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Spotted knapweed (*Centaurea stoebe*) creates a soil legacy effect by modulating soil elemental composition in a semi-arid grassland ecosystem

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ABSTRACT

Invasive plants such as spotted knapweed (*Centaurea stoebe*) are particularly detrimental to fragile ecosystems like semi-arid grasslands in the interior British Columbia, impacting aboveground and belowground ecology. Physical removal of *C. stoebe* has been one of the most popular invasive species management strategies, but the impact of *C. stoebe* removal on soil has hardly been studied. Here, we examine the legacy effect of *C. stoebe* on soil elemental composition and ecosystem function following its removal in the Lac Du Bios Grasslands Protected Area, British Columbia. First, we selected 40 paired *C. stoebe* invaded and control (uninvaded) plots and removed all vegetation from these plots. We planted *Festuca campestris* seedlings in these plots and harvested and weighed the biomass after four months. Additionally, we quantified total carbon and nitrogen in soil. We observed that *C. stoebe* invaded plots had significantly lower *F. campestris* biomass. Moreover, the total carbon and nitrogen content, and carbon/nitrogen ratio were significantly lower in *C. stoebe* invaded plots. We further analyzed 12 common soil elements and found the elemental composition was significantly different in *C. stoebe* invaded plots compared to controls. We investigated the impact of elemental composition on soil ecosystem functions (such as total soil carbon, total soil nitrogen, and *F. campestris* productivity). Our analysis revealed significant relationships amongst the elemental composition and total soil carbon and nitrogen, and *F. campestris* productivity. The results indicate that *C. stoebe* exerts a legacy effect by altering the soil elemental composition that may subsequently impacts soil ecosystem functions such as plant productivity and total carbon and nitrogen content.

1. Introduction

Since the 1970s, biological invasions across the globe have caused a cumulative economic loss of more than 1.2 trillion USD (Diagne et al., 2021). The economic loss in recent years due to biological invasions has been staggering, with an estimated 162.7 billion USD in 2017 alone (Diagne et al., 2021). Moreover, biological invasions by alien species have resulted in the extinction of organisms across major taxonomic groups (plants, amphibians, reptiles, birds, and mammals) (Bellard et al., 2016). Several studies further implicate alien species as one of the most important drivers of recent extinctions (Clavero and García-Berthou, 2005; Bellard et al., 2016; Blackburn et al., 2019), which also triggered a stern warning from the scientific community (Pyšek et al., 2020). Impacts of invasive species include disruptions of trophic level interactions (Gaertner et al., 2014; Foster et al., 2020), ecosystem processes and functioning (Kenis et al., 2009; Gaertner et al., 2014; Vilà and Hulme, 2017; Castro-Díez et al., 2019), community composition (Vilà et al., 2011; Pyšek et al., 2012; Kumschick et al., 2015; Foster et al., 2020), and even evolutionary processes (Mooney and Cleland, 2001; Suarez and Tsutsui, 2008). Thus, the influence of invasive species is extensive and can shape various ecosystem components (Gaertner et al., 2014; Gioria et al., 2014; Bowen et al., 2017). As a result, the number of studies on invasive plant species has increased rapidly but mechanisms underlying the negative impacts of invasive plant species are still largely unknown.

Recently, studies have shown that invasive plant species can affect ecosystems through soil legacy effects involving biotic (Vaccaro et al., 2009; Meisner et al., 2012; Jurand et al., 2013; Tanner and Gange, 2013) and abiotic processes (Cuddington and Hastings, 2004; Perkins and Nowak, 2012, 2013). Soil legacy effects can be persistent and influence community structure and entire ecosystems in the long-term (Del Fabbro and Prati, 2015). Changes resulting from legaciess include loss of native biodiversity and alterations to soil chemical and physical characteristics, which will have implications for invasive species management. For instance, persistence of Soil legacy effect neccessitates management efforts be focused on either prevention or early detection of invasive

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species (Kaiser and Burnett, 2010; Reaser et al., 2020). In grasslands and forests throughout western North America, one species of management concern is spotted knapweed (*Centaurea stoebe*), which has invaded millions of hectares and caused millions of dollars of control costs and forage production losses (Bucher, 1984; Duncan et al., 2004; Hirsch and Leitch, 1996; Knochel and Seastedt, 2008). In addition to reductions in aboveground productivity of native plants, *C. stoebe* invasions impact belowground processes, including disruptions of soil microbial community, nematode community (García-De la Cruz et al., 2019), and invertebrate arthropod food web structure (Foster et al., 2020; Foster et al., 2021). The microbial community, along with the soil nematodes and arthropods communities, are principal engineers of soil ecosystem processes, such as infiltration and storage of water in soil pore systems and nutrient cycling (Lavelle et al., 2006) and damage to their community composition could have severe consequences for ecosystem functioning. Since *C. stoebe* exerts substantial influence on the belowground and aboveground communities, studies disentangling its mechanism of action are necessary.

The belowground disturbances caused by *C. stoebe* invasions likely enhance its propagation (Akin-Fajiye and Gurevitch, 2020) and may exert a legacy effect on the soil. Allelopathic influence is also suggested as a mechanism of exerting legacy effect on soil by *C. stoebe,* but is not proven (Blair et al., 2006; Duke et al., 2009). Multiple studies have examined the effect of *C. stoebe* on soil nitrogen, carbon, phosphorus, and potassium (Harner et al., 2010; Knochel et al., 2010; Knochel and Seastedt, 2010; Fraser and Carlyle, 2011) and have found significant associations amongst them. However, hardly any study explores the relationship between knapweed invasion and other chemical elements in the soil or the legacy effects that result from *C. stoebe* invasions following its removal.

Most studies focus on the common soil nutrients (e.g., carbon and nitrogen), while research on the other macro- and micronutrients remain scarce. In this study, we aim to fill the research gap by quantifying 12 different elements - Aluminum (Al), Boron (B), Calcium (Ca), Copper (Cu), Iron (Fe), Potassium (K), Magnesium (Mg), Manganese (Mn), Sodium (Na), Phosphorus (P), Sulphur (S) and Zinc (Zn) in knapweed invaded and uninvaded soils. These elements have remained understudied in the context of knapweed invasions, although, they play an essential role in ecosystem functions. While Al- and Fe-oxides influence carbon cycling in soil (Khandakar et al., 2021), B, Zn, and Cu have shown a strong association with soil carbon content in Canadian prairies (Rahman et al., 2021). Ca has been reported to increase mineral-associated carbon in soils (Rowley et al., 2021). K enhances soil fertility and plant performance (Mahdi et al., 2021). Mg and Mn improve soil biochemical activity, and are associated with soil fungal diversity (Małek et al., 2021). P is a rate-limiting nutrient in most ecosystems and is essential for growth and reproduction of living organisms (Guignard et al., 2017). On the other hand, S stabilizes microbial N and impacts C utilization (Ma et al., 2021). These pieces of evidence indicate that the elements aforementioned are important and can provide critical insights into *C. stoebe* management.

Here, we explore soil legacy effects of *C. stoebe* on ecosystem functioning after rough fescue (*Festuca campestris*) transplantation in a natural, semi-arid grassland in the Lac du Bois Grasslands Protected Area in British Columbia, Canada. *C. stoebe* has been observed at Lac du Bois since the 1970s (B.C. Parks 2000). As such, it presented us with a unique opportunity to study sites that have long been impacted by knapweed invasion. We selected paired plots where *C. stoebe* was either present or absent. We then removed all vegetation from these paired plots and transplanted *F. campestris* seedlings in them. We chose *F. campestris* because it is native to these grasslands and provides quality winter forage for cattle and other wildlife (Adams et al., 2013). *F. campestris* is known to conserve water by providing canopy cover, and its litter helps to increase water infiltration (Deutsch et al., 2010). The deep roots of the *F. campestris* also increase soil stability by reducing soil erosion (Looman, 1969). The main objective of our study was to examine the legacy effect of *C. stoebe* on 1) soil ecosystem function and 2) soil elemental composition. While we studied the soil ecosystem function by measuring the productivity of transplanted *F. campestris* (dried biomass), soil carbon, and nitrogen, we also quantified 12 different elements to investigate the elemental distribution in knapweed invaded and uninvaded plots.

2. Methodology

2.1. Site description

We conducted the study in the Lac Du Bios Grasslands Protected Area, located northwest of Kamloops, British Columbia, Canada (N50°47′, W120°26′) (Fig. 1). Soils of the Lac Du Bois Grasslands Protected are classified as Chernozems (Van Ryswyk et al., 1966) following the (Canadian Agricultural Services Coordinating Committee, 1998). Within this grassland, the dominant grass species are *Festuca campestris* Rydb., *Achnatherum occidentale* (Thurb.) Barkworth ssp. *occidentale* and *Stipa richardsonii* (Link) Barkworth (Van Ryswyk et al., 1966). *Centaurea stoebe* was first observed in these grasslands approximately 50 years ago (Fraser and Carlyle, 2011), indicating its long-term influence on the ecosystem processes at the grassland.

The average annual precipitation is about 260 mm, but it increases up to 310 mm, with significant snow melting at higher elevations in the park (Carlyle et al., 2014). The highest rainfall is seen between June and August. The driest period occurs between March and April. Snowfall is mainly observed in December and January (B.C. Parks, 2000). The average annual temperature in the valley bottom is 8.4 °C and decreases by approximately 0.5° with an elevation increase every 500 m (B.C. Parks. 2000). The upper elevation grasslands in Lac Du Bois Park have higher annual precipitation and lower mean temperatures than lower and middle elevation grasslands.

2.2. Experimental design

To test the effects of knapweed (*C. stoebe*) removal, we randomly selected 40 areas invaded by *C. stoebe* and paired each with an uninvaded (control) area located no further than 5 m north of the invaded areas within the Lac Du Bois Grassland Protected Area. Knapweed invaded areas consisted of at least ten stems, with stems no further than 0.5 m from its neighbor. In addition, we ensured that the invaded areas were at least 20 m from one another. Knapweed invaded areas were categorized according to patch size, where a large patch had an area greater than 10 m^2 and a small patch had an area between 2 m^2 and 10

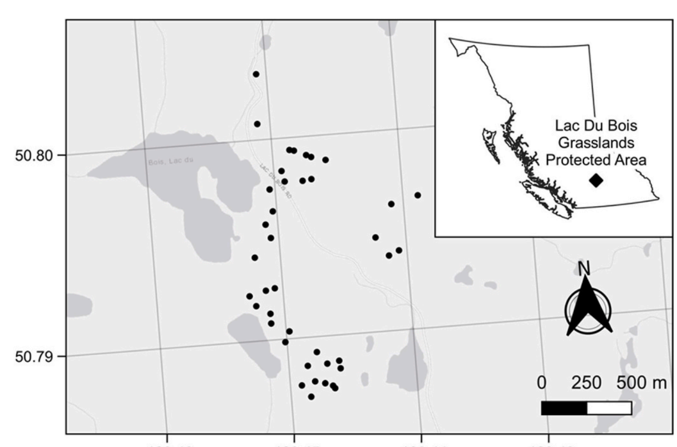

Fig. 1. Map of the Lac Du Bois Grassland Protected Area indicating the experimental plots. Each point denotes the location of the paired plots at Lac Du Bois Grassland Protected Area. Inset is the map of British Columbia to provide context.

m^2 (Fraser and Carlyle, 2011). Within each patch our experimental plots of 1 m^2 were set up. All vegetation was clipped to ground-level within each paired plot (80 plots total) in May 2011. Within each plot (1 m^2), nine seedlings of *F. campestris* were transplanted in a 3 × 3 array, spaced 30 cm apart (Supplementary Figure 2). The seedlings were about four months old, between 5 and 10 cm tall, and propagated from seed in the Research Greenhouse at Thompson Rivers University, Kamloops, BC. Seedlings with similar heights were randomly assigned for transplantation, and plots were watered to field capacity at the time of the transplant.

2.3. Sampling, measurements, and analysis

In the last week of September 2011, transplanted *F. campestris* seedlings were harvested and soil samples were collected. All vegetation was clipped to ground-level within each paired plot (80 plots total) in May 2011. Each individual of *F. campestris* was oven-dried at 75 °C for at least 48 h, and then weighed. Four soil samples from the top 10 cm of soil were collected from each corner of a plot and combined to make a single composite sample. Soils were air-dried to a consistent mass, and dry soil samples were sieved with a 2 mm mesh to separate coarse fragments, roots, and small rocks. Sieved dry soil was ground into fine powder for downstream analyses.

Total carbon (%) and total nitrogen (%) of the ground soil samples were quantified with a CE-440 Rapid Analysis Elemental Analyzer, Exeter Analytical, Inc. Elemental analysis for the concentrations of Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn were analyzed by the Environmental Sustainability and Strategic Policy Division of the Ministry of Environment, British Columbia using Inductively Coupled Plasma - Optical Emission Spectrometry (ICP-OES).

2.4. Statistical analysis

We used R programming language (R Core Team, 2021) for statistical analyses and ran linear mixed effect models (lme4 package) (Bates et al., 2015), principal component analysis and linear regressions to understand the impact of knapweed invasion on total soil carbon and nitrogen (%), carbon and nitrogen stoichiometry (C:N ratio), *F. campestris* biomass. To avoid pseudoreplication, the average biomass of the nine *F. campestris* plants from each plot was used for the analysis. We square-root transformed the biomass, total soil nitrogen and total soil carbon to satisfy the normality assumptions of the models. Every mixed effect model used knapweed invasion and patch size as fixed factors and the paired plot id as random variable.

We further assessed the impact of knapweed invasion on the elemental distribution of soil by running a multivariate analysis. We first normalized the elemental concentration with the '*decostand*' function in the 'vegan' package (Oksanen et al., 2013) and ran a principal component analysis (using '*prcomp*' function) on the normalized data. Then, we plotted the result to visualize the elemental composition of the knapweed invaded and non-invaded sites using the 'ggplot2' package. We further calculated the pairwise euclidean distance using the '*vegdist*' function in vegan between the samples. Finally, we ran a Permutational multivariate analysis of variance (PERMANOVA) using the '*adonis2*' function on the pairwise distance against the knapweed invasion to examine the statistical difference of elemental composition between knapweed invaded and non-invaded plots. We picked PC 1 because it can be considered a proxy for the 12 elements, which explained more than 50% of the variation of the elemental data. We ran pearson correlation to examine how soil elemental composition's corresponds to soil carbon, soil nitrogen, and *F. campestris* biomass. We used the 'tidyverse' package (Wickham, 2019) and associated packages for data wrangling and visualization of data (Kassambara and Mundt, 2017; Kunzetsova et al., 2017; Slowikowski et al., 2018; Xiao, 2018; Kassambara, 2020a, 2020b; Pedersen, 2020). We used QGIS to generate the map indicating the paired plots.

3. Results

The mean *F. campestris* biomass for the knapweed-infested plot was 0.343 g, and the mean biomass for the uninvaded plots was 0.390 g. The results show that the mean biomass in uninvaded sites was at least 13.7% higher (F value = 5.59; $p < 0.05$) than invaded sites (Fig. 2A).

Further, we examined the impact of knapweed invasion on soil carbon, nitrogen, and their ratio. The mean carbon percent in knapweed invaded and uninvaded sites were 5.1% and 6.29%, respectively. Our LME model established that the soil carbon (Fig. 2B) was significantly lower (F value = 7.8; $p < 0.01$) in knapweed invaded plots. Similarly, we observed significantly lower (F value = 6.9; $p < 0.05$) nitrogen (Fig. 2C) and (F value = 9.8; $p < 0.05$) carbon-nitrogen (C:N) ratio (Fig. 2D), respectively, in plots impacted by knapweed invasion. The mean nitrogen content in knapweed uninvaded and invaded plots were 0.584% and 0.484%, respectively, implying a reduction of more than 17.1% in nitrogen content when knapweed is present.

We observed that concentrations of Cu, Fe, Mg, Na, and S were significantly different in knapweed invaded plots (Supplementary figure 1). To get an overall understanding of the impact of knapweed invasion on the elemental composition, we analyzed the data using principal component analysis and found that the two components explained more than 85% of the variation. Further, we found that Mg, Ca, Al, Fe had the highest contribution to the variance associated with PCA (Fig. 3, Supplementary figure 3).We also tested the correlations amongst different elements and found none had a correlation coefficient higher than 0.66 (supplementary figure 4). Finally, we ran a PERMANOVA to examine the difference in the elemental composition of the elements in knapweed invaded and uninvaded plots. We found that the elemental composition (Fig. 3) in knapweed impacted plots was significantly different (Pseudo F = 4.77; $p = 0.007$) from the uninvaded plots. The results indicate that knapweed invasion likely affected the elemental make-up of soils.

Our analyses showed significant correlations between PC1 and plant productivity ($_r = 0.35$; $p = 0.0014$), soil nitrogen ($_r = 0.57$; $p < 0.001$), and carbon ($R^2_{adj} = 0.57$; $p < 0.001$)).

4. Discussion

Studies have shown that knapweed invasion negatively impacts the structure and function of grassland ecosystems (Tyser and Key, 1988; Fraser and Carlyle, 2011), but our understanding of the Soil legacy effects of a previous knapweed invasion is limited. This study demonstrates that the influence of C. stoebe persists following its removal and may negatively impacts ecosystem function (such as biomass of successional plants and elemental composition in soils). Furthermore, we noticed that C. stoebe impacted plots had significantly lower total soil carbon and nitrogen. Lutgen and Rillig (2004) made a similar observation where C. stoebe negatively impacts arbuscular mycorrhizae and reduces soil glomalin, a glycoprotein known to sequester a substantial amount of soil carbon and nitrogen (Treseder and Turner, 2007). Our findings indicate that the knapweed invasion most likely impacted the belowground nutrient by reducing soil nitrogen and carbon.

Moreover, *C. stoebe* increases surface runoff leading to loss of soil particulates, contributing to additional carbon loss (Lacey et al., 1989). We further observed that *F. campestris* grown in knapweed invaded plots had substantially lower biomass, which corresponded with the changes in elemental composition of the soil. Previous studies have also reported that the presence of *C. stoebe* reduced productivity of mature *F. campestris* by 88% (Watson and Renney, 1974), but our study showed that the biomass of establishing plants was reduced even after knapweed removal. While Festuca growth may also have altered soil chemistry, we tried to reduce this effect by using plants from a single ecotype, which likely did not differ in nutrient requirements.As such, we think the change in biomass is most likely due to the chemical legacy of *C. stoebe* (Fig. 2A). Although we noticed a significantly lower C:N ratio in knapweed invaded plots (Fig. 2D).we found no significant correlation

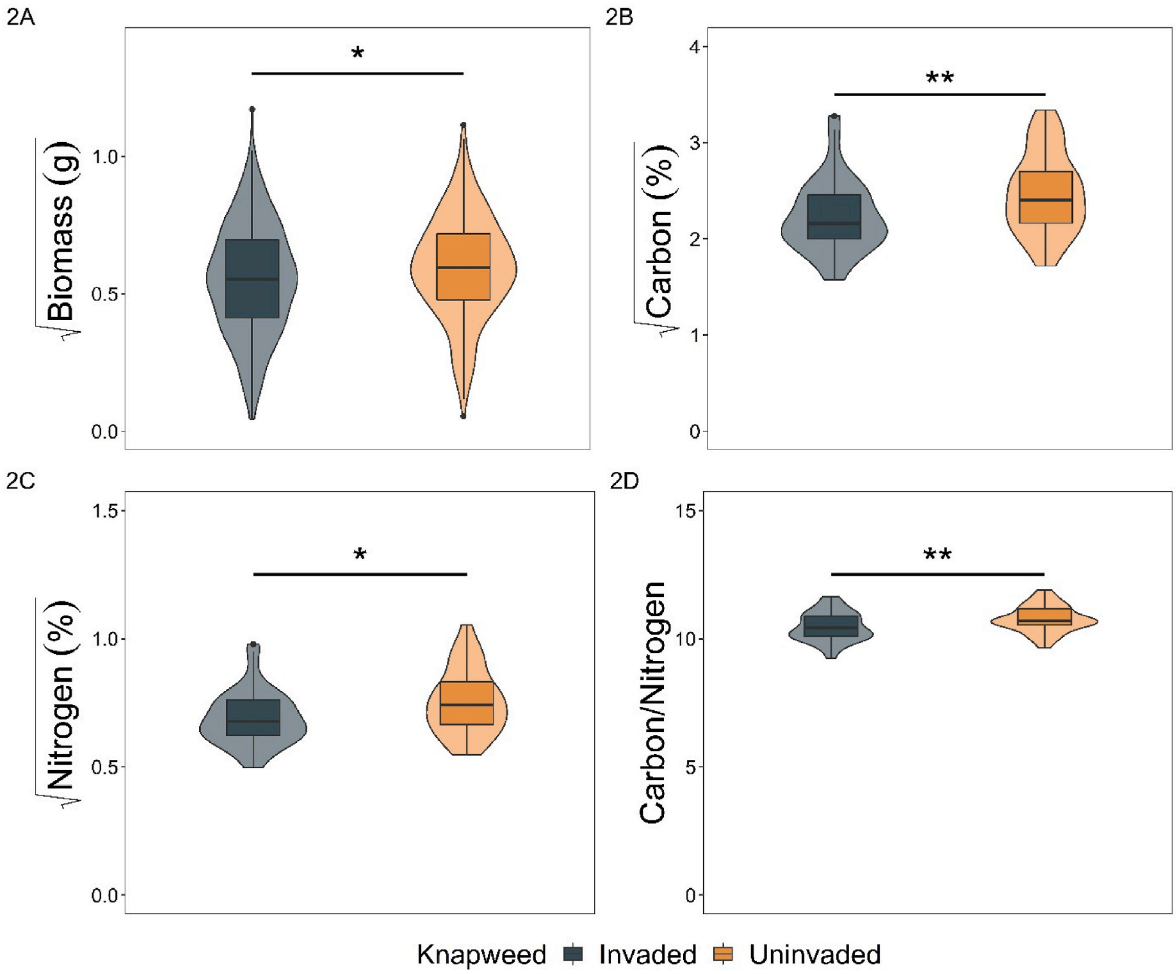

Fig. 2. Rough fescue biomass (2A), soil carbon (2B), soil nitrogen (2C), and C:N (2D) were significantly lower ($p < 0.05$) in knapweed invaded plots compared to uninvaded plots. The horizontal line in the box-whisker plot indicates the median of the responses in soils, and the whiskers indicate the interquartile range of the data. The violin plot denotes the density of the responses in soils.

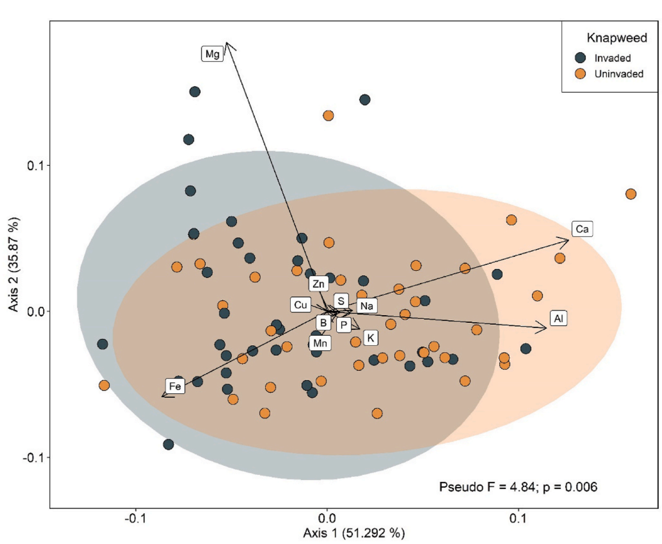

Fig. 3. Principal component analysis of the 12 major elements in soils accounts for more than 85% of the variation in the data. The first and second axis explains 51.29% and 35.87% of the variance, respectively. PERMANOVA indicates that the elemental composition is significantly different ($p < 0.005$) in knapweed invaded and uninvaded sites.

between biomass and C:N, which indicates it that the biomass is most likely impacted by the soil elemental distribution.

Besides *F. campestris*, studies have shown that *C. stoebe* also results in a decline of other forage biomass and quality (Harris and Cranston, 1979; Tyser and Key, 1988; Sheley et al., 1998). The reduction in biomass has long been attributed to the competitive advantage of *C. stoebe* due to resource utilization (Herron et al., 2001; Harner et al., 2010) and seed persistence (Davis et al., 1993) but the impacts of *C. stoebe* via the soil disturbance (soil legacy effect) largely remain understudied. Here, we examined if knapweed invasion causes soil disruption by disturbing the soil nutrient composition. We took a macro-scale view of the soil elements (Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn) by using ordination analysis (PC analysis) to investigate their composition in knapweed invaded and uninvaded soils. We found that the composition of elements was significantly different in knapweed -invaded and uninvaded soils (Fig. 3). To understand if the elemental composition had any relationship with soil carbon, nitrogen, and *F. campestris* biomass, we ran correlations and found significant relationships amongst them (Fig. 4). The significant relationship indicate that soil elemental distribution may potentially play a crucial role in determining ecosystem functions (soil carbon, soil nitrogen, and plant biomass). While it may be challenging to identify the mechanism of how knapweed impacts elemental distribution and subsequently biomass, soil carbon, and nitrogen, our results generate interesting hypotheses on the Soil legacy effect of knapweed. Our results show that knapweed invasion leave a distinct elemental fingerprint in soil (Fig. 3). Previous

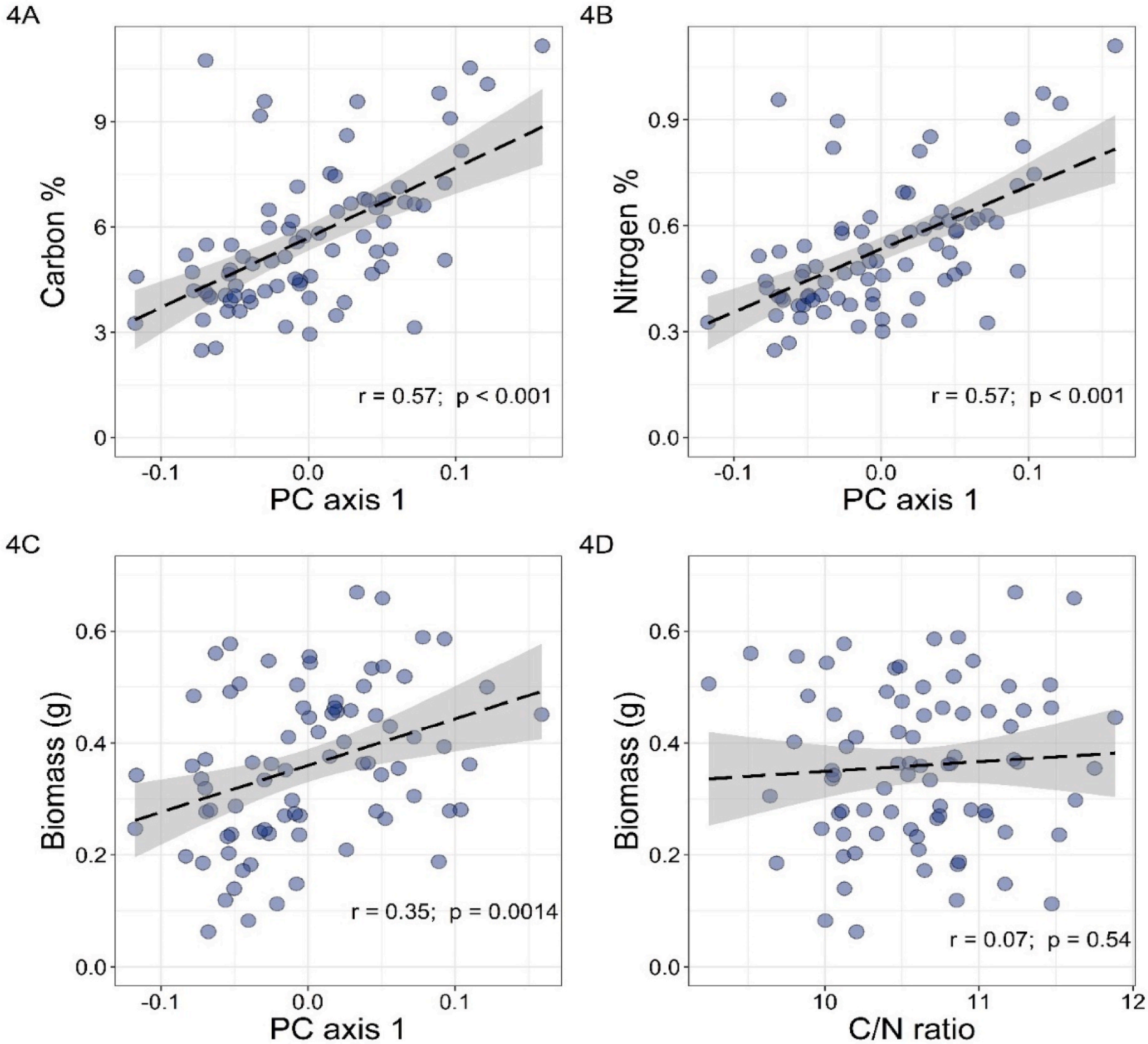

Fig. 4. Correlation analysis between PC axis 1, plant productivity (biomass), soil carbon, and nitrogen. The pearson correlation coefficients and its corresponding p values are indicated in the figure.

studies have shown that Ca, Al and Fe are important determiners of total soil organic carbon as well as mineral associated organic carbon (Mulder et al., 2001; Rowley et al., 2018; Kirsten et al., 2021) and are also known to be associated with the nitrogen content in soil (Ye et al., 2018). Mg and Mn improve soil biochemical activity, and are associated with soil fungal diversity (Małek et al., 2021). P and K enhances plant performance (Rady et al., 2020; Mahdi et al., 2021) Additionally, the overall soil composition also impacts plants biomass (Hejcman et al., 2010). These studies indicate the importance of soil elements on plant biomass, soil carbon and nitrogen. We also found the pattern of elemental distribution, which is correlated to the rough fescue biomass, and soil nitrogen and carbon suggesting a relationship among them. Since these significant relationships are based on correlations, we cannot conclusively say whether the relationship is causal or indirect. Additionally, how *C. stoebe* changes the elemental composition and how it benefits their expansion is still not known. One plausible mechanism of alteration in the elemental composition could be increased soil erosion and surface runoff (Lacey et al., 1989). Soil erosion and surface runoff can significantly impact soil nutrients (Otero et al., 2011), particularly in semi-arid areas (Dilshad et al., 1996), resulting in ecosystem disturbance. Soil parameters influence the occurrence and distribution of *C. stoebe* (Akin-Fajiye and Gurevitch, 2018), and the change in elemental composition is likely helping *C. stoebe* proliferate. Furthermore, ecosystem disturbance increases reproduction in *C. stoebe* (Akin-Fajiye and Gurevitch, 2020). Meiman et al. (2006) show that prior infestation with *C. stoebe* facilitates their emergence, which further substantiates that the Soil legacy effect exerted by spotted knapweed improves their reproductive success Therefore, it is likely that the C. stoebe promotes the alterations of soil chemistry that may in part underly this positive plant-soil feedback effect. Although it remains unclear how prior biotic legacies in the area may influence initial knapweed invasions, as historical differences in abiotic and biotic legacie can enhance or suppress invasion success of introduced species (Miller et al., 2021).

5. Conclusion

This study, to our knowledge, reports the first evidence of *C. stoebe* impacting elemental composition in soils. Overall, knapweed invasion left a legacy of changed elemental composition in the soil, which subsequently may have affected native plant biomass. We also observed significant correlations among elemental distribution, soil nitrogen and carbon but whether these relationships are causal or indirect is hard to disentangle. Perhaps, the disturbance also influences the distribution, density, and reproductive success of *C. stoebe*. Further studies on the mechanism of modification in elemental composition can untangle its benefits to *C. stoebe*. Such studies would benefit environment managers and equip them with targeted strategies for *C. stoebe* management.

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Data and codes availability

The data and codes available on GitHub https://github.com/jaymicro/knapweed_manuscript.git.

Credit author statement

Yuying Kuang: Conceptualization: Methodology, Lauchlan Fraser: Data curation: Writing – original draft preparation, Conceptualization: Methodology, Visualization, Investigation., Writing- Reviewing and Editing, Jay Prakash Singh: Data curation: Writing – original draft preparation, Visualization, Investigation., Writing- Reviewing and Editing, Laura Ploughe: Data curation: Writing – original draft preparation, Visualization, Investigation., Writing- Reviewing and Editing, Matthew Coghill: Data curation: Writing – original draft preparation, Visualization, Investigation., Writing- Reviewing and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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