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RESEARCH ARTICLE

An invasive shrub drives carbon uptake in New Zealand montane tussock grasslands, with strongest effects early in the growing season

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Abstract

1. Plants play a critical role in the carbon cycle by driving carbon uptake and release through photosynthesis and respiration, with dominant species exerting large control over these fluxes. Invasive plants can disrupt carbon cycling because of their high biomass and rapid growth, yet their influence across a growing season remains unclear. Many studies show that invasive species exhibit greater phenological plasticity than native species, which can enhance their competitive ability. Under warming, this phenological plasticity may allow invasive species to better track resource availability and capitalize on longer growing seasons, potentially disadvantaging native communities.
2. To test how warming and an invasive species interact to alter carbon dynamics, we measured plant biomass, net ecosystem exchange (NEE), gross primary productivity (GPP), and ecosystem respiration (ER) three times over the growing season in a *Calluna vulgaris*-invaded alpine community in New Zealand. We removed *C. vulgaris* and increased temperatures using open-top chambers in a factorial design.
3. With the removal of *C. vulgaris*, we found significantly lower community plant biomass and weakened ecosystem carbon sink strength due to lower GPP across the growing season. These responses reflect the removal of *C. vulgaris* itself rather than a general reduction in biomass, as biomass-corrected NEE showed the same patterns. Surprisingly, warming increased GPP in native-only plots, but not in *C. vulgaris-invaded* plots. *C. vulgaris* had the strongest effects on carbon fluxes early in the season, with influence diminishing later in the season. This seasonal shift aligns with *C. vulgaris* phenology, as late-season measurements coincided with peak flowering, a period likely characterized by reduced photosynthetic investment.
4. Overall, removal of *C. vulgaris* decreased plot-level biomass and productivity, while warming more strongly enhanced carbon uptake in native rather than in invaded plant communities. These findings indicate that invasive species can exert an outsized influence on ecosystem carbon dynamics, independent of warming,

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and these effects vary seasonally. As biological invasions and climate warming intensify, resolving their interactive and time-dependent impacts on carbon cycling will be important for improving ecosystem and carbon models.

KEYWORDS
carbon cycle, dominant plants, ecosystem respiration, gross primary productivity, invasion, net ecosystem exchange, seasonality, warming

1 | INTRODUCTION

Plants play a central role in the carbon cycle as primary producers, with ecosystem productivity strongly influenced by abiotic and biotic conditions (e.g., temperature and plant community composition (Prager et al., 2021; Wu et al., 2011)). In general, dominant species play a large role in carbon cycling (Lisner et al., 2023) as they make up the largest portion of community biomass, and their impacts tend to be proportional (Avolio et al., 2019; Grime, 1998). However, their effects can vary by species identity and environment (Sundqvist et al., 2020). In a factorial dominant species removal by warming experiment in the Rocky Mountains, USA, removing dominant species decreased productivity at one elevation but had little effect at another (Brinkhoff et al., 2026); while an experiment with the same design in Abisko, Sweden, found dominant species removal did not affect productivity (Sundqvist et al., 2020). Warming can alter carbon dynamics by increasing productivity (Ganjurjav et al., 2015), ecosystem respiration (ER) (Sundqvist et al., 2020), or both (Ganjurjav et al., 2015), but the strength and direction of these effects are context-specific.

Invasive plant species are increasingly outcompeting the native dominant species, becoming the dominant species (Bottollier-Curtet et al., 2013) and reshaping plant communities and altering ecosystem processes. On average, invasive plants increase overall plant community biomass (i.e., above-ground plant material) by 133% (Liao et al., 2008), though there are exceptions. For example, taller invaders tend to cause greater biomass increases (Martin et al., 2017). Plant biomass could be permanently impacted by invasive species, as native biomass recovery after invader removal is limited when native cover is low (Ta et al., 2024). Warming and aridity can exacerbate invasion impacts, disproportionately reducing native biomass (Ravi et al., 2022). In general, warming in cold, mountain environments causes increases in plant biomass (Huang et al., 2020; Zhou et al., 2014), though these effects may be mediated by water limitation (Bloor et al., 2010; Ma et al., 2010; Zhang et al., 2018). In warm and wet grasslands, biomass has increased since 1980, while in arid areas, biomass has decreased (MacDougall et al., 2024).

Invasive species have a pronounced effect on the carbon cycling of ecosystems, potentially increasing the strength of the carbon sink via increases in gross primary productivity (GPP) (Hamerlynck et al., 2012; Raheem et al., 2024; Zhou et al., 2015) or by decreasing ER (Duman & Schäfer, 2018; Hu et al., 2022; Xu et al., 2022). But, invasive species can also have lower photosynthetic rates than native species (Huxman et al., 2004; Ignace et al., 2007) and greater respiration (Winkler et al., 2016), potentially causing ecosystems to be more of a carbon source (Zhou et al., 2023). The variation in invasive species GPP and ER may be species-specific. However, invasive species tend to be fast-growing with greater photosynthesis (Montesinos, 2022), and a meta-analysis found that net primary productivity (i.e., the rate of biomass production) increased with invasion by an average of 83% (Liao et al., 2008). Warming temperatures can interact with plant invasion to alter the ecosystem carbon cycling, but little empirical research quantifies how they will interact to impact carbon fluxes of terrestrial ecosystems. In uninvaded ecosystems, plant community composition tends to have a larger effect on carbon fluxes than warming (Sundqvist et al., 2020), and along an elevational gradient, carbon fluxes were regulated by plant diversity and not abiotic conditions (Prager et al., 2021).

Warming and invasive species have distinct impacts on plant community biomass and ecosystem productivity across the growing season (Fridley, 2012; Wang et al., 2020). Warming can cause the growing season to be shifted earlier in the year, with increased plant productivity early in the growing season and decreased productivity later (Wang et al., 2020). Alternatively, the growing season can be shortened due to water limitation (Zhu et al., 2017). Increased temperatures can cause soils to dry, especially later in the growing season (Bloor et al., 2010). Likewise, invasive species phenology can cause disproportionate ecosystem impacts across a growing season (Engelhardt & Anderson, 2011; Fridley, 2012; Giejsztowt et al., 2020). For example, *Alliaria petiolata* (garlic mustard) tends to establish before the native understory (Engelhardt & Anderson, 2011), largely impacting productivity in the spring, while *Calluna vulgaris* (common heather) blooms later and longer than native species (Giejsztowt et al., 2020), potentially impacting productivity in autumn. Warming temperatures and invasive species phenology can also interact to have cascading effects on ecosystem productivity (Dawson-Glass et al., 2025; Zettlemoyer et al., 2019), with invasive species tending to have greater phenological plasticity than native species, potentially increasing their productivity with warming temperatures (Giejsztowt et al., 2020; Zettlemoyer et al., 2019). However, this observation is largely based on observations in temperate ecosystems in the Northern Hemisphere (Dawson-Glass et al., 2025) and tends to focus on the timing of life history traits, such as flowering or leaf-out. The seasonal impact of warming and invasive species on ecosystems' overall carbon budget (biomass pools, productivity, and respiration) is still unknown.

To understand how warmer temperatures will impact the carbon cycling of an invaded ecosystem across the growing season, we conducted a fully factorial 8-year experiment in a New Zealand montane tussock grassland where we removed the invasive species *C. vulgaris* and increased the temperature using open-top chambers (Prager et al., 2022). Specifically, we asked: Does an invasive species affect carbon dynamics in this ecosystem? Do these effects vary across the growing season? Does warming modify the effect of the invasive species on carbon dynamics? We hypothesized:

1. Overall, *C. vulgaris* intact plots will be more of a carbon sink because they increase plant biomass, and invasive species tend to have higher productivity.
2. Due to the phenology of *C. vulgaris* (late-season flowering), the plots with *C. vulgaris* removal will be a stronger carbon sink in the early season compared with plots with *C. vulgaris*. However, by the end of the growing season, the plots with *C. vulgaris* will be a greater carbon sink.
3. Warming will increase *C. vulgaris* biomass and productivity because invasive species tend to be resilient to warming, increasing the strength of the carbon sink in invaded plots. However, the native species will respond negatively to warming since they are more sensitive to warming temperatures, decreasing biomass and productivity.

Our results reveal how warmer temperatures impact the carbon dynamics of an invaded montane tussock grassland ecosystem across a growing season by measuring plant biomass and carbon fluxes in the early, peak, and late periods of the growing season.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental establishment

We conducted this experiment in an alpine plant community in Tongariro National Park, New Zealand (1071 metres, −39.294° S, 175.726° E). Tongariro National Park is a culturally and ecologically significant UNESCO World Heritage Site (Baird, 2013; Rogers & Leathwick, 1996) with high levels of plant endemism (Halloy & Mark, 2003). The park is composed of three volcanoes, Ruapehu, Ngāuruhoe, and Tongariro, resulting in dark sandy loam and loamy sand soils (Giejsztowt et al., 2020) with high drainage. High elevations are warming more quickly than sea level (Pepin et al., 2015), and New Zealand has already warmed 1.1°C and is expected to warm another 1.0°C by 2050 under a medium emissions pathway (Lawrence et al., 2022). The mean summer temperature is 14.5°C, and the park receives 150 mm of rain during the growing season on average (Prager et al., 2022). The dominant species at the study site is *C. vulgaris*, which was first introduced to the park in 1912 to increase the habitat of introduced game birds like grouse (Keesing, 1995). Now, *C. vulgaris* has largely displaced the native *Chionochloa rubra* tussock grass below 1200 metres to become the most abundant plant species (Rogers & Leathwick, 1996) and continues spreading. *C. vulgaris* produces many small (5–8 mm), bell-shaped, purple flowers and is a late-flowering species, with peak flowering starting in early February and extending until mid-March (Chapman & Bannister, 1995). Other abundant species include *Dracophyllum subulatum*, *Ozothamnus vauvilliersii*, *Veronica tetragona*, *Pentachondra pumila*, *Racomitrium* spp., *Poa colensoi*, and *C. rubra*.

We established a fully factorial warming × *C. vulgaris* removal experiment in 2015. We established eight blocks of four 2 m^2 treatment plots: control, warming, removal, and warming and removal (8 blocks × 4 treatments). Warming was conducted with 2.3 m^2 hexagonal open-top chambers, modelled after those used in the International Tundra Experiment (Henry & Molau, 1997). The chambers were deployed at the beginning of the study and have been maintained continuously since. The chambers increase the yearly mean air temperature by 1.73°C. Removal of *C. vulgaris* occurred by clipping any above-ground biomass at ground level, bagging it, and removing it. At the start of each growing season, we remove all *C. vulgaris* present in the plots and then maintain the plots as needed throughout the growing season (Prager et al., 2022). During the 2015–2016 growing season, we removed 166 ± 37.5 g of dried *C. vulgaris* in each removal plot, whereas during the 2023–2024 season, we removed only 0.9 ± 0.3 g per plot (Table S1). In January 2022, 16 additional 1 m^2 plots were established near the original experiment: eight native removal plots and eight uninvaded plots. The native removal plots removed *D. subulatum*, a functionally equivalent native shrub to *C. vulgaris*. *D. subulatum* removal also occurred by clipping above-ground biomass at ground level. Uninvaded plots were established in areas of the grassland that naturally contained no *C. vulgaris*. The additional plots help determine if the effects of *C. vulgaris* removal are due to reductions in biomass or the traits of *C. vulgaris*. We acknowledge mana whenua (indigenous people) Māori as kiatiaki (guardians) of Tongariro National Park. Fieldwork in support of this research took place within the rohe (traditional territory) and in collaboration with Ngāti Rangi and Ngāti Tūwharetoa, under the Department of Conservation Research and Collections permit #81775-RES. Data are available at the Environmental Data Initiative (EDI): https://doi.org/10.6073/pasta/591dd98298eb5ff5de78b50ce686d6aa (Vought et al., 2026).

2.2 | Air temperature, soil temperature and soil moisture measurements

We installed TMS-4 data loggers (TOMST, Praha, Czech Republic) in 16 of the 32 plots (spread out equally between the treatments) in 2021. Halfway through the season, TMS-4 loggers were added to the remaining 16. The TMS-4 probes measured soil moisture, soil temperature, and air temperature every 15 min after deployment (Wild et al., 2019). The sensors recorded air temperature at 15 cm above the soil surface and soil temperature and soil moisture at 6 cm below the soil surface.

2.3 | Plant community and plant biomass measurements

We surveyed the plant community diversity and biomass using the pin drop method (McLaren & Turkington, 2011) throughout the growing season in November 2023, January 2024, and March 2024, within a week of measuring the carbon fluxes. We placed a 0.5 m^2 frame in the centre of the plot and dropped a pin at 50 equally spaced intervals throughout the frame. We recorded the number of times the pin touched each plant species, allowing us to quantify the diversity and abundance of the plant community within each plot. In November, we flagged the location where we measured the plots to measure consistently in January and March. After collecting pin drop data in the plots, we calculated the plant biomass of each species in the plot using allometric equations developed in 2019. To develop the allometric equations, we took pin drop measurements near the experimental plots. We then harvested all the plant biomass at the ground level, separated it by species, dried it, and weighed it. Next, we calculated linear relationships between the number of hits counted using the pin drop method and the amount of plant biomass in the plots. The linear regressions have an R^2 value ranging from 0.19 (*Celmisia gracilenta*) to 0.99 (*C. rubra*), depending on the species. The average R^2 value among all the equations is 0.63, though the data for the most abundant species tend to have better fits. We use these allometric equations to estimate the total plant biomass within the plots (Table S2). In each plot, the percentage of plant hits with an established allometric equation had to exceed 80% to use the plot biomass data in subsequent analysis. Over the season, this resulted in the exclusion of one plot. To estimate the greenness of the plots, we measured NDVI (Normalized Difference Vegetation Index) using a Greenseeker handheld sensor (Trimble Incorporated, Westminster, CO, USA) on the same day we measured carbon fluxes. To measure average leaf thickness in each plot, we used a micrometre and measured in the centre of fresh and fully developed young leaves, avoiding mid-veins when present. We measured three individuals per plot of *C. vulgaris*, *D. subulatum*, *V. tetragona*, and *C. rubra*, all highly abundant species.

2.4 | Carbon flux measurements

To measure how invasive species and warmer temperatures impact carbon fluxes, we measured net ecosystem exchange (NEE), GPP, and ER three times throughout the growing season, in November 2023, January 2024, and March 2024. We recorded the change in carbon dioxide inside an airtight chamber placed over the top of the vegetation and sealed at the base using an infrared gas analyser (Li-Cor, Lincoln, Nebraska, USA). The chamber, which encompassed all of the plants in each plot, was covered with a tarp and had a volume of 0.6 m^3 and an area of 1 m^2. We measured carbon dioxide change for 2 min at four light levels: full light, two different reduced light levels, and full darkness. We used five 1500 W LED full-spectrum grow lights (Greenfingers, Livingston, Scotland) in the chamber to stimulate photosynthesis. Grow lights allowed us to measure carbon fluxes on days with variable cloud cover. We took measurements at 100% light (photosynthetic photon density (PPFD) greater than 1000 $\mu mol\, m^{-2} s^{-1}$), 75% light, 50% light, and 0% light. Full darkness is a measurement of ER. To measure PPFD inside the chamber, we used two MQ-100 Apogee PAR metres (Apogee Instruments, Logan, UT, USA) set at plant height at different points in the chamber. We made a response curve between time and carbon dioxide concentration and removed any non-linear sections. We calculated NEE ($\mu mol\, m^{-2} s^{-1}$) from the flux measurements using the equation below (Prager et al., 2021) after converting the carbon dioxide concentrations to dry model fractions:

$$NEE = \frac{\rho \times V \times (dC / dt)}{A}$$

In this equation, ρ is the air density (mol air/m^3) calculated from P/RT, where P is the atmospheric pressure (Pa), R is the universal gas constant (8.314 J·air K^{-1} mol^{-1}), and T is the air temperature (K). V is the volume of the chamber (m^3), dC / dt is the rate of change of carbon dioxide taken from the chamber ($\mu mol \cdot CO_2$ mol^{-1} air s^{-1}), and A is the ground area of the chamber (m^2). We estimated NEE at PPFD = 800 $\mu mol\, m^{-2} s^{-1}$ (NEE_{800}) to standardize our measurements over time and space. We estimated NEE_{800} by creating a light response curve with NEE against PPFD and fitting a line between our four light measurements. We then solved the equation for PPFD = 800 $\mu mol\, m^{-2} s^{-1}$ (Sundqvist et al., 2020). GPP_{800} is then calculated using the equation:

$$NEE_{800} = ER - GPP_{800}$$

with negative NEE indicating CO_2 uptake and positive NEE indicating CO_2 release.

2.5 | Data analysis

To determine the effect of warming and invasive species on plant biomass, NEE, GPP, ER, soil moisture, and NDVI throughout the growing season, we ran a linear mixed effects model using the package *nlme* (Pinheiro et al., 2023; Pinheiro & Bates, 2000) in R, version 4.15 (R Core Team, 2023). All the models had a consistent structure, with an interaction term between warming, invasive species presence, and time, which was represented numerically as the month the data were collected, as fixed effects. Plot was a random effect, and we included a correlation structure to account for temporal autocorrelation. To capture how warming modified the impact of invasive species on carbon fluxes across the growing season, we calculated the standardized mean difference (SMD) using Hedge's *d* metric of effect size using the package *effsize* (Torchiano, 2020) in R, version 4.15 (R Core Team, 2023). We calculated the effect of invasive species presence separately for ambient and warmed temperatures at the three different sampling points. For NEE, SMD <0 indicates that plots without *C. vulgaris* are more of a carbon source than the control plots. For GPP, SMD <0 indicates less productivity in plots without *C. vulgaris*. For ER, SMD <0 plots without *C. vulgaris* increased

respiration. To measure the treatment effects on NEE, independent of plant biomass, we corrected NEE for the amount of biomass by dividing the NEE value in the plot by the biomass. One plot was an extreme outlier (>1000% higher than any other plot) and was removed from the analysis. These analyses used the main plots established in 2015, which included warming and *C. vulraris* removal treatments.

In January, when we measured carbon fluxes and leaf thickness in plots with native species removal and naturally uninvaded plots, we used an ANOVA test with a post hoc Tukey test to determine the statistical difference between all six plots. We compared the differences between all six plots in plant biomass, NEE, GPP, ER, and leaf thickness. To explore the differences between plant communities in the six different plots, we calculated Bray–Curtis dissimilarity matrices from the January plant community composition data, visualized them using an NMDS, and then ran a PerMANOVA to determine statistical differences among treatments. *p*-values were corrected for multiple comparisons using the Holm method for the PerMANOVA test, and the ANOVA tests were corrected for multiple comparisons using Tukey's HSD.

3 | RESULTS

With *C. vulgaris* removal, there was 30% less total above-ground biomass ($F_{1,27}=8.51$, $p=0.007$) (Figure 1). Above-ground biomass varies significantly throughout the growing season; the average biomass was 486 g m^{-2} in November, 502 g m^{-2} in January, and 570 g m^{-2} in March ($F_{1,57}=12.65$, $p=0.007$). There were consistent effects of the treatments over time, as there was no significant interaction between time and removal ($F_{1,57}=0.75$, $p=0.390$), time and warming ($F_{1,57}=0.06$, $p=0.811$), or time, warming, and removal ($F_{1,57}=0.51$, $p=0.477$). There was no significant interaction between warming and removal ($F_{1,27}=0.11$, $p=0.746$), and warming did not significantly impact above-ground biomass ($F_{1,27}=2.98$, $p=0.134$). Removal did not significantly affect subdominant biomass (all plants except *C. vulgaris*) ($F_{1,27}=3.386$, $p=0.077$), though removal plots had 21% less subdominant biomass (Figure S1).

With *C. vulgaris* removal, there was 128% greater NEE (weaker carbon sink) ($F_{1,28}=51.53$, $p<0.001$) (Figure 2 and Figure S2). The removal effect differed over the season. Hedge's g effect size showed the largest effect of removal in November, with the effect of removal diminishing across the growing season (Figure 2). There were consistent effects of the treatments over time on NEE, as there were no significant interactions between removal and time ($F_{1,60}=2.141$, $p=0.149$), warming and time ($F_{1,60}=0.30$, $p=0.586$), or warming, removal, and time ($F_{1,60}=0.07$, $p=0.800$) (Table S3). NEE varied significantly over the season ($F_{1,60}=10.40$, $p=0.002$). November was the largest carbon sink (−0.612 μmol^{-2} s^{-1}), January was the weakest carbon sink (0.064 μmol^{-2} s^{-1}), and March was intermediate (−0.146 μmol^{-2} s^{-1}). Warming did not significantly impact NEE ($F_{1,28}=0.00$, $p=0.961$), and there was no significant warming by removal interaction ($F_{1,28}=0.57$, $p=0.456$). When correcting NEE for biomass (dividing NEE by the total biomass in the plot), there was a significant effect of removal ($F_{1,26}=12.38$, $p=0.002$, Figure S3).

With *C. vulgaris* removal, there was 40% less GPP ($F_{1,28}=15.01$, $p=0.001$) (Figure 2 and Figure S2). The effect of *C. vulgaris* removal on GPP was strongest in November, with a 46% reduction in GPP, compared with 41% in January and 29% in March (Figure 2). Warming modified the effect of *C. vulgaris* removal on GPP; under ambient conditions, removal decreased GPP by 59%, whereas GPP decreased by only 17% in the combined warming and removal treatment ($F_{1,28}=6.33$, $p=0.018$). GPP did not vary significantly over time

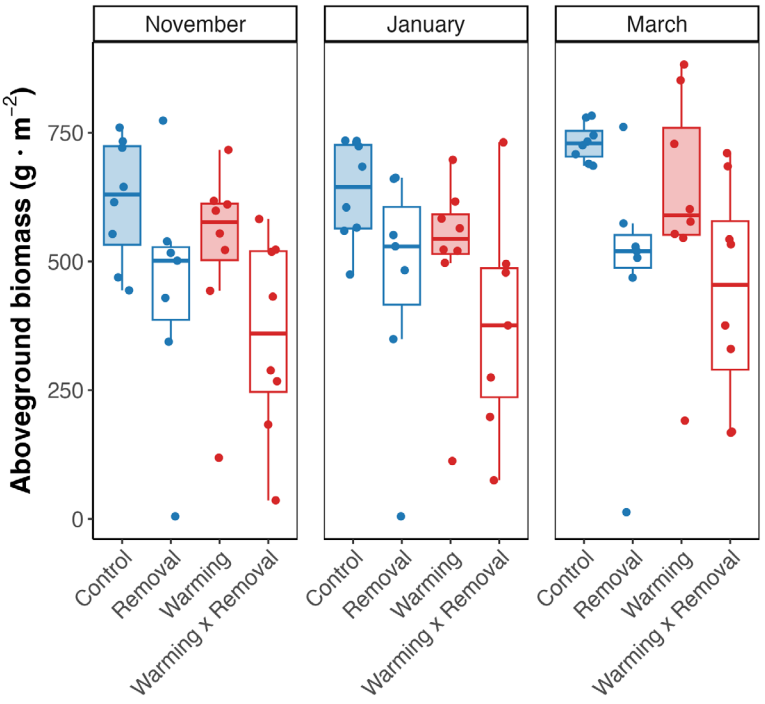


FIGURE 1 Above-ground biomass across the growing season. There was a significant main effect of time and *C. vulgaris* removal. There was no significant effect of warming and no significant interactions.

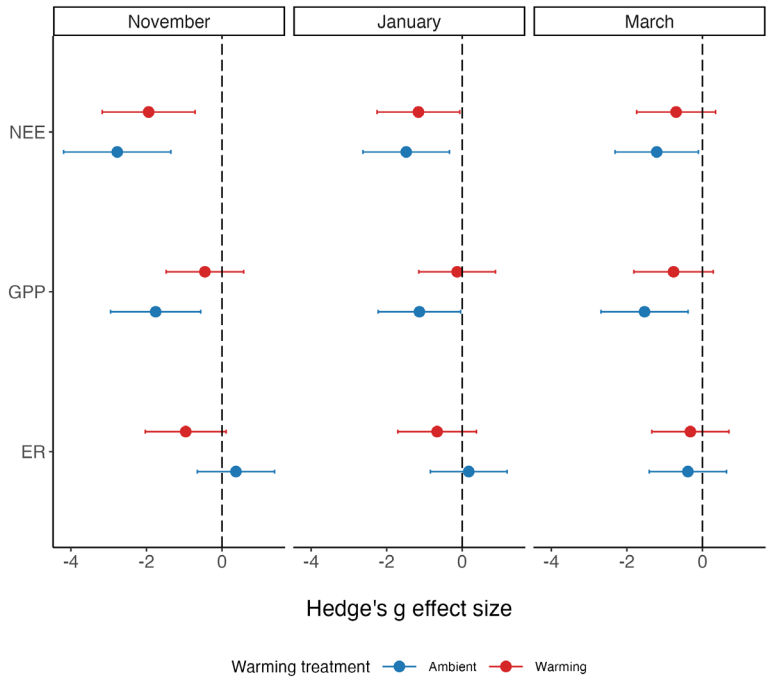


FIGURE 2 The effect of *C. vulgaris* removal on carbon fluxes across the growing season. Each effect size is calculated to compare the control from the removed plots (e.g., the ambient bar compares AC with AR, and the warmed bar compares WC with WR). This can allow us to determine how removal impacts carbon fluxes and how warming can modify the effect. For NEE, SMD <0 indicates that plots without *C. vulgaris* are more of a carbon source than control plots, for GPP SMD <0 indicates less productivity in plots without *C. vulgaris*, and for ER SMD <0 indicates that plots have increased respiration without *C. vulgaris*.

($F_{1,60}=1.72$, $p=0.192$), and warming had no significant direct effect on GPP ($F_{1,28}=0.571$, $p=0.456$). There were consistent effects of the treatments over time on GPP as there were no significant interactions between removal and time ($F_{1,60}=1.723$, $p=0.194$), warming and time ($F_{1,60}=0.55$, $p=0.462$), or warming, removal, and time ($F_{1,60}=1.51$, $p=0.225$) (Table S3). There was no significant effect of removal, warming, or the interaction between time and the treatments on ER (Figure 2, Figure S2 and Table S3). However, time had a marginally significant effect on ER ($F_{1,60}=3.82$, $p=0.056$), as ER was, on average, 0.55 $\mu mol^{-2}s^{-1}$ in November, 1.56 $\mu mol^{-2}s^{-1}$ in January, and 0.84 $\mu mol^{-2}s^{-1}$ in March.

NEE of the uninvaded and native removal plots were not significantly different from the other treatments (Figure 3). GPP of the native removal plots was significantly lower than that of the control plots ($p=0.044$). ER of the native removal plots was significantly lower than the warming × removal plots ($p=0.015$). Above-ground biomass of the uninvaded and native removal plots was not significantly different from the other treatments (Figure 3). Warming and *C. vulgaris* removal also impacted NDVI, soil moisture, leaf thickness, and plant community composition. There was significantly lower NDVI with *C. vulgaris* removal ($F_{1,28}=16.72$, $p<0.001$), but this effect diminished as the season progressed (time×removal, $F_{1,60}=21.40$, $p<0.001$) (Table S4). There was no significant effect of time ($F_{1,60}=0.03$, $p=0.860$), warming ($F_{1,28}=0.11$, $p=0.742$), warming×removal ($F_{1,28}=2.23$, $p=0.147$), warming×time ($F_{1,60}=0.74$, $p=0.393$), or warming×removal×time ($F_{1,60}=0.99$, $p=0.326$) on NDVI (Figure S4). There were no significant treatment effects on soil moisture, but soil moisture varied significantly over time ($F_{1,492}=3.91$, $p=0.049$), with the wettest weekly soil moisture 28% in the last week of January and the driest weekly soil moisture 21% in mid-March (Figure S5). Leaf thickness varied substantially with the presence and absence of *C. vulgaris*, and the community-weighted mean of leaf thickness tended to be lower when *C. vulgaris* was present. The uninvaded control plots had the thickest leaves and had significantly higher leaf thickness than the control plots ($p<0.001$), warmed plots ($p<0.001$), and native removal plots ($p=0.001$). The warmed plots had the thinnest leaves and were significantly thinner than the *C. vulgaris* removal plots ($p<0.001$) and warmed *C. vulgaris* removal plots ($p=0.001$). The *C. vulgaris* removal plots were also significantly different from the control plots ($p=0.007$) (Figure S6 and Table S4). The removal of *C. vulgaris* changed the community composition of the plots. Using a PerMANOVA (Figure S7 and Table S5), we determined that warmed plots with *C. vulgaris* removal were significantly different from those without *C. vulgaris* ($p=0.045$), unwarmed plots with *C. vulgaris* removal were significantly different from those without *C. vulgaris* ($p=0.015$) and that plots without *D. subulatum* were significantly different from the control plots ($p=0.030$).

4 | DISCUSSION

Plant invasion can have detrimental effects on ecosystems worldwide, but substantial uncertainty remains about how warming interacts with invasion to impact ecosystem processes, especially since there is often strong context dependency (Lopez et al., 2022) and seasonal variation in effects. We measured the interactive effects of *C. vulgaris* removal and experimental warming on carbon cycling in a montane tussock grassland in a long-term experiment. We found that the removal of an invasive species led to lower productivity and weakened the carbon sink, while warming alone had little effect. Although we hypothesized that *C. vulgaris* would exert its strongest influence later in the growing season due to its phenology, the largest effects occurred early in the season, and *C. vulgaris* removal consistently reduced net carbon uptake across the season. Plots with

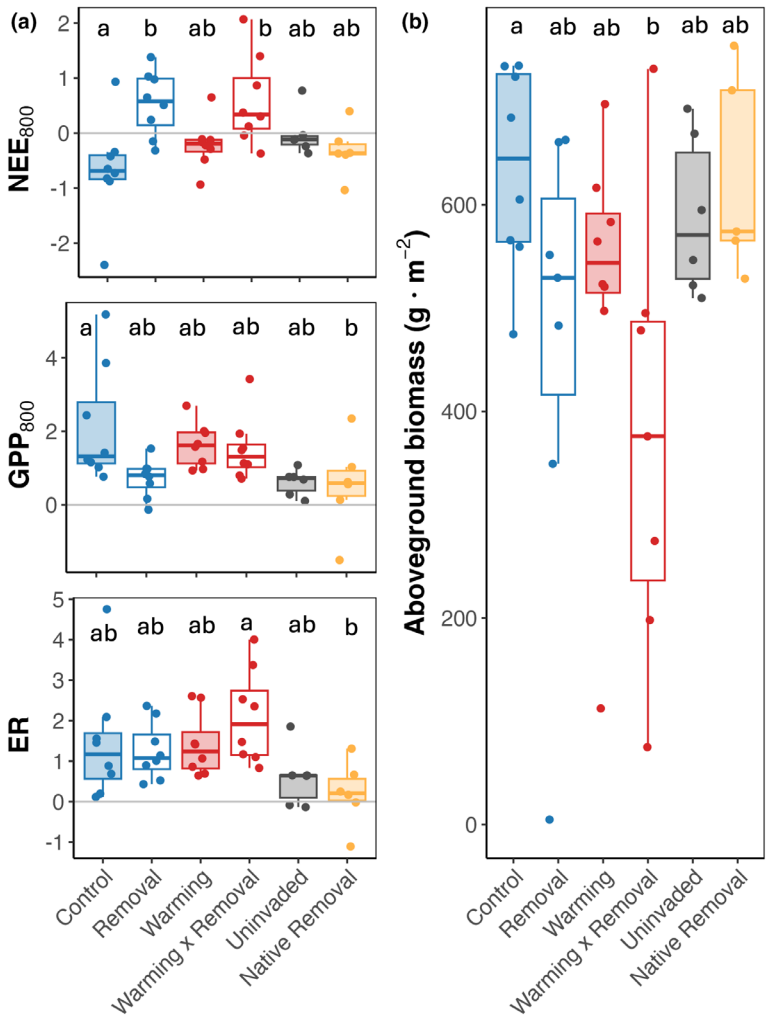


FIGURE 3 In January, the base plots and additional controls, which include uninvaded plots and plots with native plant removal, were measured. (a) NEE, GPP, and ER in the base plots and additional controls. NEE, GPP, and ER are measured in $\mu mol\, m^{-2}\, s^{-1}$. (b) Above-ground biomass in all the plots. Treatments that share a letter are not statistically different from one another.

C. vulgaris removal also had less total plant biomass. Even after accounting for plot-level biomass, native plant communities had lower productivity than invaded plots. Overall, we found that *C. vulgaris* had surprisingly consistent effects on carbon cycling and is the dominant producer in these invaded tussock grasslands.

After 8 years of *C. vulgaris* removal, total plant biomass remained significantly lower than in invaded plots and tended to be lower than the native removal plots or uninvaded plots. This lack of biomass compensation by the native plant community was unexpected, as competition theory predicts that removal of the dominant species should release subdominant species and increase community biomass (Tilman, 1987; Whittaker, 1965). However, dominant species removal does not always result in compensatory growth. For example, removal of two different dominant species led to compensation in only one of two cases examined by Souza et al. (2011), and a meta-analysis reported general declines in above-ground net primary productivity following species removal (Smith et al., 2020). Additionally, one study found that invasive species removal most strongly increases native biomass when native cover is intermediate (20%–39%), whereas recovery is limited under high or low native cover due to resource limitation or ecosystem degradation, respectively (Ta et al., 2024). The greater biomass observed in invaded plots versus removal plots likely reflects slow regeneration rates of the native community, as native shrubs primarily regenerate following disturbances such as fire (Smale, 1990), and tussock grasses rely largely on vegetative regeneration (Rose & Platt, 1990).

Contrary to our hypothesis, warming did not strongly affect plant biomass in either invaded or removal plots. Previous work found that *C. vulgaris* extends its flowering period under warmer temperatures, shifting its phenology earlier in the year and extending later (Giejsztowt et al., 2020). We anticipated this extended phenology to translate into greater biomass accumulation, but the absence of a warming effect suggests that phenological shifts do not necessarily scale to ecosystem-level changes in biomass. Warmer temperatures often increase invasive biomass more than native biomass (Chen et al., 2017; Ivison et al., 2025; Zhang et al., 2025). In a meta-analysis measuring warming effects on invasive plant species, warming had a positive effect on invasive plants' performance, but there was no effect on the native plant community (Liu et al., 2017). In our 8-year experiment, the plant community may have acclimated to elevated temperatures, dampening biomass responses. Consistent with this interpretation, plant cover data from 2015 to 2021 show that *C. vulgaris* abundance was negatively correlated with maximum air temperature in warmed plots, likely reflecting lower drought

tolerance, though there was no overall warming effect (Leon-Garcia et al., 2025). In relatively cold, montane ecosystems, where temperature typically constrains growth, warming often increases biomass (Hobbie et al., 1999; Madani et al., 2020; Peñuelas et al., 2004), but water limitation can offset these gains, resulting in no net change (Peñuelas et al., 2004).

We found that plots with *C. vulgaris* removed had less GPP and greater NEE without a significant effect on ER. Invasive plants tend to increase ecosystem productivity (Liao et al., 2008; Raheem et al., 2024; Zhou et al., 2015) as invasive species are generally highly productive (Montesinos, 2022); thus, the removal of *C. vulgaris* would reduce productivity, aligning with our results. Many of the studies measuring NEE in response to species invasion have focused on wetlands, where invasive species often strengthen carbon sinks (Duman & Schäfer, 2018; Huang et al., 2025; Zhou et al., 2015; Zhu et al., 2024), sometimes increasing carbon storage up to 86% (Huang et al., 2025). Our results extend this pattern to a terrestrial grassland ecosystem. Interestingly, the stronger carbon sink in plots with *C. vulgaris* was driven by enhanced GPP rather than changes in ER. Although root biomass may persist following above-ground removal, the consistency of ER across all treatments suggests that below-ground respiration was not strongly altered and that removal effects were driven primarily by changes in above-ground productivity. Though other studies have also found larger effects of invasive species on productivity (Zhu et al., 2024), many also find that invasive species impact carbon cycling through changes to respiration (Duman & Schäfer, 2018; Hamerlynck et al., 2012; Hu et al., 2022). The absence of an ER response suggests that below-ground processes are relatively resilient to changes in above-ground species composition in this system.

Although warming often benefits invasive species (Liu et al., 2017), and *C. vulgaris* was a major driver of C-fluxes in our experiment, we measured no direct effects of warming on ecosystem NEE, GPP, or ER. Warmer temperatures often do not affect NEE, as they tend to positively impact GPP and ER, causing there to be no net change in NEE (Wu et al., 2011), but surprisingly, we did not see an effect on any of the carbon fluxes. There was a significant interaction between warming and *C. vulgaris* removal on GPP, such that the native plant community increased productivity with warming, but it had no effect on the GPP of the *C. vulgaris*-invaded plant community ($F_{1,28}=6.33$, $p=0.018$). This finding demonstrates the resilience of the native plant community to higher temperatures. In plots where *C. vulgaris* is removed, leaves are significantly thicker (Figure S6), and plants with thicker leaves tend to be more resistant to warming temperatures (Leigh et al., 2012).

Although there was less total plant biomass and lower GPP in plots with *C. vulgaris* removed, the reduction in biomass cannot be explained by the differences in GPP, but rather by the absence of *C. vulgaris*. Even after correcting NEE for biomass, plots without C. vulgaris remained weaker carbon sinks (Figure S3). Historically, productivity was assumed to scale with biomass at a 2:1 ratio (Beer et al., 2010). However, subsequent work shows that productivity more closely tracks photosynthetically active biomass, with fast-growing plants fixing more carbon per unit mass (Poorter et al., 1990). Invasive plants often have higher specific leaf area (Lake & Leishman, 2004) and rapid growth rates (Lagos et al., 2017; Montesinos, 2022), resulting in greater photosynthetic capacity relative to total biomass. In our experiment, plots with *C. vulgaris* had thinner leaves (Figure S6) and higher GPP. Moreover, naturally uninvaded plots showed GPP comparable to removal plots, reinforcing the conclusion that observed differences reflect the presence of *C. vulgaris*. These findings highlight a key management trade-off: while invasive species can enhance ecosystem carbon uptake, their persistence may undermine biodiversity, alter long-term soil carbon dynamics, and increase surface energy absorption (Colberg et al., 2024; Nuñez et al., 2021). Therefore, we suggest caution in interpreting these effects of *C. vulgaris* invasion on carbon fluxes as beneficial to the ecosystem overall.

Although we expected *C. vulgaris* to have the largest effect on NEE later in the growing season, due to its extended flowering under warming (Giejsztowt et al., 2020), the largest effect occurred early in the growing season and decreased over time. Because biomass removal was minimal during the 2023–2024 growing season and preceding years, these seasonal patterns are unlikely to reflect transient release from disturbance and instead likely reflect phenological differences. Since *C. vulgaris* tends to flower later in the season, carbon is likely allocated toward reproduction, meaning that less is allocated toward vegetative growth (Lundgren & Des Marais, 2020; Reekie & Bazzaz, 1987). With less energy allocated towards vegetative growth, *C. vulgaris* could have less production later in the season relative to the native plant community, though floral production is at its peak. Additionally, the carbon allocation to flowers, which respire but do not photosynthesize, could increase ER compared with GPP. Interestingly, warming did not change the seasonality of NEE, GPP, or ER fluxes, and there were similar differences between native and invaded plant communities for the whole season. Although invasive species are often more phenologically sensitive to warming than native species (Dawson-Glass et al., 2025; Zettlemoyer et al., 2019), data linking invasion to seasonal dynamics of carbon fluxes remain scarce. Our results provide rare evidence that seasonal carbon flux patterns can remain stable, even with changing plant phenology.

5 | CONCLUSIONS

In this long-term experiment, we demonstrate that removal of an invasive shrub reduced GPP and weakened the carbon sink of a montane tussock grassland across a growing season. Warming increased productivity only in native plant communities and had little effect in invaded plots. Although studies increasingly document warming effects on invasive plant phenology, their consequences for ecosystem carbon cycling, especially in terrestrial ecosystems, remain poorly understood. As biological invasions and climate warming continue to intensify, explicitly accounting for invasive species in carbon cycling models will be essential for improving ecosystem-scale predictions.

AUTHOR CONTRIBUTIONS

Julie R. Deslippe and Aimée T. Classen designed the study and methodology. Olivia K. Vought, Julie R. Deslippe, Indira V. Leon-Garcia, and Janelle A. Veenendaal performed the research. Olivia K. Vought analysed the data. Aimée T. Classen and Julie R. Deslippe acquired the funding. Olivia K. Vought wrote the original manuscript draft, and all co-authors contributed to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Environmental Data Initiative (EDI) at https://doi.org/10.6073/pasta/591dd98298eb5ff5de78b50ce686d6aa (Vought et al., 2026).

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SUPPORTING INFORMATION

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

Figure S1. Subdominant biomass (biomass of all plants besides *Calluna vulgaris*) through time.

Figure S2. (A) Net ecosystem exchange (NEE) across the growing season. There was a significant main effect of time and *C. vulgaris* removal. There were no significant interactions. (B) Gross primary productivity (GPP) across the growing season. There was a significant main effect of *C. vulgaris* removal and a significant interaction between warming and *C. vulgaris* removal. (C) Ecosystem respiration (ER) throughout the growing season. There were no significant effects of the treatments or time.

Figure S3. NEE across the season, with each plot divided by the biomass in the plot. The Y-axis was adjusted to omit plot 26, which had a corrected NEE of ~0.2.

Figure S4. NDVI through time.

Figure S5. Soil moisture through time, yellow arrows indicate sampling time.

Figure S6. Leaf thickness in all the plots, calculated as a community-weighted mean of the four most abundant species. Letters indicated statistical significance, with shared letters meaning no statistical difference.

Figure S7. NMDS of the plant communities from all the treatments in January. Using a PerMANOVA, WR v WC, AR v AC, and AC v ADR were statistically different from one another (statistics are in Table S5). Treatment codes are: WR = warmed and *Calluna vulgaris* removal, WC = warmed, AR = *C. vulgaris* removal, AC = no treatment, ADR = *Dracophyllum subulatum* removal (native equivalent to *C. vulgaris*), and A = naturally no *C. vulgaris*.

Table S1. Average *C. vulgaris* removed across removal plots each growing season. Standard error is calculated among all plots.

Table S2. Allometric equation for each species to calculate grams of above-ground biomass.

Table S3. The effect of warming, removal, and time on carbon fluxes and biomass. Time represents which sampling point in the season the data were collected (collection one was in November, collection two in January, and collection three in March).

Table S4. The effect of warming, removal, and time on subdominant biomass, NDVI, soil moisture, and scaled NEE. Time represents which sampling point in the season the data were collected (collection one was in November, collection two in January, and collection three in March). Scaled NEE omits plot 26, which is an extreme outlier.

Table S5. Results of a PerMANOVA analysis comparing the plant communities of the different plots during January. Treatment codes are: WR = warmed and *Calluna vulgaris* removal, WC = warmed, AR = *C. vulgaris* removal, AC = no treatment, ADR = *Dracophyllum subulatum* removal (native equivalent to *C. vulgaris*), and A = naturally no *C. vulgaris*.

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