone, as biomass allocation of tundra vegetation shift towards above-ground at higher temperatures (DeMarco et al., 2014; Hollister & Flaherty, 2010). Furthermore, it is likely that lower root productivity with warming was also partly dictated by the observed OTC-induced cooling of the upper soil, which plausibly originated due to shading of denser plant canopies and/or higher evaporation (Hollister et al., 2022). While high-severity flooding or warming alone decreased root productivity, surprisingly root productivity in wet tundra that was both flooded at high-severity and warmed did not differ from unmanipulated conditions. As our data do not help interpret the mechanisms underlying these contrasting responses, further research is warranted. Regardless, these results are relevant because shifts in below-ground biomass may impact carbon and nutrient cycling by modifying the net amount of litter input into the soil (Wang et al., 2016). Our estimate of root productivity in the upper 7.5cm of soil (~18$\,\mathrm{g\,m^{-2}}$ summer^{-1}) are comparable to previous estimates in wet sedge tundra (e.g., ~75$\,\mathrm{g\,m^{-2}}$ found in the upper 30cm of soil after 1-year incubation; Nadelhoffer et al., 2002).

While our findings are valuable to predict short-term plant-community shifts in response to increasing tidal floods and summer warming, longer-term alterations of coastal high-latitude wetlands will likely be much larger (and potentially different) than those demonstrated here. Relative sea level for the region of Alaska is projected to increase up to 1.8m and 3.3m by 2100 and 2150, respectively (Sweet et al., 2022), indicating that current tidal wetlands in the Y-K Delta may be converted into permanently inundated marshes (Jorgenson & Ely, 2001). This, combined with increased storminess and storm surges (Sepp & Jaagus, 2011; Vermaire et al., 2013), also suggests that oceanic, more saline water could be regularly pushed into the inner part of coastal deltaic systems, thereby converting freshwater-to-oligohaline wetlands into brackish-to-saline wetlands. For instance, the five most extreme floods of the last century in the Y-K Delta all occurred in the past 20years, with oceanic water reaching areas 21–32km from the coast (Terenzi et al., 2014; A. Joshua Leffler, *data unpublished*) and resulting in the extensive salt-kill of vegetation (Jorgenson et al., 2018; cf. also Lantz et al., 2015). Finally, other processes—including permafrost degradation and related subsidence, erosion, and sedimentation—contribute to landscape changes in coastal ecosystems, such as the Y-K Delta (Jorgenson et al., 2018), further complicating predictions of flooding-induced shifts in plant communities over longer time scales.

This study explored plant-community responses to projected near-term flooding and warming for the freshwater-to-oligohaline coastal wetlands of the Y-K Delta in western Alaska (Figure 6), one of the most productive high-latitude systems on Earth (Frost et al., 2021). We hypothesized that more frequent high-tide floods would cause small net changes in plant-community biomass by promoting graminoid growth whilst suppressing shrub growth. In direct opposition to our prediction, despite weak negative effects on shrubs, flooding increased graminoid biomass to such an extent that total live biomass also increased. What is striking is the rate at which flooding-induced alterations have occurred, becoming largely apparent after only two monthly flood events in the first year of the experiment. Additionally, and in contrast with our hypothesis, high-tide floods did not constrain the effect of warming, which was shown to increase more graminoid biomass than shrub biomass in the focal wet sedge-shrub meadow. As PFGs differ sharply in their growth rates and patterns of carbon and nutrient allocation (Aerts & Chapin, 2000), shifts in PFG abundances can produce substantial modifications in ecosystem functioning (McLaren & Turkington, 2010; Wookey et al., 2009). Here, the increase in graminoid biomass and relative abundance, coupled with the enhanced turnover of standing-dead biomass, suggest that more frequent floods could affect carbon and nutrient cycling of coastal tundra wetlands, as graminoids are characterized by relatively nutrient-rich, fast degradable litter (Hobbie, 1996). This finding is relevant because tundra wetlands store large amounts of soil carbon (Nahlik & Fennessy, 2016), and thereby play a disproportionate role in the ecosystem-climate change feedback loop (Kreplin et al., 2021). We urgently need a better understanding of how flooding and warming may affect other plant communities, such as coastal upland tundra heaths, which, like brackish meadows, account for large parts of the Y-K Delta (Figure 1b) and are already experiencing more frequent flood events.

AUTHOR CONTRIBUTIONS

Karen H. Beard, A. Joshua Leffler and Katharine C. Kelsey conceived the idea and all authors designed experiments and methodology. Matteo Petit Bon and Tyler J. Williams collected the data. Matteo Petit Bon analysed the data and led the writing of the manuscript, for which all authors contributed critically and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting this study are available at the Arctic Data Center: https://doi.org/10.18739/A2K93180P (Petit Bon et al., 2024).

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14418.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1.

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