An invasive plant does not escape negative soil feedback near the northern limit of its invaded range

Vicki Mengyuan Zhang (vickizhang97@gmail.com)
University of Toronto - Mississauga https://orcid.org/0000-0002-7426-723X
Peter M. Kotanen
University of Toronto Mississauga

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Abstract

In the Canadian subarctic, the non-native plant *Linaria vulgaris* has invaded human-disturbed soils in and around the town of Churchill, Manitoba (58.8ºN), but has failed to spread into nearby tundra and taiga communities. This lack of spread over decades suggests that interactions with native soil communities might be a barrier to *L. vulgaris*, in contrast to areas where this plant has been long established; however, no local evidence for plant-soil feedbacks yet exists. In one of the first studies to investigate the role of plant-soil feedbacks in an invasion at high latitudes, we planted *L. vulgaris* in soil serially inoculated with live and sterilized field-collected soil that was sampled either from invaded or uninvaded plots, and measured plant performance (biomass) over three greenhouse generations. We also conducted soil chemical analyses on all soil samples to determine whether pH, and carbon, nitrogen, and phosphorous contents may contribute to feedbacks.

There was no significant difference in soil chemistry detected between invaded and uninvaded areas. Additionally, there was no initial difference in plant biomass between soil treatments in the first two generations. However, by generation three, we found that sterilization significantly increased *L. vulgaris* biomass in invaded soils, indicating feedback gradually becomes more negative in invaded soils compared to uninvaded soils. These results suggest both that this non-native plant is not modifying the soil biota to its benefit in invaded soils, and that feedbacks in native-dominated soils do not represent a barrier to further range expansion. Thus, explanations for the restriction of this species to anthropogenically modified areas must lie elsewhere.

Introduction

Interactions between plants and the soil can play a significant role in community assembly and the invasion process (Klironomos 2002, Kardol et al. 2006). Plant-soil feedbacks (PSF) occur when a plant modifies soil biota or soil properties, subsequently affecting itself and other plants in the community (Bever et al. 1997). It has been postulated that plants typically experience negative soil feedback in their native range due to the presence of their generalist and specialist pathogens and herbivores, resulting in species coexistence (Bever et al. 1997, Callaway et al. 2004b, Kulmatiski et al. 2008, Inderjit and van der Putten 2010, Suding et al. 2013).

In invaded ranges, non-native plants may encounter novel soil biota, which can affect the ability of the non-native species to invade (Reinhart et al. 2003, Reinhart and Callaway 2006). The enemy release hypothesis, which hypothesizes that non-native species escape their natural enemies when invading new regions (Elton 1958, Keane and Crawley 2002), has been cited as a possible explanation for reduced negative effects of soil biota in invaded areas (Keane and Crawley 2002, Reinhart and Callaway 2006). Many studies have in fact documented that highly invasive species experience reduced negative feedback, accumulating pathogens at a slower rate than in their native ranges, and thus reaching higher densities in the invaded range (Reinhart and Callaway 2004, Callaway et al. 2004a, Knevel et al. 2004). However, pathogens or soil-borne antagonists in the invaded range may be able to adapt to non-native

species, leading limited or no release from enemies (Beckstead and Parker 2003), while mutualistic soil biota such as mycorrhizal fungi and symbiotic bacteria in invaded ranges may be less beneficial (Nuske et al. 2021), countering the benefits of reduced negative feedbacks. Non-native species that are highly invasive at first may also decline in performance over time as pathogens accumulate (Nijjer et al. 2007), and feedback becomes more negative (Diez et al. 2010, Dostál et al. 2013). Finally, invaders themselves have been found to change soil properties and nutrients (Gibbons et al. 2017, Zhang et al. 2019), and even alter bacterial diversity (Torres et al. 2021), potentially affecting future invasions and the native community (Schittko and Wurst 2014, Verbeek and Kotanen 2019). Thus, soil biota and its interactions with non-native species can either facilitate or impede invasion, and belowground feedbacks during invasions can be variable (Wolfe and Klironomos 2005). Understanding the below-ground interactions between plants and soil during invasion can aid in understanding why some plants are invasive in particular habitats, while others fail to invade, even given numerous subsequent introductions.

Polar regions are relatively resistant to invasions (Wasowicz et al. 2020, Guo et al. 2021). Invasions are a leading threat to native biodiversity in temperate regions (Vitousek et al. 1997, Colautti et al. 2006, Ricciardi et al. 2013), but boreal forests are relatively uninvaded, and northern tundra ecosystems are almost free of invasive plants (Alsos et al. 2015, Conservation of Arctic Flora and Fauna and Protection of the Arctic Marine Environment 2017). At high latitudes, the range limits of non-native plants may be set by barriers such as unsuitable environmental conditions, including soil quality, resulting in poorer non-native plant performance (Kent et al. 2018). These barriers are poorly understood as few studies have investigated invasions in boreal or tundra ecosystems (Smith et al. 2012), or the degree to which such barriers may be reduced by anthropogenic stressors including future climate change (Chen 2012, Myers-Smith et al. 2019).

Churchill, Manitoba (58.8°) represents a unique and suitable site for research into northern invasions, and specifically into limits to invasions. Located in the north-western corner of the Hudson Bay coast (Fig. 1), over a hundred non-native plants have been recorded in Churchill in surveys since 1959 (Beckett 1959, Staniforth and Scott 1991, Kent et al. 2018), reflecting its history as a railway link and a grain and shipping port. Many of these plants have persisted for decades in the Churchill townsite and other human-disturbed areas, but almost none have spread from this reservoir into the boreal forests and tundra ecosystems (Beckett 1959). This region therefore offers the ideal opportunity to investigate factors preventing further invasion of non-native species into northern regions.

This study uses a greenhouse experiment to investigate local-scale feedbacks between the soil community and one of the most locally abundant invaders, *Linaria vulgaris* Mill. (Common Toadflax). *L. vulgaris* is an conspicuous herbaceous perennial originating from Europe and Asia; in North America, it is a problematic weed, and has invaded a wide range of habitats, especially disturbed areas (Saner et al. 1995). Churchill lies at the northern edge of its known central North American range. Although *L. vulgaris* is commonly seen in Churchill and around the surrounding areas, periodic surveys indicate that it consistently fails to produce viable seed (Staniforth and Scott 1991); instead, it apparently persists from a deep, creeping root and rhizome system. Feedback between this root system and the local soil

microbiota with which it interacts could influence both the local persistence of *L. vulgaris*, if this plant cultivates a beneficial soil community in invaded sites that is absent elsewhere, and its failure to spread, if interactions with native soil communities are more negative. To date there has been no study exclusively investigating the relationship between *L. vulgaris* and soil biota in its invaded range.

We tested the following hypotheses:

H_1 *Linaria vulgaris* initially performs better in soil inoculated with microbiota from locations where this species occurs than in sites where it has failed to invade.

H_2 Performance of inoculated *L. vulgaris* decrease over time, indicating the occurrence of negative soil feedbacks.

H_3 Any such negative feedbacks are strongest where *L. vulgaris* has failed to invade.

We also conducted soil chemical analyses on soil samples to see if differences in soil nutrients between invaded and uninvaded sites exist, however we did not set out to explicitly test hypotheses on soil nutrients.

Methods

Field sampling

In August 2020, field soil was collected from 14 sites invaded by *Linaria vulgaris* in the Churchill area (Fig. 1). These sites were spaced at least 10 meters apart and were drawn from three general locations: 6 sites within the Churchill townsite, 6 sites on roadsides near the airport, and 2 sites on roadsides near the Churchill Northern Studies Centre (CNSC). Overall, samples ranged from an almost purely mineral soil to almost entirely organic.

Within each site, soil was sampled at two plots: the first plot was within a population of *L. vulgaris* (referred to as “invaded”), and the second plot was approximately 2 meters away from the population (referred to as “uninvaded”). Both plots supported similar vegetation, excluding *L. vulgaris*; additionally, abiotic factors (e.g., soil, moisture, temperature, and sunlight exposure) did not differ substantially within each pair. To document sampling sites, GPS locations were recorded, and photographs of the plots were taken. After surface litter was removed, samples were collected using a trowel (depth of 15 cm) and stored separately in Ziploc™ bags and express-mailed back to the University of Toronto Mississauga in an insulated chilled container. Soil was kept in a refrigerator (4°C) prior to use.

Soil chemical analyses

Each sample of soil was analyzed for total carbon (% dry), nitrogen (% dry), phosphorus (mg/kg), and pH. Chemical analyses of C, N, and P were done by the Agriculture and Food Laboratory (AFL) at the

University of Guelph. Three separate pH measurements were taken for each sample using an HQd Portable pH meter (IntelliCAL™ Rugged Field Kit), and these measurements were averaged.

Feedback experiment

Spring-like conditions were maintained in the greenhouse (60% humidity, 14-hour daily lighting, 17°C:10°C day:night temperature cycle) for the duration of the experiment. Seeds for our experiment were collected from two locations where populations were present in late autumn 2020: Koffler Scientific Reserve in Newmarket (44°2' 5"N, 79°32' 25"W), and Kipling subway station (43°38'26"N 79°32'27"W); since *L. vulgaris* does not set seed in Churchill, northern population must be derived from such temperate genotypes. Seeds were removed from capsules, mixed, and then rinsed in a distilled water bath, surface-sterilized using 70% ethanol, and rinsed again to remove excess alcohol. Seeds were placed on moist filter paper in a petri dish wrapped in parafilm, and stratified at 5°C for eight weeks prior to planting (Nadeau et al. 1992). During this time, seeds were rehydrated if necessary, and any mold was removed by alcohol. After stratification, seeds were planted on moist filter paper. Upon radicle growth, seeds were planted in sterile potting soil. After germination, seedlings at the cotyledon stage (2–4 leaves) were transferred into conical containers (SC10 Ray Leach Super Cell, Stuewe & Sons). Any seedlings that did not survive three days post-transfer was replaced.

From each field soil sample, 50 mL was sieved and double-sterilized using an autoclave under a gravity cycle (referred to as “sterile”); a second 50 mL of soil sample was sieved but not sterilized (referred to as “live”). Ten mL of this sterilized or unsterilized soil was then used to each inoculate four replicates of approximately 230 mL of sterilized potting soil (2 soil:1 sand:1 peat by volume). This proportion of inoculum represents about 4% of the volume of the container, and is unlikely to introduce unwanted changes in the abiotic properties of the soil inocula (Vandegehuchte et al. 2010). Soil from different sites was not mixed in order to control for between-site variation (Reinhart and Rinella 2016). This resulted in a total of 224 replicates: 14 sites · 2 soil invasion types (invaded and uninvaded) · 2 sterile types (live and sterile) · 4 replicates.

For the first greenhouse generation, individuals were left to grow for 6 weeks, and seedling height (cm) was measured every seven days. After 42 days, and before flowering parts were produced, above- and below-ground plant material was harvested from the initial experiment and dried at 60°C for 48 hours, and biomass was weighed (mg). Above- and below-ground biomass were measured twice for each individual seedling; any repeated measurements that varied by over 2 mg was re-weighed. Seedling height and biomass measurements were made while blind to soil treatment, and replicates were be randomized within the greenhouse.

Serial inoculations were performed to document pathogen build-up (MacKay and Kotanen 2008, Brinkman et al. 2010, Gundale et al. 2019). After above- and below-ground plant material was harvested, 10 mL of sub-surface soil were collected from each conical container. Each new soil sample was used to inoculate 230 mL of sterile soil in a new conical container for a seedling, following the same germination methods as above. The same measurements were taken for this second generation, including cotyledon

length: height (cm) was measured every seven days and biomass (mg) was measured after above- and below-ground plant material was harvested and dried. This inoculation process and all measurements were then repeated for a third time. Note that soils were sterilized only prior to the experiment; "sterile" soils in generations 2 and 3 were drawn from the previous "sterile" iteration and does not contain soil biota from original sampling sites. However, the 2nd and 3rd generations of soils may contain greenhouse-acquired microbes.

Statistical Analyses

All statistical analyses were completed using R (Version 1.4.1717). Wilcoxon signed rank test on paired samples from the package $rstatix$ were used to compare soil properties (C, N, P, pH); a non-parametric test was used as soil nutrient data were not normally distributed. Soil properties were then analyzed with correlation-based principal component analysis (PCA) from the package $stats$, and visualized with the two first principal components. Non-metric dimensional scaling (NMDS), using the $vegan$ package, was run on the soil samples to investigate whether samples can be grouped based on invaded status, based on Euclidean distances. Plant-soil feedback data was analyzed using generalized linear mixed effects model from the package $lme4$ to assess the effect of invaded versus uninvaded soils on *L. vulgaris* growth. We fit the following generalized linear mixed effects model: biomass = invasion type · sterile type + initial height + site. Preliminary analysis indicated that nesting by general location (town, airport, CNSC) did not significantly alter experimental results; therefore only "site" (N = 14) was included to account for spatial variation. Invasion and sterile status were treated as fixed effects, while initial height and site were treated as random effects to account for variation between individuals and between sites, respectively. Type III Sums of Squares were used to test the overall effect of each variable.

Results

Analyses of the soil nutrient and pH data show no significant differences between invaded and uninvaded plots, but a tendency ($0.1 > p > 0.05$) for invaded soils to contain higher C and N (Fig. 2, Table 1). A Wilcoxon signed rank test on paired samples found no differences in carbon (percent dry) between invaded and uninvaded plots ($W_{13} = 74$, $p = 0.0504$). Additionally, there were no differences in nitrogen (percent dry) between invaded and uninvaded plots ($W_{13} = 62$, $p = 0.0776$). There were also no differences in phosphorous (mg/kg dry) ($W_{13} = 58$, $p = 0.402$), or pH ($W_{13} = 34$, $p = 0.268$) between invaded and uninvaded plots.

Table 1
Results from paired Wilcoxon signed rank tests comparing carbon, nitrogen, and phosphorous in the soil between invaded and uninvaded plots.

	invaded (n = 14)		**uninvaded (n = 14)**				
	Mean	SD	Mean	SD	*df*	*W*	*p*
Carbon (% dry)	11.700	8.071	8.017	3.861	13	74	0.050
Nitrogen (% dry)	0.770	0.793	0.435	0.448	13	62	0.078
Phosphorous (mg/kg dry)	57.184	38.003	48.478	40.713	13	58	0.402
pH	7.460	0.195	7.496	0.2070	13	34	0.268

Two major axes in the PCA explained 84.93% of the variation (Fig. 3). Soil carbon, nitrogen, and phosphorus had negative loadings on component 1, while average pH had positive loadings; average pH and soil phosphorus had positive loadings on component 2 (Table 2). Invaded plots tended to score lower values on Axis 1, suggesting higher nutrient levels, but extensively overlapped with uninvaded plots. Non-metric dimensional scaling (NMDS) of soil properties, clustered by invaded status (Fig. 4) also shows substantial overlap between invaded and uninvaded plots based on soil chemical analyses. Note that, for the soil nutrients, this soil chemical analysis only shows *total* carbon, nitrogen, and phosphorous, and may not reflect available forms.

Table 2
Soil chemical analyses loadings on four principal components axes. Largest |loading| for each PC indicated in bold.

	PC1	**PC2**	**PC3**	**PC4**
Nitrogen (% dry)	**-0.5713**	0.1657	-0.2459	**-0.7653**
Average pH	0.4264	**0.8914**	-0.1284	-0.0840
Phosphorus (mg/kg)	-0.4561	0.3488	**0.8033**	0.1579
Carbon (% dry)	-0.5326	0.2372	-0.5270	0.6184

There were no significant predictors of total biomass between the four soil treatments (invasion · sterilization) in generation 1 or in generation 2 (Table 3). Interaction plots also suggest no effect of sterility or invasion in generation 1 or in generation 2, though there was a non-significant ($p > 0.22$) tendency towards lower biomass in invaded soils in generation one (Fig. 5). Generation 1 had the highest average biomass, while generation 2 had the lowest biomass and greatest mortality. The reason for this difference is unclear, though we suspect seasonal differences in daylight and growing conditions; this is one reason we chose to analyze each generation independently as an internally consistent trial. In generation 3, however, biomass depended on both treatment and invasion status (Table 3). Overall, biomass was significantly higher in sterile soils than inoculated soils ($p = 0.01$), though this effect was

small (Fig. 5). Biomass also tended to be slightly higher in uninvaded soils than invaded soils ($p = 0.09$). Importantly, the interaction between sterility and invasion was significant ($p = 0.02$): sterilization significantly increased *L. vulgaris* biomass in comparison with biomass in uninvaded soils.

Table 3
Results from a generalized linear model testing the difference of total *L. vulgaris* biomass in all three generations between soil treatments, with "Invaded status" and "Sterile status" as fixed effects, and site and the initial height of seedlings as random effects.

Biomass (generation 1)				
Predictors	*Estimates*	χ^2	Df	*P*
Invaded status	26.26	1.4904	1	0.2222
Sterile status	6.24	0.1081	1	0.7423
Invaded status * Sterile status	-1.93	0.0045	1	0.9463
Biomass (generation 2)				
Predictors	*Estimates*	χ^2	*Predictors*	*P*
Invaded status	2.31	0.0318	1	0.8584
Sterile status	9.24	0.5156	1	0.4727
Invaded status * Sterile status	8.25	0.2089	1	0.6476
Biomass (generation 3)				
Predictors	*Estimates*	χ^2	Df	*P*
Invaded status	27.10	2.8829	1	0.0895
Sterile status	39.60	6.4553	1	**0.0111**
Invaded status * Sterile status	-54.77	5.8094	1	**0.0159**

Discussion

The ability of a non-native species to modify the soil biota of its invaded range may influence its invasiveness. Our study found no significant differences in soil chemistry between soils invaded by *Linaria vulgaris* and uninvaded plots, but we did find evidence that negative plant-soil feedbacks were stronger in invaded soils than in uninvaded soils, contrary to our expectations. Our results suggest that while feedbacks exist, they are not sufficient to explain the persistent failure of *L. vulgaris* to invade natural communities: instead, there is no evidence of greater resistance by uninvaded soils.

Soil chemical analyses

There were no significant differences in the soil chemical analyses between invaded and uninvaded plots, though total N and C tended to be more abundant in invaded soils. These results differ from those of Kent et al. (2018), who clearly found higher levels of ammonium and phosphorus (but not nitrate) in sites that were invaded versus sites that were uninvaded. This difference may be due to different soil chemical analyses, as we tested for total amounts, not available forms as in Kent et al. (2018), because the sites sampled were different, and because our sample sizes were small. Nonetheless, the small differences between invaded and uninvaded soils in our study coupled with the small volume of our inocula suggests that the results from our plant-soil feedback experiment were not influenced by differences in soil nutrients between invaded and uninvaded samples.

Feedback experiment

This experiment was completed in the greenhouse, not in the field. Because of this, as in all greenhouse studies, we may be missing one or several important factors that are not present in a controlled greenhouse setting (Dawson and Schrama 2016). As well, soil pathogens may change at different stages of invasion, from establishment to persistence and spread (Day et al. 2015), and at different plant history stages, from seedling to maturation (Moyano et al. 2021). Finally, plant-soil feedbacks may be mediated by above-ground biotic interactions, such as herbivory (Kirchhoff et al. 2019). Despite these limitations, our results suggest that *L. vulgaris* is vulnerable to negative soil feedback in previously invaded plots.

In generation one and two, we found no evidence that soil biota initially affected the performance of *L. vulgaris* in either invaded or uninvaded soils, contrary to our Hypothesis 1. We did, however, find evidence that negative feedbacks developed over time, supporting our Hypothesis 2. This indicates that *L. vulgaris* has not escaped harmful soil feedback in its invaded geographic range, in contrast with the results of Maron et al. (2014) who found that *L. vulgaris* performed better in the invaded range in comparison to the native range. This discrepancy may have occurred because their study did not sample previously invaded soils in both native and non-native regions, while we explicitly tested locally invaded and uninvaded soils in the invaded range. The inclusion of presently uninvaded plots in our study means that we can compare differences in currently invaded and currently uninvaded areas that may be colonized in future years.

Importantly, we found that feedback depended on the invasion history of the soil sampled: specifically, that by generation three, sterilization improved plant performance more for invaded soils than for previously uninvaded soils. This suggests that *L. vulgaris* gradually cultivated a harmful soil biota originating in invaded soils but absent from uninvaded soils, directly contradicting our Hypothesis 3. Thus, there is no evidence that further spread of *L. vulgaris* is being prevented by biotic resistance in the invaded community. Instead, our results mirror studies that suggest invaders can experience reduced negative feedbacks in previously uninvaded soils (Reinhart and Callaway 2006, Gundale et al. 2014).

Measuring effects of the entire soil community integrates the effects of both antagonists (bacterial and fungal pathogens) and mutualists (mycorrhizae, beneficial rhizosphere bacteria) in soil. Therefore, the

relatively more positive effect of sterilization in invaded soils versus uninvaded soils in principle could result from both the removal of soil pathogens from invaded soils and the removal of mutualists from uninvaded soils. In fact, trendlines suggest a slight decline in growth with sterilization in uninvaded plots versus an increase in invaded plots (Fig. 5). Invasive species can depend on mutualistic microorganisms, such as mycorrhizal fungi, in the invaded range (Moyano et al. 2021). However, the fact that *L. vulgaris* relies on relatively generalist AM mycorrhizae (Pendleton and Smith 1983) suggests that mycorrhizal partners may occur in most otherwise suitable habitats. As well, it is hard to understand why suitable mutualists would be more common in largely ericoid-mycorrhizal natural landscapes than in previously invaded soils. Consequently, we believe our result is more likely to be driven by species- or habitat-specific pathogens than specialized mutualists.

At the edge of its range, a plant species may be limited by more than just one factor, such as unsuitable abiotic conditions paired with strong species interactions (DeWalt et al. 2004, Brown and Vellend 2014, Wan et al. 2016, Armitage and Jones 2020). However, non-native species may exhibit a greater ability to invade and spread if they suffer less from negative feedbacks compared to natives in the invaded range (Van Grunsven et al. 2007, Engelkes et al. 2008). Although populations of *L. vulgaris* at the edge of its range may develop negative feedback over time, uninvaded areas may represent initially more biotically suitable habitat. Lack of seed production in our study area currently may be the main restriction on such spread, though we have observed plants establishing in transported soil, presumably from rhizomes. Ongoing climatic warming may also alter flowering phenology (Mulder et al. 2017), and the potential of *L. vulgaris* to set seed in the Churchill area along with lack of biotic resistance by in uninvaded soils may accelerate further range expansion.

Declarations

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Competing Interests

The authors have no competing financial or non-financial interests to declare.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection, and analyses were performed by Vicki M. Zhang. The first draft of the manuscript was written by Vicki M. Zhang, and all authors commented in previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

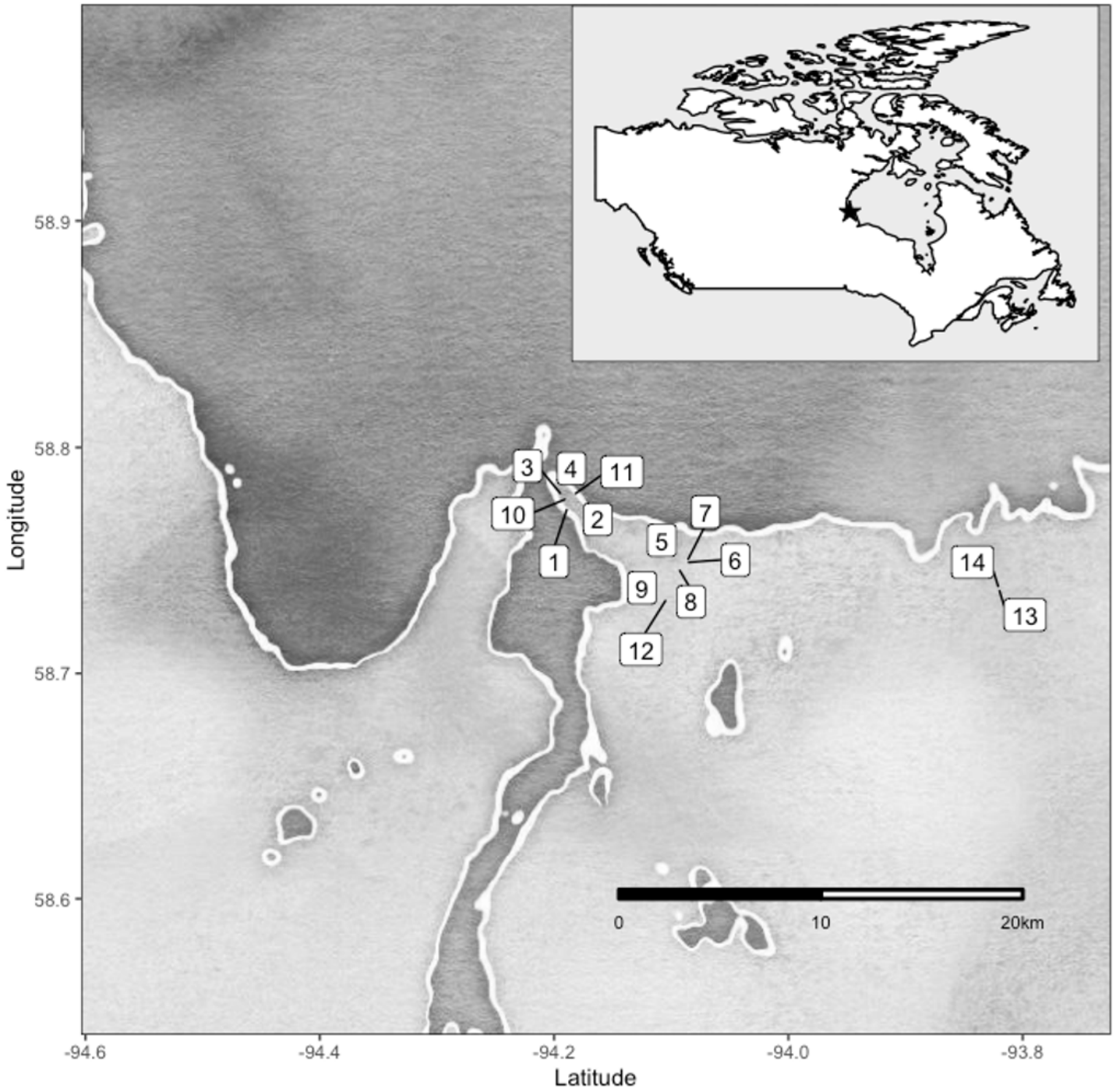

Figure 1

Main: The fourteen sampled sites in Churchill, numbered: 6 in the Churchill townsite, 6 along roadsides east of the Churchill Airport, and 2 on Launch Road next to the Churchill Northern Studies Centre. Inset: Location of Churchill, Manitoba, indicated by the star.

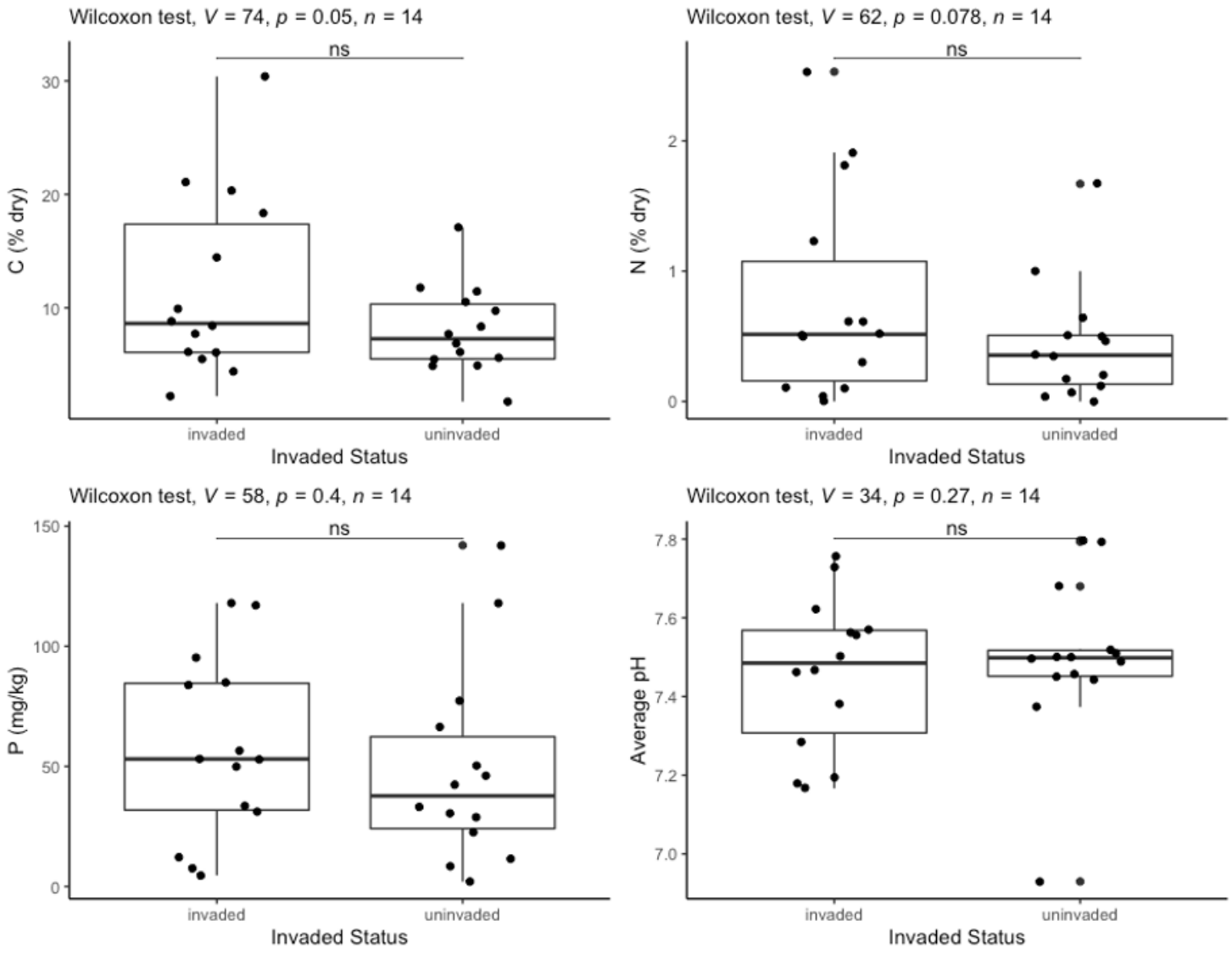

Figure 2

Median, 25th and 75th percentile of carbon (C; % dry), nitrogen (N, % dry), phosphorus (P, mg/kg dry), and average pH in soil samples collected from plots invaded by *L. vulgaris* and uninvaded plots. Statistics from paired non-parametric two-sided Wilcoxon tests are reported.

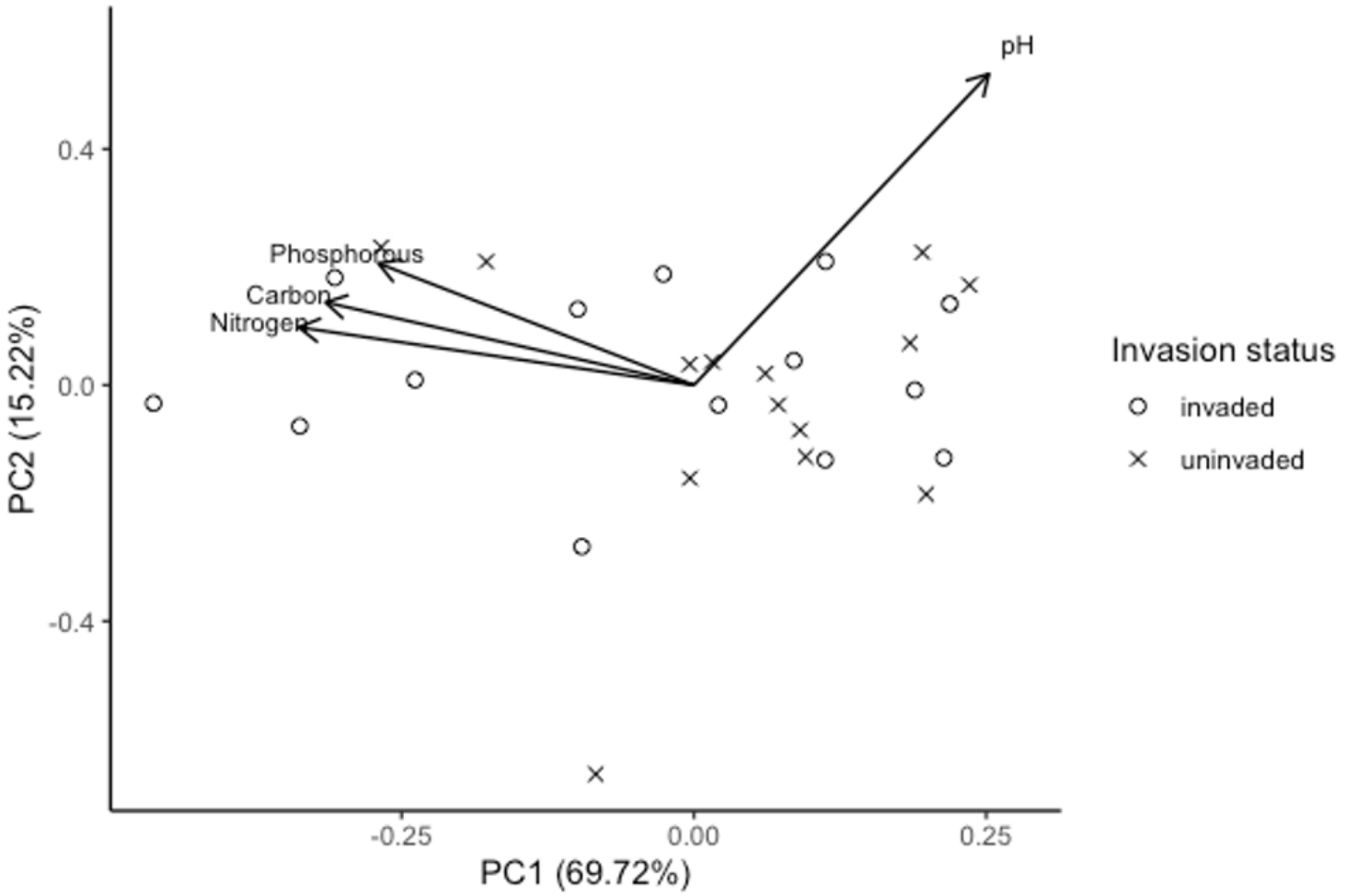

Figure 3

Loading plot of the first two components of a PCA from soil chemical analysis data of 14 invaded (open circles) and 14 uninvaded plots (crosses).

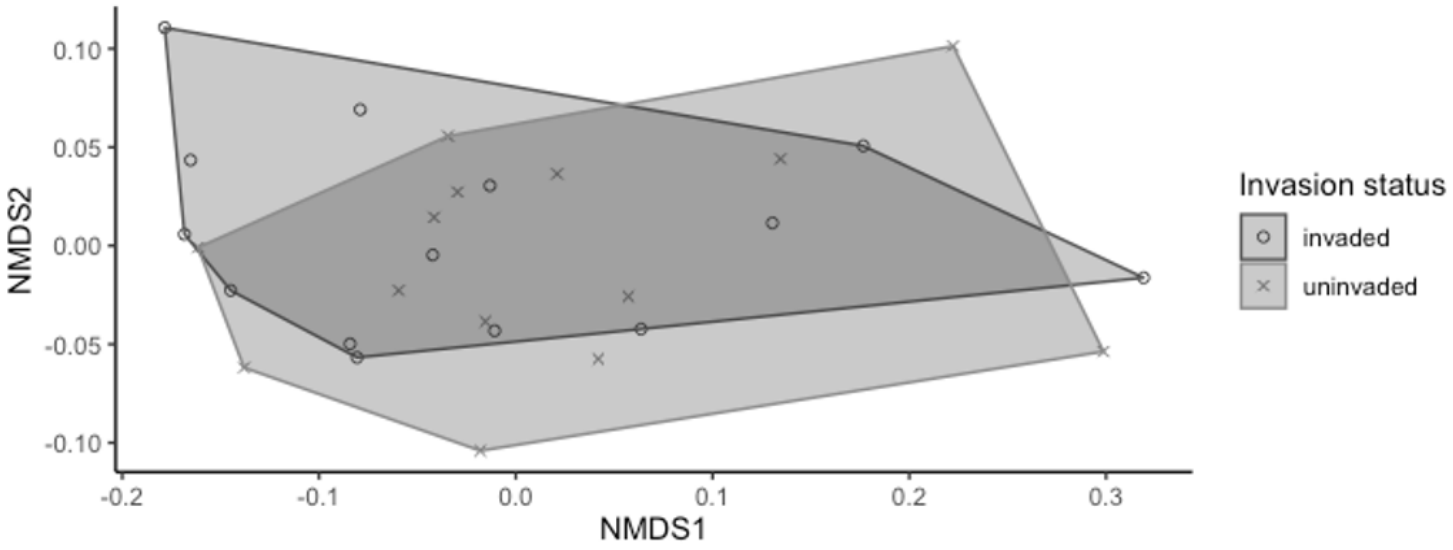

Figure 4

Non-metric dimensional scaling of soil variables based on Euclidean distances. Fourteen sites were samples, with paired samples collected from invaded (open circles) and uninvaded (crosses) plots at each site; invaded plots clustered in dark grey and uninvaded plots clustered in lighter grey.

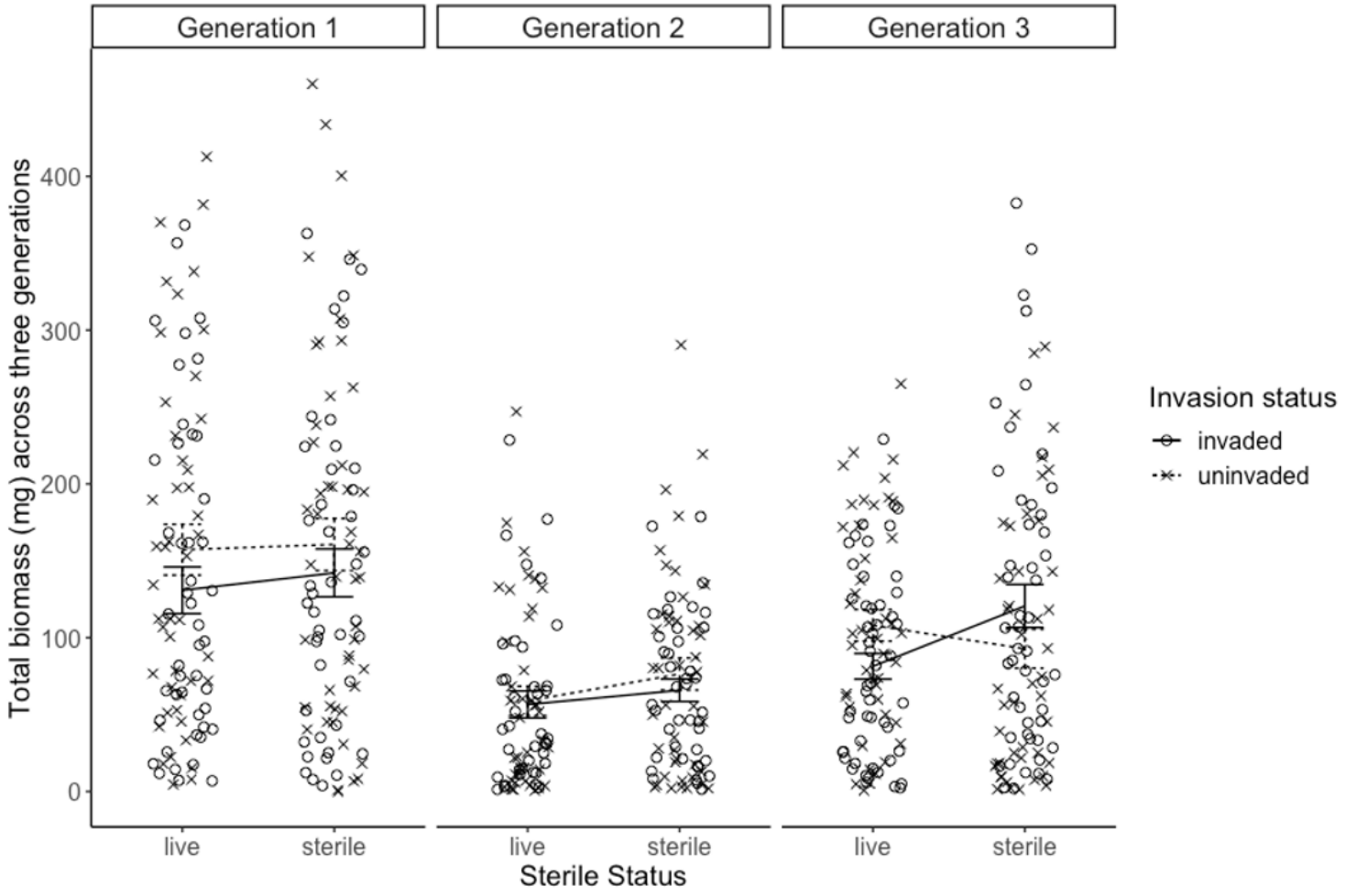

Figure 5

Total *L. vulgaris* biomass grouped by greenhouse generation, and distinguished by invaded (open circles, solid lines) and uninvaded soils (crosses, dashed line). In generation one (left) and two (middle), there were no significant effects of invasion, sterility, or their interactions ($p > 0.2$; Table 3) on total biomass. In generation three (right), live soil inhibits growth more when sampled from invaded plots than when sampled from uninvaded plots (invasion ´ sterility interaction $p < 0.02$; Table 3), indicating negative feedback is stronger in invaded soils.