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ORIGINAL PAPER

Nutrient addition increases non-native plant growth but not survival in a subarctic treeline environment

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Abstract High-latitude ecosystems are relatively uninvaded by non-native plant species compared to mid-latitudes. An exception is in some human-disturbed areas, where non-native species may benefit from an increase in soil nutrients following anthropogenic disturbance. In the subarctic settlement of Churchill, Manitoba, Canada, over a hundred non-native plant species have been recorded within town and other human-associated disturbed areas, and while some of these species have persisted for decades, almost none has spread into the surrounding natural ecosystems. We used a field experiment to investigate the effects of annual additions of nitrogen (N) and phosphorous (P) on the survival and growth of three perennial non-native species (*Linaria vulgaris*, *Plantago major*, *Taraxacum officinale*). We found that nutrient addition increased non-native plant growth, but had no positive effect on their survival. Instead, survival rapidly decreased over time, irrespective of nutrient addition. This suggests that nitrogen or phosphorous limitations are not the sole barriers to successful northern invasions, though they may limit the growth of any surviving plants. Instead, nutrient supply likely interacts with factors such as microclimate to determine when populations of non-natives can persist.

Keywords Non-native species · Plant invasions · Nutrient addition · Tundra · Subarctic

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Introduction

Arctic and subarctic ecosystems generally are nutrient-poor (Henry et al. 1986; Lang et al. 2021), and nitrogen fixation can be low and variable, even in the summer (Alexander and Schell 1973). In these high-latitude ecosystems, net primary productivity (NPP) is limited by low nitrogen and phosphorous availability (Haag 1974; Ngai and Jefferies 2004) and the slow release of nutrients from organic matter (Jonasson et al. 1999). Consequently, the growth and biomass production of plants is limited (Chapin et al. 1986), resulting in plant communities that are dominated by slow-growing native vegetation adapted to these conditions, with specialized mycorrhizae or other low-nutrient adaptations (Read 1991). Changes to the nutrient composition of such soils can alter the growth of plants (Shaver and Chapin 1995), and the richness and diversity of plant communities (Tilman 1987; Theodose and Bowman 1997;

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Gharajehdaghipour et al. 2016). For instance, soil nutrient uptake may differ between species, allowing colonization by plant species that are able take advantage of increases in nutrients (Robinson et al. 1998); such effects can also differ across plant communities (Henry et al. 1986; Theodose and Bowman 1997).

Increased nutrient content in soils can benefit non-native species through several different mechanisms. In general, an intermediate influx of nutrients can increase the diversity of a plant community and the growth of individuals (Gurevitch et al. 2006). However, nutrient increases can provide an additional advantage of growth to non-natives, which often include weedy, nutrient-demanding species. Such ruderal, fast-growing non-native species can outcompete native species for these resources, and these non-native species can produce greater biomass with increased resources (Milberg et al. 1999). The benefit of increased nutrients may favour non-native plants even further when coupled with other factors facilitating invasions, for instance by allocating these additional resources for growth while in the absence of natural enemies (Blumenthal 2006; Heckman et al. 2016). Finally, non-native species, once established, may also be able to increase nutrient availability and thus facilitate future invasions (Ehrenfeld 2003). Thus, any increase in nutrients can change the plant community composition, resulting in opportunities for non-native species to successfully invade.

Anthropogenic disturbance can change the amount of soil nutrients in a community. Human activity and land use can increase the resource availability in an area by adding nutrients (Vitousek et al. 1997; Dukes and Mooney 1999), or increasing nutrient mineralization which can increase nutrient availability, leading to increased plant growth (Hobbie et al. 2002). Higher levels of available soil nutrients can disproportionately benefit fast-growing and weedy non-native species, especially since these species are typically generalists to a wide range of habitats (Hobbs and Huenneke 1992; Davis et al. 2000; Lake and Leishman 2004; Dawson et al. 2012). However, nutrient addition can also decrease plant growth or biodiversity (Eskelinen 2008; Isbell et al. 2013). In the Arctic and subarctic especially, increased human activity is a major source of nutrient deposition in a historically nutrient-limited region, which can alter plant communities (Shaver and Chapin 1995). However, few studies have directly investigated how non-native plant species may respond to nutrient increases in high latitude ecosystems.

Using a field experiment, we focus on the role of increased soil nutrients, specifically nitrogen (N) and phosphorous (P), on non-native transplants in a subarctic environment. We hypothesized that artificially enriching soils with nutrients will increase the survival, growth, and biomass of established non-native plants. Such a result could help to explain the local persistence of non-natives on anthropogenic soils, but not in unmodified tundra or boreal sites.

Methods

Study Area

Churchill, Manitoba, Canada (58.5°N) is a subarctic treeline town, with a long history as a grain and shipping port (Brandson 2011). Local natural ecosystems have previously been demonstrated to be N- and/or P-limited (Ngai and Jefferies 2004; Gharajehdaghipour et al. 2016). In contrast, in disturbed areas within town and associated areas, such as in landfills, soils are visibly darker than the natural sandy tundra soil, indicating previous organic enrichment, including nutrient-rich domestic and agricultural waste (Kent et al. 2018). These sites are currently dominated by non-native species that do not occur in the surrounding tundra and boreal forest ecosystems. Previous measurements of nutrients within soils invaded by non-native plant species in Churchill have confirmed slightly elevated levels of nitrogen and phosphorous (Kent et al. 2018; Zhang and Kotanen 2023), however these studies only investigated the association of soil nutrients and non-native species, and did not directly test the effect of increased nutrients.

Study species

We used locally-collected non-flowering transplants of three weedy non-native perennials: *Plantago major* L. (common plantain), *Linaria vulgaris* Mill. (common toadflax), and *Taraxacum officinale* F.H. Wiggers (common dandelion, sensu Brouillet 2006). All three species are introduced from and widely distributed in Europe, but have occurred in the Churchill area for over 60 years (Beckett 1959). Using transplants in our experiments allows us to describe the

survival and growth of established plants, including those originating as root or rhizome fragments. All of these species are Eurasian in origin, but are common in nutrient-enriched habitats in temperate southern Canada, including lawns, disturbed waste areas, and agricultural fields.

Nutrient addition experiment

In August 2022, a 30 m × 20 m site was established in an open tundra-boreal edge habitat (58º 44′ 16" N, 93º 49′ 25" W, ~ 15 m ASL) next to a meteorological building near the Churchill Northern Studies Centre (CNSC), approximately 20 km east of the Churchill town. This study site was previously disturbed during the construction of the building and neighbouring anthropogenic structures, but has now been recolonized by native species; soil N and P remain scarce. Fifty 50 cm × 50 cm plots, each separated by at least 1 m from neighbours, were disturbed to remove native vegetation, and the top 5 cm of soil was raked. The fifty plots were then divided into two treatments. Nutrients dissolved in water were applied to one treatment, resulting in an influx of 10 g m^{-2} $year^{-1}$ of nitrogen (added as urea $CO(NH_2)_2$), and 5 g m^{-2} $year^{-1}$ of phosphorous (added as calcium phosphate monobasic monohydrate $Ca(H_2PO_4)_2SO_4$). The amounts and kinds of nutrients added have been reported to produce changes to tundra plant biomass (e.g., Gharajehdaghipour, et al. 2016, Lang et al. 2021), and are the same or within the ranges of other nutrient addition experiments in northern ecosystems (Shaver and Chapin 1980, Gough and Hobbie 2003). The remaining 25 plots received water but no nutrients. This nutrient application was then repeated at the start of the growing season during each year that the experiment was run (June 7, 2023, and June 7, 2024); adding nutrients at the start of the season simulates the nutrient pulses during snowmelt and with warmer temperatures (Stanton et al. 1994).

Within each plot, three transplants each of *P. major*, *L. vulgaris*, and *T. officinale* were planted, resulting in a total of 75 individuals of each species transplanted into either the 25 nutrient addition or the 25 control plots. Initial performance data of these three species were collected: height was measured for *L. vulgaris*, and the length of the longest leaf for *P. major* and *T. officinale* was measured. The transplants in these plots were sampled in the summer of 2023 and 2024 for survival by recording emergence at the beginning of the growing season. If transplants emerged earlier in the summer but died in the same summer, the individual was recorded as dead for the year. Performance metrics were recorded individually for each transplant at the end of the season: plant height and the number of ramets was recorded for *L. vulgaris*, and length of the longest leaf and number of leaves were recorded for *P. major* and *T. officinale*. After the final sampling in August 2024, all surviving transplants were harvested, 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 mixed effects models with the fixed effects of nutrient treatment, year, and their interaction as categorical variables, and with the random effect of "plot", using the 'lme4' package (Version 1.1–30; Bates et al. 2015). We created additional models by removing the random effect using the 'stats' package (Version 4.1.1). We performed model comparison of Restricted Maximum Likelihood (REML) fitted models using Akaike's Information Criterion corrected for small samples (AICc; Johnson and Omland 2004) to select the model with the lowest AICc; if there were multiple best-performing REML models for a measurement of a particular species (AICc difference of less than 2), we selected the model with the same formula as a model for a similar metric or for a different species, so that the models used were consistent. We present results ($\alpha = 0.05$) using Type 3 analysis-of-variance from the 'car' package (Fox and Weisberg 2019) for the maximum likelihood (ML) fitted best-performing model (See Table S5 for a summary of all models used). We conducted post-hoc tests on the fixed effects of the best-performing model by computing estimated marginal means (EMMs) using the 'emmeans' package (Lenth et al. 2021).

A binomial generalised linear model was used to test for the additive fixed effect of nutrient treatment and year on survival, with a random effect of plot, resulting in the formula: ~ nutrient treatment + year + (1|plot). A linear mixed effects model was used to analyse the effect of

nutrient addition, year, and their interaction on plant growth, with plot as a random effect and the initial size of the transplant as a covariate: ~ nutrient treatment + year + treatment: year + initial size + (1|plot); the exception are the models for *T. officinale* growth, which had a lower AICc (difference greater than 2) than the model with the interaction, so the interaction term was dropped: ~ nutrient treatment + year + initial size + (1|plot). We assessed growth between nutrient treatments and between time from 2023 to 2024, but did not compare transplant sizes to the initial pre-transplant size measured in 2022. To test for the effect of nutrient addition on total dry biomass, we used a linear regression model with initial transplant size as a covariate, but dropped plot as a random effect, as models with plot as a random effect had a higher AICc (difference greater than 2), resulting in the model: ~ nutrient treatment + initial size. We natural log-transformed all measurements of growth and biomass for all three species to meet the assumption of normality of residuals.

Results

Nutrient addition had no effect on survival for transplants of *L. vulgaris* or *T. officinale* (Fig. 1, Tables S1 and S2), but nutrient addition did have a significant, negative effect on the survival of *P. major* transplants. Survival also rapidly decreased over time for all species regardless of nutrient treatment. The number of surviving transplants of *P. major* decreased over time, from 52 individuals in the control treatment and 45 individuals in the nutrient addition treatment in 2023, to 40 individuals in the control treatment and 24 individuals in the nutrient treatment by 2024. There were three *P. major* individuals in the control plots and one *P. major* individual in the nutrient addition plot that were marked as dead in 2023, but were found alive again in 2024. Out of the 75 individuals of *L. vulgaris* that were transplanted into each treatment, 52 individuals of each treatment survived in 2023, but this decreased by 2025, to 17 individuals in the control treatment and 34 individuals in the nutrient treatment. For *T. officinale*, survival also decreased over time, from 48 individuals in 2023 to 16 individuals in 2024 in the control plots, and 33 individuals in 2023 and 15

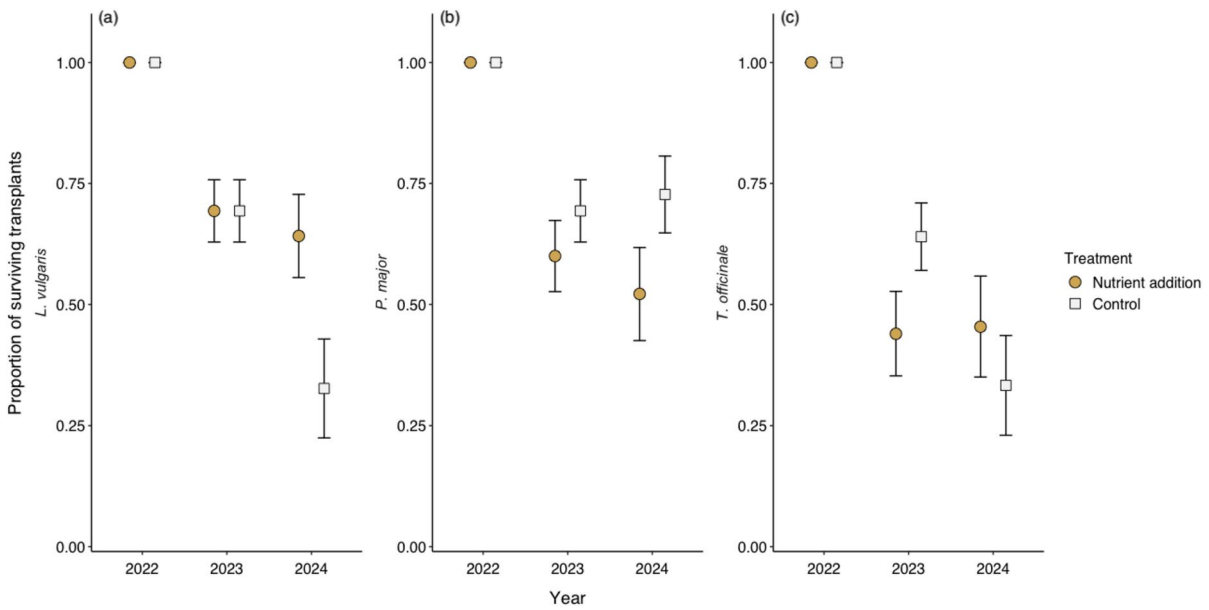

Fig. 1 Mean survival (±standard error) of transplants each year in nutrient addition (square yellow points) and control plots (round white points), separated by species **a** *L. vulgaris*; **b** *P. major*; **c** *T. officinale*. A total of 75 individuals of each species was transplanted into both the nutrient addition and control treatments in 2022, as indicated by the 100% survival post-transplant. Survival decreased over time for all three species; nutrient addition further decreased survival of *P. major* ($p < 0.05$). For *p*-values, see Table S2

transplants survived in 2024 in the nutrient addition plots.

Nutrient addition improved the growth of transplants, and this benefit was observed over both years of sampling (Fig. 2a–c, Table S3). Transplants of *L. vulgaris* had significantly greater stalk height in the nutrient addition plots, with an average height of 4 cm in 2023 and 7.3 cm in 2024, compared to 3.6 cm in 2023 and 2.2 cm in 2024 in the control plots. There was also a significant interaction between nutrient addition and time on *L. vulgaris* ramets, where nutrient addition had a significant benefit in 2024: on average, there were 2.0 ramets in the control plots and 2.3 in the nutrient plots in 2023, which decreased to 1.6 cm in the control plots and increased to 2.9 cm in the nutrient plots by 2024. Similarly, there was a significant interaction between nutrient addition and year on the average length of *P. major* leaves, where nutrient addition improved growth over time. However, there was a significant, negative effect of time on the size of *P. major* transplants. The average length of the longest leaf was 3.3 cm in the nutrient plots and 3.6 cm in the control plots in 2023, while in 2024, the average length of the longest leaf was 3.5 cm in the nutrient plots and 2.8 cm in the control plots. Transplants of *T. officinale* also benefitted from the added nutrients. The average leaf length (cm) of *T. officinale* significantly increased from an average of 3.2 cm in the control treatment to 4.4 cm in the nutrient addition treatment in 2023, and 3.7 cm in the control treatment to 7.0 cm in the nutrient treatment in 2024. The average number of leaves of *T. officinale* also significantly benefitted from the added nutrients, increasing from an average of 2.5 leaves in 2023 and 2.2 leaves in 2024 in the control plots, to an average of 3.8 leaves in 2023 and 3.5 leaves in 2024 in the nutrient addition plots. There was also a significant negative effect of time on the average length of the longest leaf of *T. officinale* transplants. Only transplants in nutrient addition plots flowered (Table S1): two individuals of *L. vulgaris* and two individuals of *T. officinale* flowered in 2023, and five individuals of *L. vulgaris* and four individuals of *T. officinale* flowered in 2024. No transplants of *P. major* flowered.

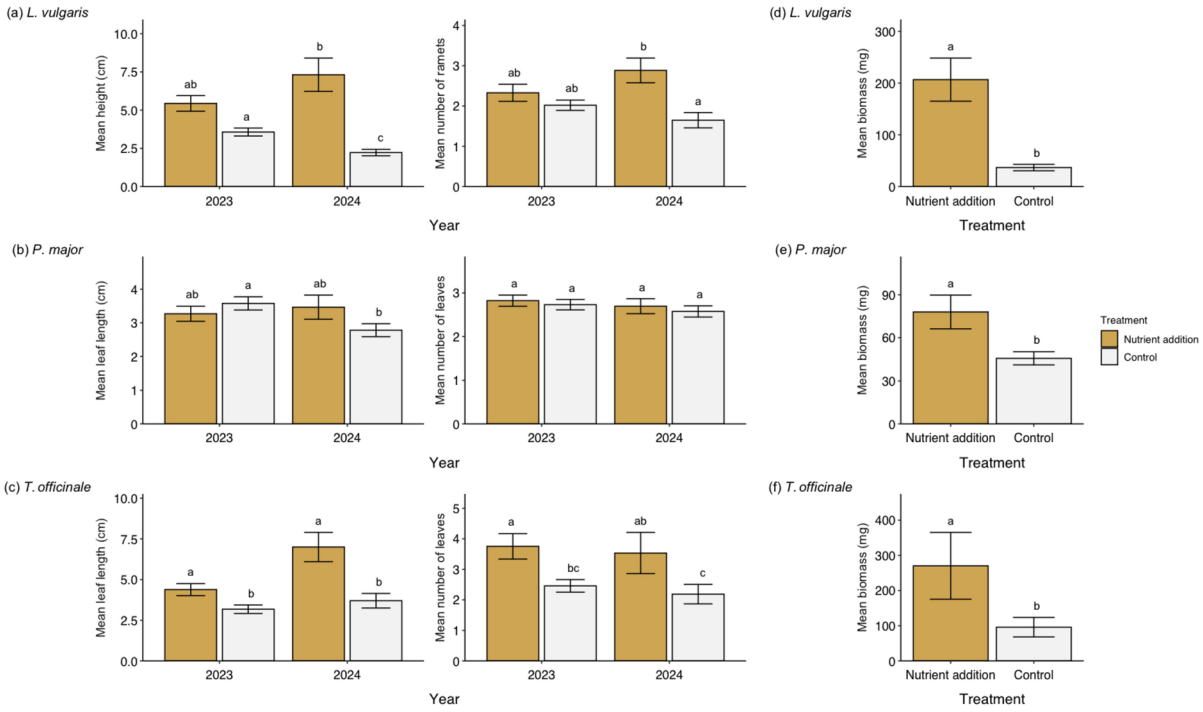

Fig. 2 Mean growth (±standard error) of transplants each year in nutrient addition (yellow) and control (white) plots. The size of transplants is plotted in panels (**a**), (**b**), and (**c**), and the biomass produced by transplants are plotted in panels (**d**), (**e**), and (**f**). Bars that do not share letters differed significantly ($p < 0.05$). For p-values, see Tables S3 and S4

Finally, the total dry plant biomass in nutrient addition plots was significantly larger for all three species (Fig. 2d–f, Table S4). Average dry biomass of *L. vulgaris* transplants averaged 207 mg in the nutrient addition treatment and 37 mg in the control treatment. Average dry biomass of *P. major* weighed 78 mg in the nutrient addition treatment, and 46 mg in the control treatment. Average dry biomass of *T. officinale* was 270 mg in the nutrient addition treatment and 96 mg in the control treatment.

Discussion

In this study, we investigated the effect of nutrient enrichment in soils on the survival and growth of three non-native plant species the tundra. Nutrient addition increased growth and biomass for transplants three of these species. However, nutrient addition was overall associated with a pattern of decreased survival of all three species, with a significant decrease in *P. major*.

Transplants of non-native species benefitted significantly from the elevated nutrients, suggesting that non-native species can take advantage of the increased nutrients, allocating these resources into growth and biomass addition. There is evidence that non-native species benefit more from nutrient increases compared to native species (Milberg et al. 1999; Blumenthal 2006; Heckman et al. 2017). This is also reflected in the town of Churchill, where the individuals of our focal non-native species can reach exceptionally large sizes, likely given the constant nutrient pulses within the Churchill townsite. As some non-native species may be dispersed via rhizomes (e.g., *L. vulgaris*; (Nadeau et al. 1992) or root fragments (e.g., *Silene alba*; (McNeill 1977) buried within the soil (Syed et al. 2023), this positive effect of nutrient addition on transplants likely occurs in many human-disturbed areas where plant fragments of non-native species have been transported, as well as sites where plants have established from seed.

Although we found a positive effect of nutrient addition on non-native plant growth, there is still limited evidence of soil nutrients as sufficient for successful invasion, due to the low survival rates detected regardless of nutrient addition treatment. We found a neutral or negative effect of nutrient addition on transplant survival, depending on the plant species, which contrasts with other studies that found a positive effect of nutrient addition on non-native species survival (Leishman and Thomson 2005). Instead, in our experiment, transplant survival rapidly decreased over time irrespective of nutrient amounts. This suggests that exposure to the subarctic climate remains too harsh to allow non-native plants to capitalize on nutrient addition, instead driving the high rates of mortality of non-native transplants. Other impacts associated with human activity can also contribute to the increased risk of non-native plant invasions into surrounding high latitude ecosystems (Alsos et al. 2015; Bazzichetto et al. 2021). For instance, in Churchill, disturbed areas where non-native species are commonly found are not only associated with nutrient increases (Kent et al. 2018; Zhang and Kotanen 2023), but also have other ameliorated abiotic conditions, such as shelter and warmer temperatures (Da Silva and Kotanen 2024; Zhang and Kotanen 2025a).

It is highly unlikely that the entire amount of experimentally added soil nutrients reached the non-native plants. For instance, in nutrient-poor areas, such as in the subarctic, moderate to high amounts of added nutrients may result in a smaller growth response compared to temperate regions, due to uptake and immobilization of nutrients by microbes (Chapin et al. 1986; Rinnan et al. 2007). In addition, fertilization can benefit native species as well, they can take advantage of the higher amounts of nutrients to increase vegetative growth (Henry et al. 1986; Klokk and Rønning 1987; Robinson et al. 1998), potentially outcompeting the non-native species in this study. Although we did not measure rates of growth of native species, our observations suggest that native vegetation recolonized after their initial removal and site disturbance in 2022, leading to a visible decrease in bare ground. This pattern of native species recolonization contrasts the typical trend of invasion success following an increase in soil nutrients in temperate regions, sometimes at a cost of the diversity of native plant species, however, it does reflect the pattern observed in Churchill. Across many previously human-disturbed but currently abandoned and uninhabited areas in or around Churchill, this is a common process: without constant physical disturbance in addition to the associated nutrient pulses, the reversal back to native species dominance occurs, although slowly

(Staniforth and Scott 1991). This suggests that non-native populations are transient, requiring consistent nutrient pulses and perhaps additional anthropogenic ameliorations (Rinnan et al. 2007; Zhang and Kotanen 2025b); otherwise, they can be outcompeted by native species adapted to the harsh subarctic conditions (Cavieres et al. 2018).

Global change can increase nutrient availability through many different processes, such as atmospheric deposition (Grennfelt and Hultberg 1986), increased nutrient mineralization (Nadelhoffer et al. 1991; Hobbie et al. 2002; Dawes et al. 2017), the disposal of garbage and waste (Vaverková 2019), agricultural fertilization (Galloway et al. 1995), and increased run-off (Carpenter et al. 1992), amongst others (Vitousek et al. 1997). The impact of changes in soil nutrients may depend on other associated consequences of climate change, such as elevated temperatures (Gough and Hobbie 2003; Flores-Moreno et al. 2016; Doetterl et al. 2022) or increased rainfall (Robinson et al. 1998). These types of anthropogenic disturbance can change the nutrient amount and availability, affecting plant communities (Eskelinen 2008) and elevating the risk of non-native species invasions (Bartlett et al. 2021). Nutrient addition alone may not in itself be sufficient to support non-native plants adapted to more southern climates. However, in combination with other human-mediated factors, such as continuous physical soil disturbance (Lembrechts et al. 2016), removal of native competitors, the sheltering and warming effect of buildings (Da Silva and Kotanen 2024), and elevated temperatures (Zhang and Kotanen 2025a), increased nutrient levels may help to explain persistence of these species within the town of Churchill, and also may contribute to the future success of these non-native species in increasingly anthropogenically-modified subarctic ecosystems.

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Data availability The data that support the findings of this study will be deposited into an open-source repository after the publication of the manuscript, and will also be available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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