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ORIGINAL RESEARCH

Low temperatures reduce establishment of new populations of invasive plants in a subarctic treeline environment

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Abstract

Biological invasions are a serious global issue, but invasions are relatively less common at high latitudes, likely due to harsh environmental conditions and limited accessibility. An exception to this is human-settled and disturbed towns that may promote invasions and risk acting as sources of non-native species into the surrounding natural areas. For instance, Churchill, Manitoba, Canada (58ºN), is a treeline subarctic town and port connected by a railway to temperate North America. More than a hundred non-native plant species have been recorded within the town footprint and associated areas. While some have persisted for decades in these areas, none has spread into nearby tundra or boreal forest ecosystems. We used a greenhouse warming experiment to investigate the importance of increased growing season temperatures on three perennial non-native species (*Linaria vulgaris*, *Plantago major*, *Taraxacum officinale*), and used a transplant experiment to investigate non-native survival and growth after manual translocation to tundra and boreal forest roadside over several full years. We found that non-native plants were able to survive temporarily after manual translocation to roadsides adjacent to natural areas, with higher survival in warmer boreal forest roadsides. When we experimentally increased temperature, non-native seed germination increased, and non-native transplants trended toward increased survival and growth, again suggesting that temperature is a limiting factor. However, survival and growth of these non-native species consistently declined over time. Future global and climate change that results in increased warming therefore may shift these non-native species from invasion failure to success.

Keywords Invasive species · Non-native plants · Subarctic ecosystems · Tundra · Boreal forest · Climate change · Warming

Introduction

Although invasions are a widespread and serious problem throughout temperate zones in Canada (Colautti et al. 2006) and elsewhere (Guo et al. 2021), boreal forests currently are relatively uninvaded and tundra ecosystems are almost free of non-native plants (Alsos et al. 2015; CAFF and PAME 2017; Guo et al. 2021). At high latitudes, the lower risk of invasion reflects the harsh climate (Barry et al. 2013), low propagule pressure (CAFF and PAME 2017), and strong competition and limited nutrients (Lembrechts et al. 2016). Anthropogenic climate change may alter this picture. High latitudes are warming at a rate much higher than the global average (Serreze and Barry 2011; Overland et al. 2014). As well as directly improving conditions for invaders imported from more temperate latitudes, this rapid warming is expected to lead to increased human travel, trade, settlement, and disturbance, enhancing pathways for invasions into human-disturbed and settled areas (Hulme 2009; Ibáñez et al. 2009; Kalwij et al. 2015; Dainese et al. 2017; Wilson et al. 2009).

Once a potential invader arrives at a site, human activities can also change local abiotic factors from limiting to promoting invasion (Rew et al. 2020; Fuentes-Lillo et al. 2021). For instance, buildings can improve abiotic conditions by increasing shelter and warming the immediate area (Da Silva and Kotanen 2024), resulting in settlements with high occurrences of non-native species (Bartlett et al. 2021). Roadsides often are especially vulnerable to invasions by non-native species due to consistent disturbance coupled with the importation of seeds by soil or vehicle movement (Rauschert et al. 2017; Yang et al. 2021; Syed et al. 2023).

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Frequent dispersal of non-native species by vehicles along roadsides can lead to the spread of invaders into new areas (Lippe and Kowarik 2007; Lembrechts et al. 2014), especially if the road is unpaved and requires grading (Rauschert et al. 2017). For example, non-native plants have spread widely throughout the road network in the Canadian Northwest Territories (Oldham and Delisle-Oldham 2017).

A settlement with unusually high numbers of non-native species for its latitude is the subarctic town of Churchill, Manitoba, Canada (58.8° N, 94.2° W). Over a hundred non-native plants have been recorded in the Churchill area, including both the town and nearby compost dumps and landfills (Beckett 1959; Scott 1996). Many of these species have persisted for decades; however, very few have escaped this reservoir into the surrounding boreal forest and tundra ecosystems (Beckett 1959; Staniforth and Scott 1991; Kent et al. 2018), possibly reflecting unfavorable conditions outside of anthropogenically modified sites. Thus, Churchill offers the ideal opportunity to investigate whether environmental constraints such as temperature currently are preventing further invasion of non-native species into northern regions.

We tested whether growing season temperatures are limitations to invasion outside the town of Churchill using two controlled multi-year field experiments. In the first (Cross-Biome) experiment, we measured the performance and survival of non-native seeds and seedlings planted on roadsides in both tundra and boreal forest areas. This tests whether these plants fail to spread from town into uninvaded areas, because they are unable to establish even after reaching an apparently suitable site; it also tests whether boreal and tundra sites are equally hostile to establishment. The second (Warming) experiment used open-top greenhouses to determine whether low growing season temperatures may be the factor inhibiting establishment of seeds and seedlings. By comparing performance of seeds and seedlings, both experiments test whether failure of these plants to spread occurs at the germination stage, or because of subsequently poor growth and survivorship.

Materials and methods

Site description

Churchill, Manitoba is located on the north-western corner of the Hudson Bay coast. Churchill lies at the treeline, and the surrounding subarctic climate supports both tundra and boreal forest ecosystems. The area is undergoing isostatic uplift following most recent glaciation, and soils are young and poorly developed, originating in glacially deposited marine sediment (Johnson 1987). The area is thus relatively flat, and the plots within our study area are all within 10–30 m above sea level. The growing season is short, and dates of snowmelt vary substantially year to year; for the duration of the experiments reported here, snowmelt began in May, the landscape was clear of snow by mid-June, and freeze-up occurred at the end of October.

Although the town has no roads connecting to southern Canada, it has had a railway link since 1929 servicing the town's grain port (Brandson 2011). Grain shipments can be a major source of weed seeds (Ikeda et al. 2022). In Churchill, grain was cleaned prior to export, and weed seeds and other contaminants were dumped locally, resulting in the area around the railway terminal and the grain elevators being especially heavily exposed to non-native seeds and plant material (Kent et al. 2018). Consequently, many non-native species can be found around town buildings and in other anthropogenically disturbed areas.

Study species

In both the Cross-Biome and the Warming Experiments, we used locally collected transplants and seeds of three weedy non-native perennials: *Plantago major* L. (common plantain), *Linaria vulgaris* Mill. (common toadflax), and *Taraxacum officinale* (L.) Weber. (common dandelion). In addition, for the Warming Experiment, we used locally collected seeds of three additional persistent non-native species found in Churchill: *Silene latifolia* subsp. *alba* (Mill.) Greuter & Burdet (white campion), a perennial, and *Capsella bursa-pastoris* L., (shepherd's purse) and *Thlaspi arvense* L. (field penny-cress), both annuals. All six species are introduced from and widely distributed in Europe, but have occurred in the Churchill area for over 60 years (Beckett 1959). All are commonly found in roadsides and waste places in North America (Cody 2000), and some are also commonly contaminants in crop seed (McNeill 1977; Saner et al. 1995). All produce seeds in the fall; however, seeds of locally occurring *L. vulgaris* are rarely viable (Staniforth and Scott 1991), and consequently may instead rely on rhizome fragments for spread (Nadeau et al. 1992); *S. alba* potentially also may regenerate from fragments as well as seeds. Although the potential for these non-native species to establish is low, we ensured that all non-native plant material, roots, rhizomes, and soil with seed added were removed from all plots at the completion of each experiment, and follow-up surveys in subsequent years failed to find any surviving non-native plants.

Cross-Biome Experiment

In mid-August 2021, 80 individuals of *L. vulgaris*, *P. major*, and *T. officinale* were collected from various invaded sites in the Churchill area associated with anthropogenic disturbance. These plants were transplanted to eight experimental sites along the roadsides near the Churchill Northern Studies Centre (CNSC, Fig. 1), located approximately 20 km east of the Churchill townsite. *P. major* and *T. officinale* were collected and transplanted as complete rosettes, and we recorded the initial size of the transplants by measuring the length of the longest leaf for each individual. We controlled the length of *L. vulgaris* rhizomes by cutting the rhizomes to 5 cm each, and only planted one ramet per individual. Four sites were set along roadsides in lichen-heath tundra dominated by plants including *Arctostaphylos* spp. (bearberry) and other species of Ericaceae, *Dryas integrifolia* (arctic avens), and *Salix reticulata* (snow willow). Another four sites were along roadsides in boreal forest, dominated by *Picea glauca* (white spruce), mosses, and lichens. In both habitats, the disturbed roadsides used were largely exposed gravel with a few pioneer species, notably *Dryas* and mosses such as *Dicranum* spp. This gravel originated from local surface excavations, and consisted of Pleistocene glacial till dominated by Paleozoic limestone fragments (Dredge 1992) mixed with sand, with a very low organic content. Use of these roadside sites reduced differences between habitats in soil development and cover.

Sites were separated by approximately 1 km by road. At each site, 30 transplants (ten of each species) were randomized and evenly divided between both sides of the road. Individuals were spaced at least 15 cm apart to reduce competition. In August 2022, 300 seeds of *L. vulgaris*, *P. major*, and *T. officinale* were added into two replicated 25 × 25 cm plots at each roadside site, resulting in eight plots in the tundra and eight plots in the boreal forest; this resulted in 600 seeds per species per site. Seeds were added to ground surfaces at the end of the growing season, rather than buried under the gravel and soil, to approximate both the seasonal timing and spatial positioning of naturally dispersing seeds. A temperature datalogger (iButtonLink Technology © 2024) was buried 1–2 cm below the soil surface at each site to

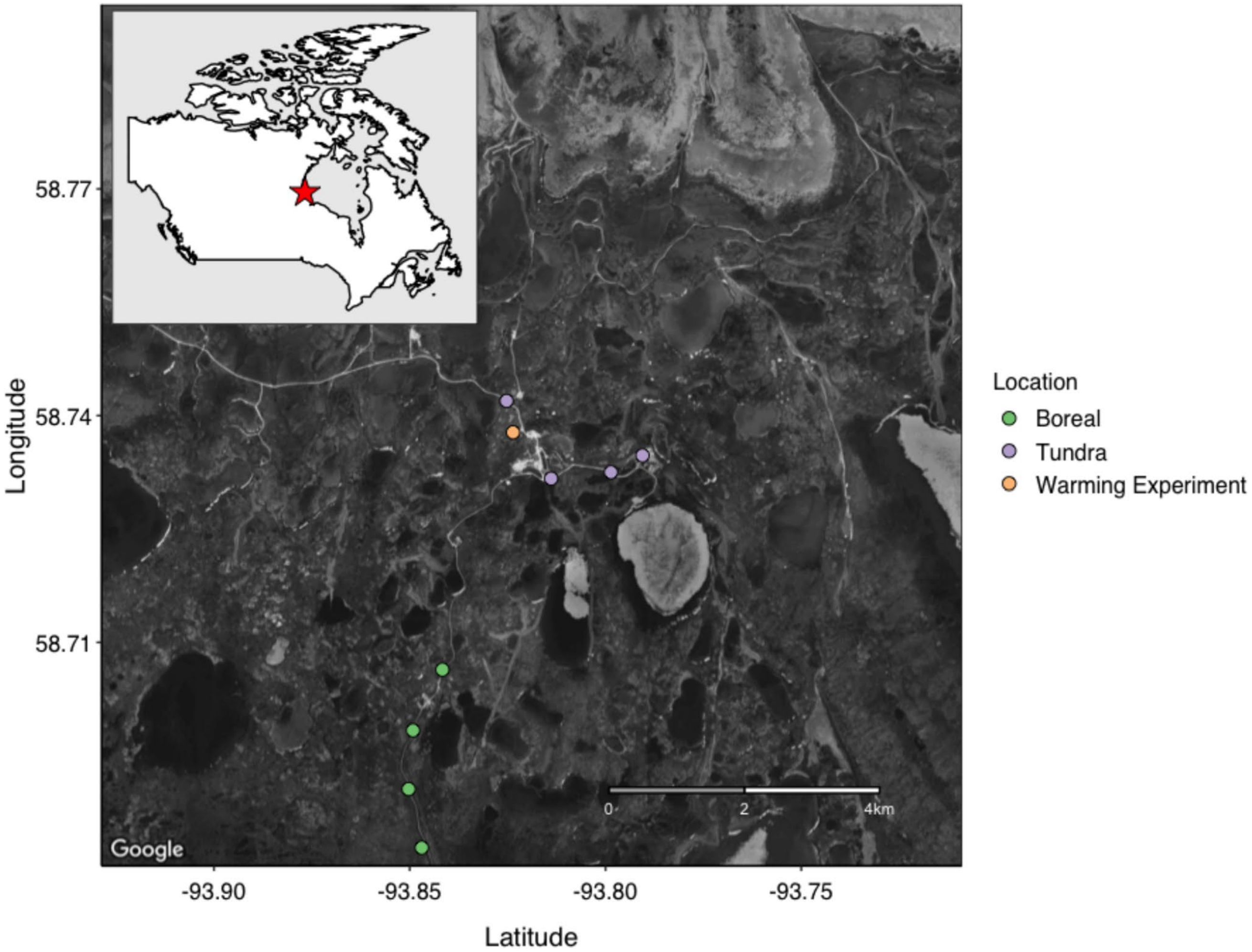

Fig. 1 Boreal forest (green) and tundra (purple) sites in the Cross-Biome Experiment, and the location of the Warming Experiment (orange) near the Churchill Northern Studies Centre, approximately 20 km east of the Churchill town area. Imagery: Google Earth (2024)

capture hourly temperatures, resulting in 4 deployed in the tundra and 4 in the boreal forest.

These plots were sampled in August from 2022 to 2024. Transplants were surveyed for survival by recording emergence and survival aboveground. If transplants emerged but died in the same summer, the individual was recorded as dead that year. Performance metrics were recorded to capture the total size of each surviving individual at the end of each growing season: for each *L. vulgaris* transplant, the height of the tallest ramet and the number of clonal ramets was recorded; for each *P. major* and *T. officinale* transplant, the length of the longest leaf and number of leaves were recorded. As all three perennial study species locally are hemicryptophytes (Hawthorn 1974; Saner et al. 1995; Verduijn et al. 2004), all measures of size represent growth that occurred during that year's growing season. Flowering success of transplants was recorded each subsequent year, and seeds of flowers were collected for germination trials and to prevent seed dispersal. Germination of added seeds was also monitored throughout the growing season in 2023 and 2024, and the total number of germinants was recorded for each year. In 2024, all transplants were removed, dried in an oven at 60 °C for 48 h, and weighed for above- and belowground biomass.

Warming Experiment

In early August 2022, a 20 m by 10 m site was established in an open-disturbed treeline area (58.73° N, 93.82° W; Fig. 1) next to a meteorological building near the CNSC. Similar to the Cross-Biome Experiment, the ground surface was dominated by bare gravel with an admixture of colonizing species. Forty 50 × 50 cm plots were marked, and the top 5 cm of vegetation and topsoil were removed to limit competition with native species. Twenty portable greenhouses (Ningbo Wonderful Plastic Industry and Trade Co., Ltd., Ningbo, Zhejiang, China, obtained through Amazon.com Inc.) were deployed randomly into half of the plots. These greenhouses were modified into open-top chambers (OTC) by partially removing their tops and the upper portion of their side panels, similar to chambers used for the International Tundra Experiment (ITEX) (Henry and Molau 1997). Initially, in August 2022, the height of these side panels was 30 cm; however, this increased temperatures by only 0.5–1 °C in treatment plots. Thus, after this first month, they were replaced by OTCs with 50 cm sides; these raised the temperature by the desired 1–2 °C, which is within the range of the estimated increase in mean summer temperature in the Arctic from the last baseline period (1981–2005, as measured by the Intergovernmental Panel on Climate Change) to mid-century (Post et al. 2019). A temperature datalogger was buried 1–2 cm under the soil surface in the center of each plot to measure hourly temperature. To test whether OTCs affected soil moisture within plots, approximately 5 g of soil was collected from each plot 48 h after the most recent rainfall in 2023. Collected soil was weighed immediately after collection, then re-weighed after 48 h in a 60 °C oven, and then, we calculated gravimetric water content (%): difference between wet and dry mass ÷ dry mass × 100%. The OTCs were removed in late August and replaced in early June each year, so that they were in place for nearly the entire active growing season.

In mid-August 2022, three transplants of *P. major*, *L. vulgaris*, and *T. officinale* were planted in half of each plot, and 300 seeds of each of the six species were added to the soil surface of the other half. Similar to the Cross-Biome Experiment, seed addition was intended to approximate the timing and positioning of naturally dispersed seeds. We again measured the initial size of each individual prior to transplant in 2022, and the same measurements of survival, performance, and flowering of transplants and seed germination were recorded as described for the Cross-Biome Experiment in late summer of 2023 and 2024. After the final sampling in 2024, all transplants were removed, dried in an oven at 60 °C for 48 h, and weighed for above- and belowground biomass.

Statistical analyses

All statistical analyses were conducted in R (Version 4.1.1; R Core Team 2021). For all parametric tests, we initially created fully crossed mixed effects models using the `lme4` package (Version 1.1–30; Bates et al. 2015), with the initial size as a covariate (height for *L. vulgaris*, and length of the longest leaf for *P. major* and *T. officinale*), and the blocking effect of site/plot. We created additional models by removing fixed and random effects using the `stats` package (Version 4.1.1). All fixed effects were evaluated using Type III tests from the `car` package (Version 3.1-2, Fox and Weisberg 2019). As measurements of survival and growth were performed each year, we used the `emmeans` package (Lenth et al. 2021) to perform post hoc comparisons of treatments within levels of year. We performed model comparison using Akaike's Information Criterion corrected for small samples (AICc; Johnson and Omland 2004), and we present results ($\alpha = 0.05$) from the model that performed equally or better during model selection; if there were several best-performing models for a metric of a particular species, we used the same formula as a model for a similar metric or for a different species, so that the models used were consistent.

For the Cross-Biome Experiment, a Poisson generalized linear model was used to test for the effect on seed germination using the habitat (tundra or boreal forest) and year after transplant as a factor (2022, 2023, or 2024) as fixed terms: ~ habitat + year; and a binomial generalized linear model was used to test for an effect on survival with habitat, year, and their interaction: ~ habitat + year + habitat:year.

To test for an effect on size and biomass of transplants, we used linear mixed effects models with habitat and year as fixed terms, with the initial size of the plant as a covariate and the site as a random factor: ~ habitat + year + initial size + [1|site]. Similarly, for the Warming Experiment, we used a Poisson generalized linear mixed model when testing for an effect on survival, and a binomial generalized linear mixed model to test for an effect on seed germination; both tests used the treatment (warming or control), year as a factor (2023, or 2024), and their interaction as fixed terms, and plot number as a random effect: ~ treatment + year + treatment:year + [1|plot]. We again used linear mixed effects models to test for the effect on size and biomass with treatment and year as fixed terms, and plot number as a random effect: ~ treatment + year + initial size + [1|plot]. The gravimetric water content (%) in control and warming plots was non-normal, so a Wilcoxon Rank Sum Test was used to test whether soil moisture differed between warming and control plots.

Results

Cross-Biome Experiment

The average difference in summer temperature (°C) between the tundra and boreal plots was approximately 1–2 °C (Fig. 2A, B). The boreal forest roadsides were consistently warmer than tundra roadsides.

Seed germination was very low for *P. major* and *L. vulgaris* in 2023 (Fig. 3A): in total, there were only three germinants of *L. vulgaris* in the boreal forest, and one in the tundra; there were two successful germinants of *P. major* in both biomes. *T. officinale* had the highest germination rates, especially in boreal sites: there were 274 germinants in the boreal forest, compared to 70 in the tundra, a significant difference ($\chi^2_{(1,4)} = 103.83$, $p < 0.0001$, Table S1). None of these seedlings grew large enough to flower or survived into the next summer, and there was no successful seed germination in 2024. Survivorship of transplanted individuals was lower in the tundra for all three species (Fig. 3B, Table S2, Table S3, Table S4). Transplants of *L. vulgaris* had the highest survivorship in the boreal forest followed by *P. major* and *T. officinale*. Survival was marginally lower in the tundra than the boreal forest for *L. vulgaris* ($\chi^2_{(1,40)} = 3.23$, $p = 0.07$), and significantly lower for *P. major* ($\chi^2_{(1,40)} = 5.49$, $p = 0.02$) and for *T. officinale* ($\chi^2_{(1,40)} = 10.16$, $p = 0.001$). Overall, survivorship of transplants of all three species was low in the tundra, with *T. officinale* disappearing by 2023 and *L. vulgaris* by 2024; only a few *P. major* survived until the end of the experiment. Over time, the number of surviving individuals decreased significantly for *L. vulgaris* ($\chi^2_{(1,40)} = 9.78$, $p = 0.008$), *P. major* ($\chi^2_{(1,40)} = 30.62$, $p < 0.0001$), and *T. officinale* ($\chi^2_{(1,40)} = 32.50$, $p < 0.0001$). Two transplants of *L. vulgaris* re-emerged after being marked as dead in 2023, and 4 transplants re-emerged after being marked dead in 2024; it is likely that this re-emergence was from rhizome fragments.

Measurements of individual size indicated that transplants became smaller over time (Fig. 4, Table S5). Size in 2021 simply reflects the size of initial transplants, rather than any habitat effects; plants never recovered to this original size. Average height of *L. vulgaris* transplants significantly decreased over time since transplantation in 2021 ($F_{(2,115)} = 43.44$, $p < 0.0001$), dropping to an average of 6.54 cm in the boreal forest and 3.35 cm in the tundra by 2022, and 1.80 cm in the boreal forest in 2024; there were no more surviving *L. vulgaris* transplants in the tundra by 2024. The mean number of ramets per *L. vulgaris* individual decreased over time since transplant, from 3.4 in both the tundra and in the boreal forest in 2022 to 1 ramet in the tundra by 2023, and 2.9 ramets in the boreal forest by 2024 ($F_{(2,198)} = 19.76$, $p < 0.0001$); note that only one ramet per individual was transplanted in 2021, and there were no more surviving *L. vulgaris* transplants in the tundra by 2024. Transplants of *P. major* individuals significantly decreased in size since transplant in 2021 ($F_{(2,132)} = 59.16$, $p < 0.0001$): the length of the longest leaf per individual decreased to a length of 6.17 cm in the boreal forest and 6.43 cm in the tundra in 2022, and to 2.88 cm in the boreal forest and 3.94 cm in the tundra by 2024. Transplants of *P. major* also decreased in the number of leaves per individual since transplant ($F_{(2,149)} = 12.81$, $p < 0.0001$), from an average of 5.1 leaves in the boreal forest and 3.8 leaves in the tundra in 2022, to 2.9 leaves in the boreal forest and 3.1 leaves in the tundra in 2024. The average length of the longest leaf on *T. officinale* transplants similarly decreased significantly over time since transplant ($F_{(2,77)} = 24.49$, $p < 0.0001$), but there was no significant effect of time on the number of leaves. Transplants of *T. officinale* in the boreal forest were 4.48 cm in 2022, and 3.80 cm in 2024. There were no surviving *T. officinale* individuals in the tundra by 2023. Flowering success was low: in 2022, 3 *P. major* and 8 *T. officinale* transplants flowered in the boreal forest, and 2 *L. vulgaris*, 5 *P. major* and 2 *T. officinale* transplants flowered in the tundra; in 2023 and 2024, only the same *P. major* transplant flowered both years in the tundra (Table S2). Collected seeds of flowering transplants were non-viable from the germination trials. Biomass of individuals was not significantly different between habitats in 2024 for *P. major* transplants ($F_{(1,40)} = 0.0024$, $p = 0.96$, Table S6, Figure S1). The average weight of *P. major* transplants in the boreal forest was 117.6 mg, while transplants in the tundra were 118.8 mg. There were no observed effects of transplant location on the biomass of *L. vulgaris* and *T. officinale* as there were no surviving transplants in the tundra by the end of the experiment.

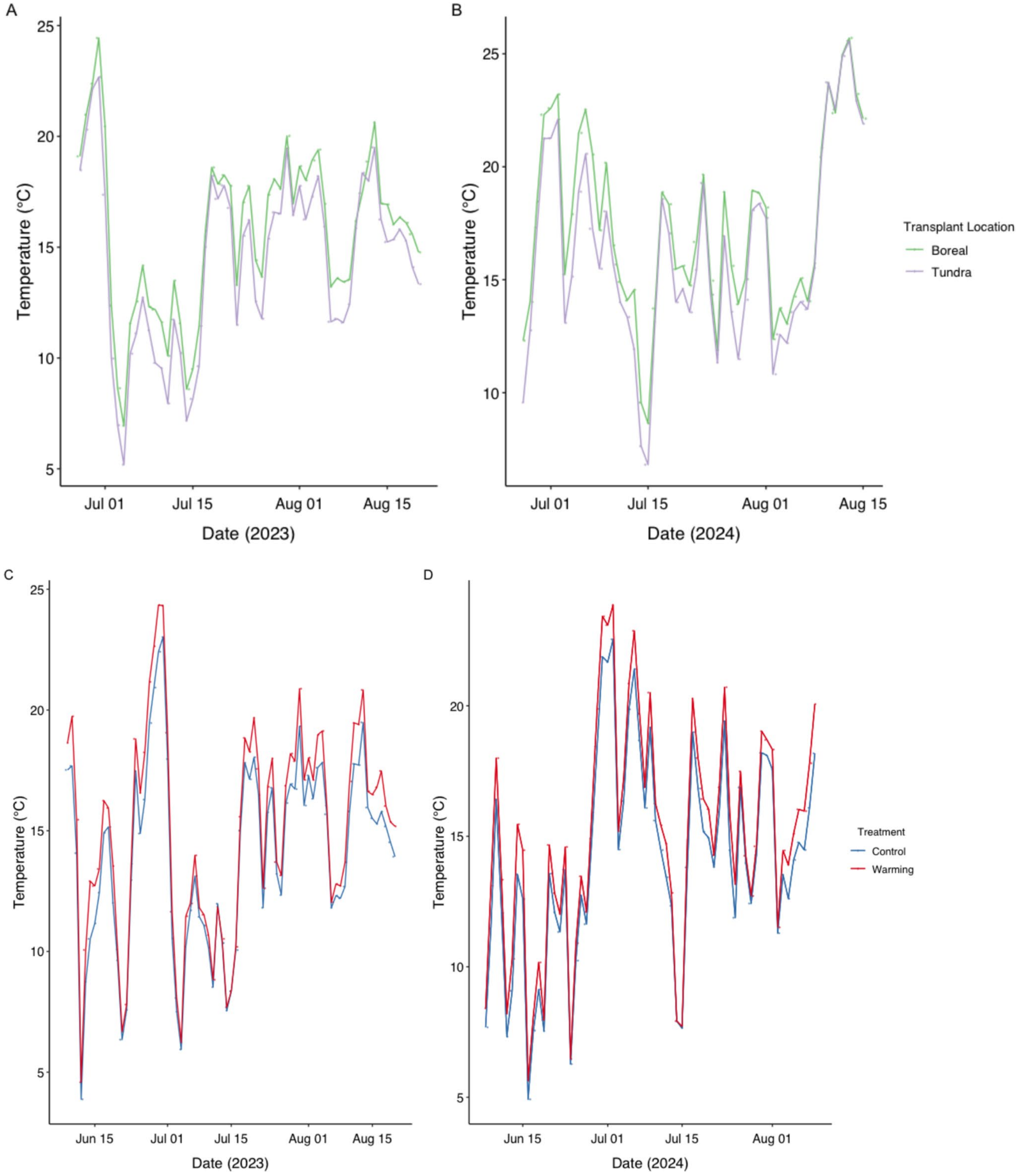

Fig. 2 Mean sub-surface soil temperature (°C), averaged daily (from midnight) from hourly temperature measurements from dataloggers. **A** Temperature averaged 14.4 °C in tundra (purple) and 15.6 °C in boreal forest plots (green) plots in 2023; **B** temperature averaged 16.2 °C in tundra plots and 17.3 °C in boreal forest plots in 2024. **C** Temperature averaged 14.0 °C in control (blue) and 15.0 °C in warming (red) plots in 2023; **D** temperature averaged 14.1 °C in control and 15.1 °C in warming plots in 2024

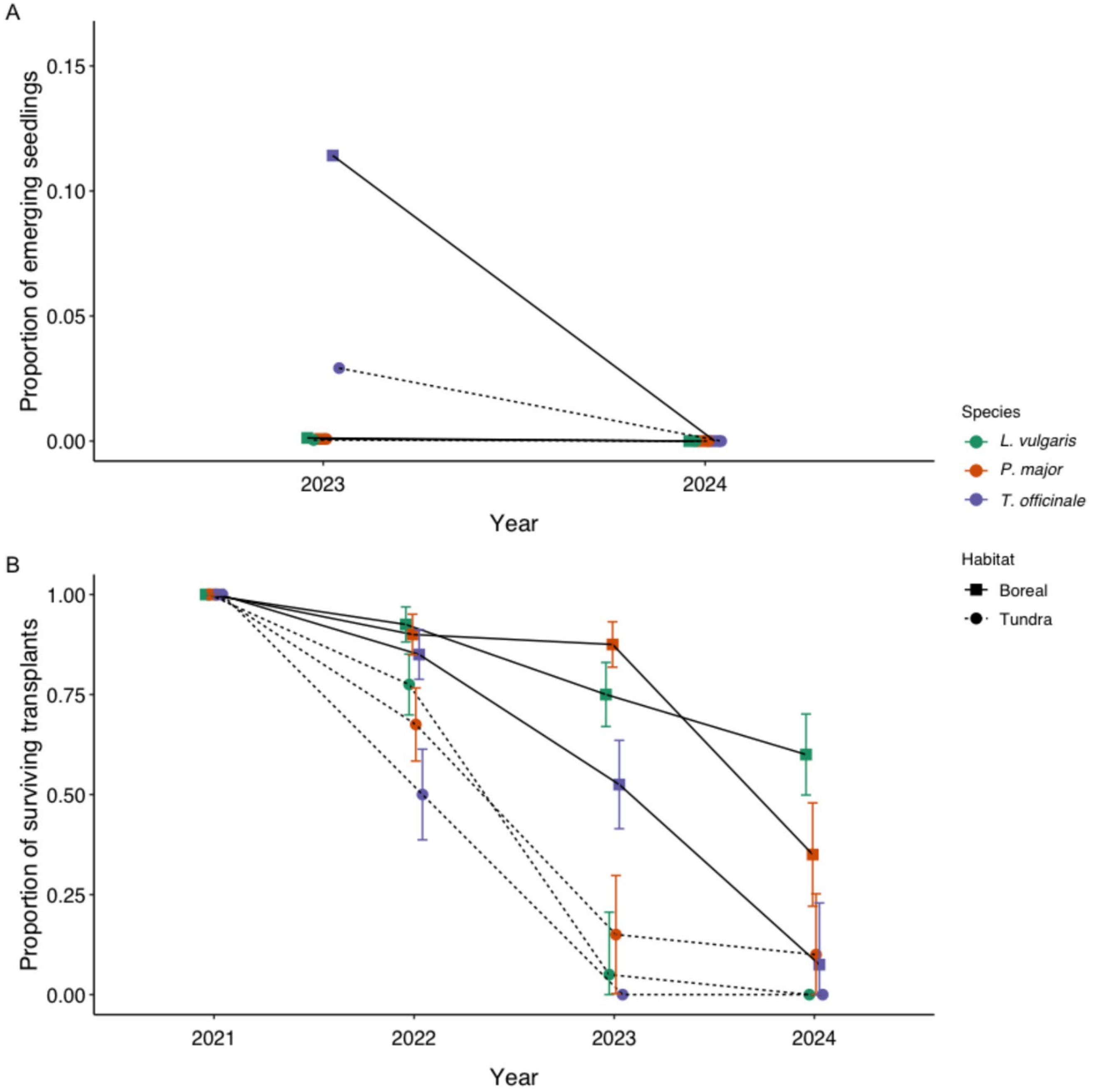

Fig. 3 Proportion of **A** emerging seedlings and **B** surviving transplants (with standard error) each year out of the original cohort following transplant in the tundra (circles, dotted lines) and boreal forest (squares, solid lines) for the Cross-Biome Experiment. Germination of *T. officinale* was significantly higher in the boreal forest ($p < 0.0001$). Survival of transplants was significantly lower in the tundra for *L. vulgaris* in 2023 ($p = 0.0002$), and for *P.* major in 2022 ($p = 0.05$) and 2023 ($p < 0.0001$). Survivorship declined significantly for all three species ($p < 0.0001$)

Warming Experiment

The OTCs increased temperature within the enclosed area by 1–2 °C (Fig. 2C, D). Gravimetric water content was lower in the warming plots compared to the control plots (Figure S2, Mann–Whitney $U = 297$, $p = 0.008$).

Seed germination was low for all species in 2023, and almost zero in 2024 (Fig. 5A, Table S7). Seed germination in 2023 was significantly higher in the warming treatment for *P. major*, with 13 germinants compared to two in the control treatment ($\chi^2_{(1,40)} = 4.94$, $p = 0.03$); as well, germination in 2023 was significantly higher in the warming treatment for

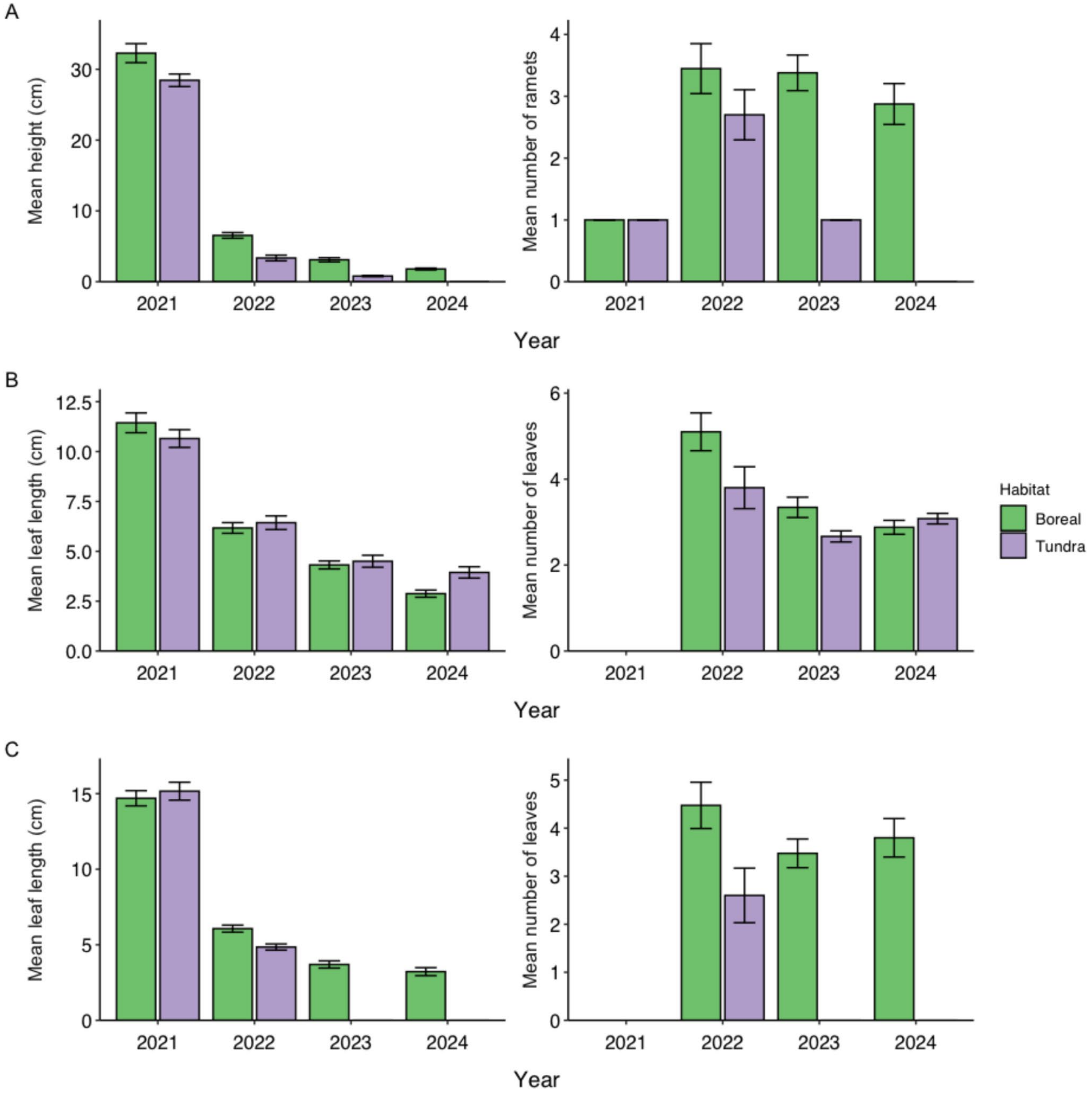

Fig. 4 Mean measures of performance and standard error across individual transplants in the boreal forest (green) and tundra (purple) sites for the Cross-Biome Experiment, measured at the end of the growing season. **A** *L. vulgaris* mean plant height (cm) decreased significantly over time ($p < 0.0001$), and individuals were smaller in height in the tundra ($p = 0.0009$), but there was no difference in the average number of ramets per surviving individual. Note that only one ramet per *L. vulgaris* individual was transplanted in 2021, and the subsequent increase in the mean number of ramets represents clonal growth. **B** *P. major* decreased significantly in the mean length of the longest leaf (cm, $p < 0.0001$) and number of leaves per individual ($p < 0.0001$) over time. **C** *T. officinale* decreased significantly in the mean length of the longest leaf (cm, $p < 0.0001$), and were slightly smaller in the tundra ($p = 0.06$), but there was no difference in the number of leaves per individual. Note that there were no initial measurements of leaf number of *P. major* and *T. officinale* after transplant in 2021

T. officinale with 515 germinants compared to 166 in the control ($\chi^2_{(1, 40)} = 9.51, p = 0.002$). Differences between treatments were non-significant for *L. vulgaris* (four germinants in the warming treatment, and one germinant in the control treatment in total in 2023) nor for *S. alba* (36 germinants in the warming treatment and 29 germinants in the control treatment in total in 2023). None of these seedlings grew large enough to flower or survived into the next summer.

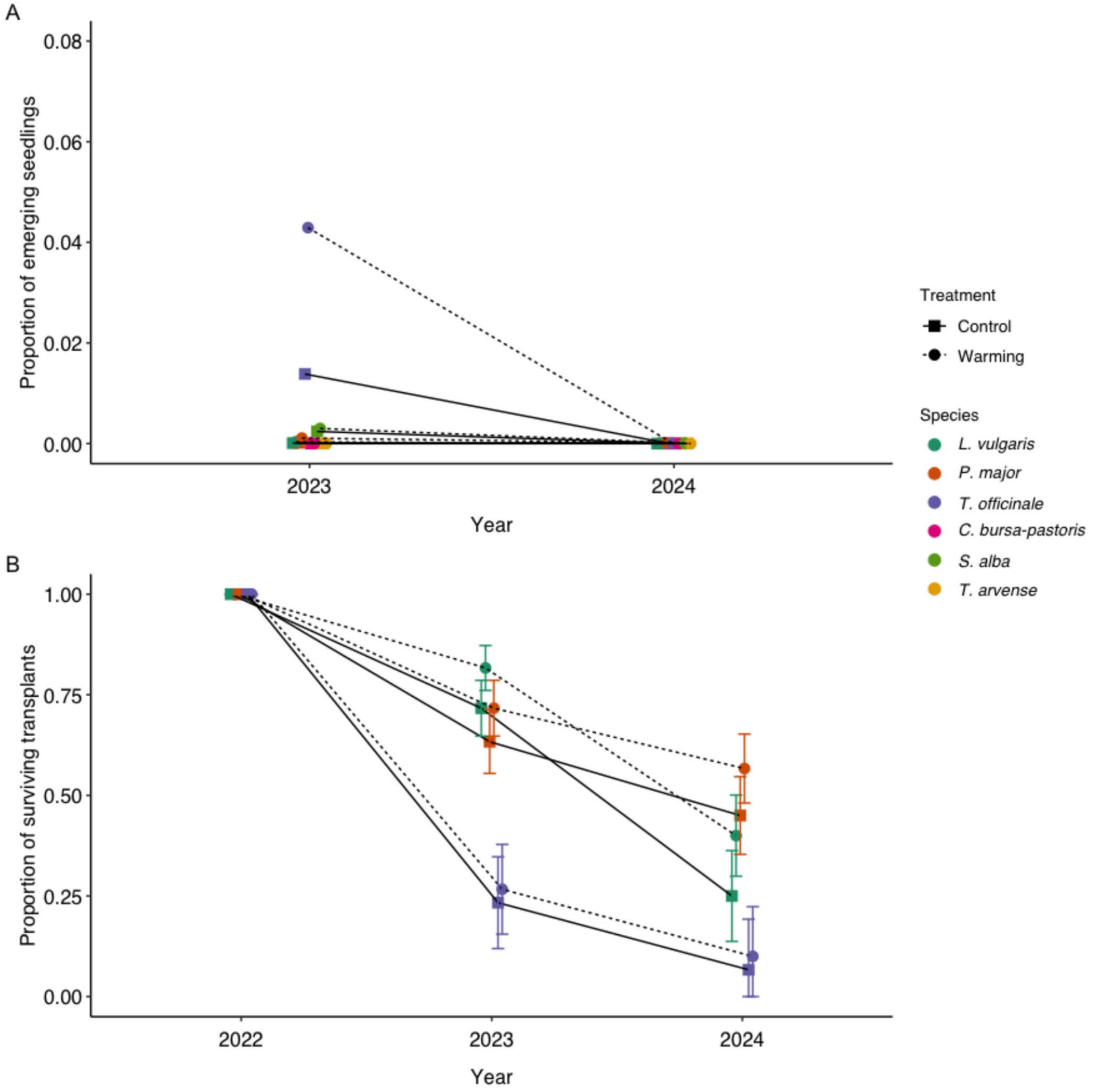

Fig. 5 Proportion of **A** emerging seedlings, and **B** surviving transplants (with standard error) each year out of the original cohort following transplant into the warming (circles, dotted lines) and control (squares, solid lines) treatments for the Warming Experiment. Germination was significantly higher in the warming treatment for *P. major* ($p = 0.03$) and *T. officinale* ($p = 0.002$) seeds. There was no evidence of germinating *C. bursa-pastoris* or *T. arvense*. Survival decreased significantly over time for transplants of *L. vulgaris* ($p < 0.0001$), *P. major* ($p = 0.02$), and *T. officinale* ($p = 0.01$)

There were only four seeds that successfully germinated in 2024, and all germinated in warming plots: two *P. major* seeds, one *S. alba* seed, and one *T. officinale* seed.

Transplant survivorship was higher in the warming treatment for all three species, and the number of surviving individuals again decreased significantly over time, from 2023 until 2024, for all three species (Fig. 5B, Table S8, Table S9, Table S10). Survival was highest for *L. vulgaris*: in the first year, 49 transplants survived in the warming plots, and 43 transplants survived in the control plots; the number of surviving individuals decreased significantly in 2024, to 24 transplants in the warming plots and 15 transplants in the control plots ($\chi^2_{(1,\,60)} = 24.38$, $p < 0.0001$). Survival of *P. major* also decreased significantly over time, from 43 in warming plots and 38 in control plots in 2023, to 34 in warming plots and 27 in control plots in 2024 ($\chi^2_{(1, 60)} = 5.72$, $p = 0.02$). Survival was the lowest for *T. officinale* transplants, with 16 transplants surviving in the warming plots and 14 transplants surviving in the control plots; these values dropped significantly in 2024 to 6 surviving transplants in the warming plots and 4 surviving transplants in the control plots ($\chi^2_{(1, 60)} = 6.89$, $p = 0.01$). There were no effects of warming or treatment x year interactions on survival.

Over time, transplants of all three species became smaller (Fig. 6A–C, Table S11). Average height of *L. vulgaris* transplants significantly decreased from 4.66 cm in the warming treatment and 4.63 cm in the control plots in the first year to 3.21 cm in the warming treatment and 2.41 cm in the control treatment by the end of the experiment ($F_{(1, 108)} = 17.08$, $p = < 0.01$). The average number of ramets per *L. vulgaris* individual also decreased slightly over time, from 3.3 in warming plots and 3.0 in control plots to 2.8 in warming plots and 2.0 in control plots by 2024 ($F_{(1, 113)} = 3.86$, $p = 0.052$). The average length of the longest leaf of *P. major* individuals significantly decreased over time ($F_{(1, 112)} = 42.42$, $p < 0.0001$), from 4.0 cm in warming plots and 3.58 cm in control plots in 2023, to 2.91 cm in warming plots and 2.47 cm in the control plots. Transplants of *P. major* also significantly decreased in the number of leaves per individual over time ($F_{(1, 112)} = 15.22$, $p = 0.0002$), from an average of 3.5 leaves in warming plots and 3.2 leaves in control in 2023, to 3.0 leaves in the warming plots and 2.5 leaves in the control plots by 2024. The average length of the longest leaf and number of leaves of *T. officinale* transplants also decreased, from 3.58 cm and 3.9 leaves in warming plots to 2.27 cm and 2.2 leaves by 2024, and from 3.68 cm and 3.1 leaves in control plots to 2.25 cm and 2.3 leaves by 2024 ($F_{(1, 35)} = 6.87$, $p = 0.013$).

There was no effect of warming on any individual measure of plant size, although transplants of all species were slightly larger in warming plots. Flowering success again was low: 2 *L. vulgaris* and 3 *P. major* transplants flowered in 2023, and 1 *L. vulgaris* and 3 *P. major* transplants flowered in 2024 (Table S8). All successful flowering transplants were in the warming plots, and there was no successful flowering transplant of *T. officinale* or of individuals in the control plots. Biomass of individuals was slightly higher in warming plots (Fig. 6D–F, Table S12), although there was no significant effect of warming. The average final biomass of *L. vulgaris* transplants in the warming treatment was 89.93 mg, while 74.54 mg in the control treatment. Transplants of *P. major* had an average biomass of 60.54 mg in warming plots, and 59.32 mg in the control plots. Finally, *T. officinale* transplants were an average of 47.68 mg in the warming treatment, and 32.45 mg in the control treatment.

Discussion

At high latitudes, non-native species are challenged by a suite of factors that limit their success and spread. We investigated whether summer temperatures limit non-native plant invasions in the tundra-boreal habitat of Churchill, contributing to their failure to spread from persistent populations in areas of human settlement into the surrounding tundra and boreal forest. This was done by experimentally introducing non-native species into warmer microsites and roadsides, which are potential entry points for further subarctic invasion.

In our Cross-Biome Experiment, we found that seeds of non-natives in both boreal forest and tundra sites had very low germination rates, did not grow larger than the seedling stage, and rarely were unable to survive the winter. When we circumvented this barrier to establishment by instead introducing individuals at the post-seedling stage as transplants (as can happen with soil movement: Syed et al. 2023), we found that although most could survive for at least a year in both tundra and boreal sites, their persistence was generally short-lived. Individuals of all species do occasionally occur on roadsides and other disturbed sites well outside of town (Kent et al. 2018, *pers. obs.*), suggesting successful dispersal of seeds and/or rhizomes does occasionally occur, but, as in our experiment, this seems insufficient to lead to local spread. Thus, temporary colonization of non-native species on roadsides does not provide successful invasion routes to adjacent natural habitats.

Exposure to the harsh subarctic climate is presumably the strongest cause for the failure of most experimental seeds and plants (Chapin et al. 1995; Smith et al. 2012). Consistent with this, transplants in the boreal forest had higher rates of survival over time, while almost all transplanted individuals died in the tundra sites. This suggests that establishment is more likely to occur in the boreal forest than in the tundra. This is consistent with the warmer microclimate of open roadsides in the boreal forest (Jobbágy and Jackson 2000), and the shelter of the forest stands (Resler et al. 2005), but also possibly might reflect correlated factors such as slightly better developed roadside soils (though our sites were all on bare gravels, rather than natural forest or tundra soils). In addition, the tundra is more open and closer in distance to Hudson Bay, making it more exposed to the Bay's harsh winds and colder temperatures (Brandson 2011). Finally, there are many more opportunities for non-native species to be transported by humans into the boreal forest (Mortensen et al. 2009; Rauschert et al. 2017), for example as a result of frequent human disturbance due to recreational activities and roadside maintenance (Langor et al. 2014), or via

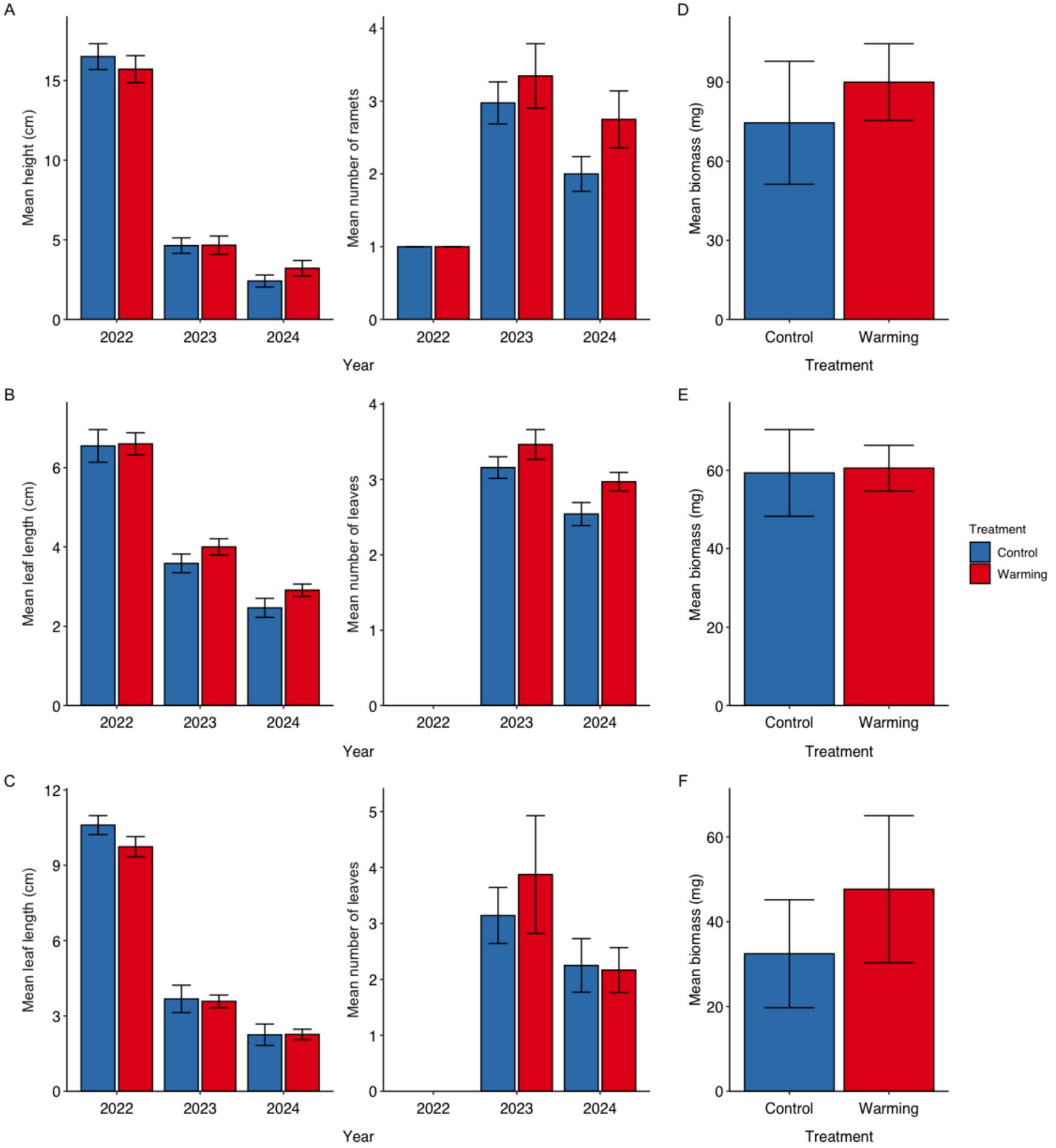

Fig. 6 Mean measures of performance and standard error across individual transplants in control (blue) and warming (red) plots for the Warming Experiment, measured at the end of the growing season. Different letters denote significant pairwise differences. **A** *L. vulgaris* transplants decreased over time in mean height (cm, $p=0.002$) and mean number of ramets for each individual ($p<0.0001$). Note that only one ramet per *L. vulgaris* individual was transplanted in 2022, and the subsequent increase in the mean number of ramets represents clonal growth. **B** *P. major* decreased significantly in mean length of the longest leaf (cm, $p<0.001$) and number of leaves per individual ($p=0.005$) over time. **C** *T. officinale* mean length of the longest leaf (cm) and number of leaves were not significantly different between treatments or over years. There were no initial measures of leaf number for *P. major* and *T. officinale*. Mean biomass (mg) of surviving transplants was not significantly different between treatments for **D** *L. vulgaris*, **E** *P. major*, and **F** *T. officinale*, measured at the end of the 2024 growing season

introductions through resource extraction, such as logging (Sanderson et al. 2012), occasionally resulting in persistent populations (Rose and Hermanutz 2004). For all of these reasons, boreal regions are more likely to be more vulnerable to invasion than tundra ecosystems.

Our Warming Experiment also provided evidence for the importance of summer temperatures. Although non-native seeds had low germination rates, and did not grow larger than the seedling stage, warming strongly increased germination of *T. officinale*. This species is abundant in town, where it preferentially occurs in warmer microsites (Da Silva and Kotanen 2024). It is common for human-disturbed areas to be hotspots for non-native species at high northern and southern latitudes (Frenot et al. 2005; Laruelle et al. 2019; Wasowicz et al. 2020; Bartlett et al. 2021) for a complex of reasons including warmer local temperatures (Laruelle et al. 2019; Da Silva and Kotanen 2024), as, while the colder climate outside of towns (Laruelle et al. 2019) may act as a barrier to their successful establishment and spread. Growth of *P. major* and *L. vulgaris* transplants also improved slightly in warmer temperature treatment; however, the number of surviving transplanted individuals and the growth of these individuals still declined over time, suggesting that unfavorable conditions will ultimately drive such populations toward extinction. Increasing temperatures may improve performance, but the 1–2 °C difference we experimentally achieved was not enough to tip the balance.

Colder environments and shorter seasons represent significant barriers to survival and growth of plants (Billings and Mooney 1968), while limiting successful regeneration (Müller et al. 2011). However, conditions vary from year to year, with especially important consequences for species near their range limits and at the treeline (Stevens and Fox 1991; Holtmeier and Broll 2019). We have observed that many non-native species have variable population sizes from year-to-year in the town of Churchill. It is likely that high interannual variation and low seedling recruitment rates often lead to transient non-native populations (Hawthorn and Cavers 1976; Staniforth and Scott 1991). Conversely, multiple introduction events may have been required before these species encountered a year that allowed them to germinate, grow, and reproduce, and disperse their own propagules (Lockwood et al. 2005; Alsos et al. 2007). If warmer temperatures increase the reliability of germination and survival, they may eventually reduce this variation and lead to greater establishment and persistence of non-natives.

Currently, the number of weedy non-native species peaks at mid-latitudes (Guo et al. 2021), and their ranges are constrained at higher latitudes by stressful abiotic environments. However, these range limits are changing due to climate warming (Chen 2012; Pauchard et al. 2016; Myers-Smith et al. 2019; Rew et al. 2020), shifting species into new, previously uninvaded regions (Beerling 1993; Walther et al. 2009; Smith et al. 2012; Bradley et al. 2024) and into higher latitudes (Zhang et al. 2023). Many plant species are already moving to higher latitudes and altitudes (Wallingford et al. 2020; Iseli et al. 2023); in particular, non-native species can benefit more from warming than native species (Welshofer et al. 2018). Abiotic constraints may already be locally ameliorated in the Churchill town footprint, for instance in warmer, sheltered microsites (Da Silva and Kotanen 2024), resulting in persistent populations. As regional temperatures continue to increase, so will the risk that these populations will spread from this original source.

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Author contribution statement VMZ and PMK conceptualized the study and developed the methodology. VMZ conducted the investigation, collected the data, completed the formal analysis and visualizations, and wrote the original draft of the manuscript. All authors contributed feedback and comments to the final manuscript.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

Highlighted student paper We investigate factors that cause failed invasions in natural ecosystems. We replicate across the tundra-boreal edge for several years and find evidence that low summer temperatures inhibit invasions.

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