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Research article

Invasive plants grow taller under experimental warming, but mediated effects of biotic interactions are species-specific

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Understanding the responses of non-native plants to climate change while accounting for biotic interactions is key to predicting and mitigating future invasion risks. Non-native invasive plants may benefit from or decline in the face of climate change, relative to native competitors. Non-native plants might also suffer less than native plants from natural enemies such as herbivores, which could give non-natives a competitive advantage. However, we lack an understanding of how non-native plants will compete with native plants in a warming climate, while accounting for the effects of herbivore pressure. To test the potential interactions between warming, herbivore pressure and competition, we set up a common-garden experiment in Trondheim, Norway, using five non-native plants growing either alone or in competition with a native plant community. These plants were subjected to herbivore exclusion and artificial warming treatments, using open-top chambers. We found that under warming, three non-native species had greater biomass and all five species were taller than when grown without warming. Competition with native species reduced the biomass of three non-native species and herbivore exclusion resulted in taller plants for three non-native species. Native community biomass was not affected by either warming or herbivore exclusion. Furthermore, the native community was not affected by competition with any non-native plant except *Centaurea montana*, which resulted in lower native community biomass, suggesting that *C. montana* is likely to be the most detrimental of these non-native species to native communities. Competition with natives reduced the positive effects of warming on biomass for only one species, *Alchemilla mollis*. Our study strongly suggests that a warming climate may benefit invasive plants more than native plants, but for some species these effects will be mediated by biotic interactions in idiosyncratic ways, depending on the identity of both native and non-native species. This will present a challenge to predicting plant invasion success under climate change while accounting for biotic interactions.

Keywords: climate change, herbivory, interactions, native competition, non-native plants, warming



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Introduction

Climate change has been predicted to influence non-native plant success (Liu et al. 2017), and non-native plants were found to perform better than native plants under both increased temperature and atmospheric CO₂ concentration (Liu et al. 2017). In addition, global warming is likely to lengthen the suitable seasons during which an introduction could happen and extend the range in which an invasive plant could survive. Longer warm periods also mean invasive plants may be able to produce fruit and reproduce within the growing season in areas with climates which, in the past, would not have supported such quick growth (Liu et al. 2017). High-latitude regions, such as Norway, are warming at a faster rate than elsewhere in the world (IPCC 2014, Taylor et al. 2022), which makes research into the response of non-native species to warming in these locations even more important. Based on a survey carried out in 2018, Norway is currently home to over 2000 non-native species, around half of which are naturalised and stably reproducing and over 70% of which are plants (Sandvik et al. 2019). In fact, Norway was found to have the most naturalised plant species of all European countries except the UK (Sandvik et al. 2019) with the potential for the introduction and establishment of many more invasive plant species (Iverson et al. unpubl.). Understanding the response of non-native species to warming in highly-invaded locations such as Norway is therefore even more important to predict how the threat of these plants may develop.

However, non-native plants do not grow in isolation. It is important to consider how other biota in these invaded ecosystems might influence non-native plant performance and therefore modulate their response to climate change. One form of biotic interactions experienced by non-native plants is competition with the native plant community. The outcompeting of native plants is a frequently described ecological impact of non-native plants within their invaded community (Mack et al. 2000), and it has been found that non-native species often possess greater competitive ability than native species (Gioria and Osborne 2014). For example, Lee et al. (2021) found that non-native dandelions outcompeted their native competitors in a pairwise experiment, and Corbin and D'Antonio (2010) found that native plant productivity in a Californian grassland was reduced when native plants were in competition with non-native grasses. However, there are also documented effects of native species impacting non-native species performance. A review of pairwise experiments showed that although non-native plants affect native plants strongly, there was still some effect of native competition on non-native plant performance (Vilà and Weiner 2004). Using native species to revegetate disturbed land was found to suppress non-native plant establishment and re-invasion (Schuster et al. 2018), and non-native species biomass was reduced when in competition with either native or naturalised non-native species (Haeuser et al. 2019). In one study, native plants were even found to outcompete their non-native competitors in a pairwise experiment using native and invasive populations of *Alliaria petiolata* (Bossdorf et al.

2004). The competitive balance between native and non-native plants can therefore vary between systems and species.

Insect herbivory is another biotic factor which may influence non-native plant success. One of the leading hypotheses in invasion ecology is that the success of non-native plants is in part due to the relative lack of effects of natural enemies such as specialist herbivores in areas where the non-native plants are introduced (enemy release). The effects of herbivory on plant success include reducing plant survival and reproduction (Huang et al. 2012) and limiting the range that a plant can expand into (Van Der Putten et al. 2010). However, there are mixed results from tests of the enemy release hypothesis in the literature (Fenner and Lee 2001, Wolfe 2002, Siemann et al. 2006) which suggests that enemy release is extremely system-specific and cannot be applied to all non-native plant scenarios.

If enemy release is indeed occurring, this may affect how plants perform under climate warming. For example, the herbivory levels of native plants may increase proportionally with warming-induced increased growth. However, if non-native plants are generally suffering lower levels of herbivory, there will be fewer limitations on their growth and they may therefore be able to exhibit a much stronger positive response to warming compared with natives. In addition, competition with native biota may suppress non-native plants' response to warming. There are very few studies which consider the interactive effects of warming, herbivory and competition on non-native plants. Such studies include field experiments by Lu et al. (2016) who found that native species gain the competitive advantage over non-native species under artificial warming but only in the presence of a biocontrol beetle herbivore, and Zhang et al. (2021) who found that warming increased plant performance of two aquatic non-native plants in China but that the competitive balance between them was dependent on the ecosystem zone (tropical/temperate) and the presence of biocontrol herbivores. However, these studies both focused on biocontrol herbivores rather than native herbivores, and therefore do not indicate how general herbivory might mediate the effects of warming.

In this study, we aimed to answer the following questions: 1) how does warming, herbivore exclusion and competition with a native plant community affect the performance of five non-native plant species in Norway? 2) Is there an interaction between these three factors in the response of non-native plants? 3) How does the response to warming, herbivore exclusion and competition differ between non-native plants and a native plant community? To achieve this we created a common-garden experiment containing warming and herbivore exclusion treatments within which we planted non-native species and a native species community both individually and together. The exclusion of herbivores allowed us to determine whether enemy release benefits non-native species, and how enemy release for both native and non-native plants affected their response to warming. In addition, our design allowed us to investigate both the effects of a native plant community on non-native plants and the effect of non-native plants on a native community.

Material and methods

Study species

We chose five non-native species for this experiment: *Arabis caucasica*, *Alchemilla mollis*, *Centaurea montana*, *Cerastium tomentosum* and *Hesperis matronalis* (Table 1). We also chose three native species (*Trifolium pratense*, *Silene dioica* and *Festuca rubra*) to represent a community of common native grassland species within Norway. Our non-native plant species are all ranked as high- or very high-risk in Norway according to the Norwegian Biodiversity Information Centre's assessment (Artsdatabanken 2023). They also have a short germination time (4 weeks or less) and maximum ground cover area (i.e. of fully-matured plant) of less than roughly 30 cm² due to limited space within the experiment. We checked germination times of each species on plant information websites (Plants For A Future; Thompson and Morgan (accessed January 2021)), and ground cover area was based on expert knowledge (Vange unpubl.). *Arabis caucasica* became naturalised around 1912 and has approximately doubled its occurrence every 20 years since, found to displace native species particularly in shallow soils. *Alchemilla mollis* was first found in Norway in 1938 and is now widespread across Norway and throughout Troms og Finnmark, the northernmost Norwegian county. *Centaurea montana* and *Cerastium tomentosum* both became naturalised within Norway in the late 1800s and began to expand their ranges in the 1940s. The latter can form large mats which displace native species. *Hesperis matronalis* began to expand its range in Norway around 1830 and since 1900, rate of occurrences have increased by 20 to 50% every decade (Artsdatabanken 2023).

Study site and experimental layout

We set up a common-garden experiment in the Norwegian University of Science and Technology (NTNU) Ringve Botanical Gardens in Trondheim, Norway (63°26'45.6"N, 10°27'14.4"E). The experiment was positioned on a grass lawn with little or no shading from trees. Within the experiment we created ten replicate blocks, each containing four treatment combination plots in a fully factorial design; control (no warming or herbivore exclusion), herbivore exclusion only, warming only and warming + herbivore exclusion (Fig. 1). The treatment combinations were randomly assigned to plots within each block. Each of the ten replicate blocks comprised a 2.5 × 2.5 m raised bed filled with topsoil. The warming treatment was achieved by using open top chambers

(OTCs), hexagonal structures made of clear plastic which typically warm inside air temperature by 1–3°C (Molau and Mølgaard 1996). Herbivore exclusion was achieved by creating six-sided insect-proof mesh covers roughly one metre tall, fitted over six bamboo canes tied together at the top to form a point. For treatments which did not include herbivore exclusion, we attached insect-proof mesh covers to the same bamboo structures but with open gaps at the bottom and top as a procedural control for light, wind and precipitation which may be affected by the mesh. For the herbivore exclusion treatment, excess mesh at the base of the structures was tucked inwards under either the base of OTCs in plots which included warming, or under six lengths of bamboo fixed to the ground using metal staples in exclusion-only plots. We built up a layer of soil with a depth or approximately 2 cm around the base of the herbivore exclusion structures to prevent aboveground invertebrate access to the plants (Fig. 1).

Plants were grown from seeds sown in trays and placed in a glasshouse at the end of April 2022 (trays contained a bottom layer of 90% potting soil (phosphorus 40 mg l⁻¹, calcium 220 mg l⁻¹ and nitrogen 950 mg l⁻¹) and 10% perlite, and a 5 cm top layer of less fertile seed-starting soil (phosphorus 30 mg l⁻¹, calcium 150 mg l⁻¹ and nitrogen 750 mg l⁻¹). We thinned out and re-potted seedlings at least once before planting them into the experiment pots, with the exception of the grass *F. rubra*. The non-native *A. mollis* seeds did not germinate and too few seeds of *C. montana* germinated, so instead we transplanted *A. mollis* seedlings and *C. montana* ramets (young lateral rosette plants with roots that were cut away from the maternal plant) growing within the garden for these two species. All *A. mollis* plants were therefore transplanted from the garden, but *C. montana* plants included both seed-grown and transplanted individuals.

From the 10–13 June 2022, we transplanted plants into two litre experimental pots containing 90% potting soil (phosphorus 40 mg l⁻¹, calcium 220 mg l⁻¹ and nitrogen 950 mg l⁻¹) and 10% perlite. Each of the four treatment plots across ten replicate blocks contained eleven pots: five containing one of each non-native species only (no competition for non-natives), five containing one of each non-native species potted with one each of all three native species (competition), and one pot containing one each of all three native species (no competition from the non-natives) (Fig. 1). In total, there were 440 pots across the experiment containing 1120 plants. The grass *F. rubra* was very dense within the seedling trays so we transplanted clumps of grass 1 cm² in area into experiment pots. Immediately prior to transplanting plants into the experiment, we recorded the following per

Table 1. Non-native species chosen for common-garden experiment including species family and native range (POWO 2022). Risk ratings are according to the Norwegian Biodiversity Information Centre (Artsdatabanken 2023). For full native and non-native distributions see the Supporting information.

Species	Family	Native range	Risk rating
<i>Arabis caucasica</i>	Brassicaceae	NW Africa, SE Europe and Arabian Peninsula	high
<i>Alchemilla mollis</i>	Rosaceae	Romania to Caucasus	very high
<i>Centaurea montana</i>	Asteraceae	Western and central Europe	high
<i>Cerastium tomentosum</i>	Caryophyllaceae	Italy	very high
<i>Hesperis matronalis</i>	Brassicaceae	Southern Europe and Caucasus	high

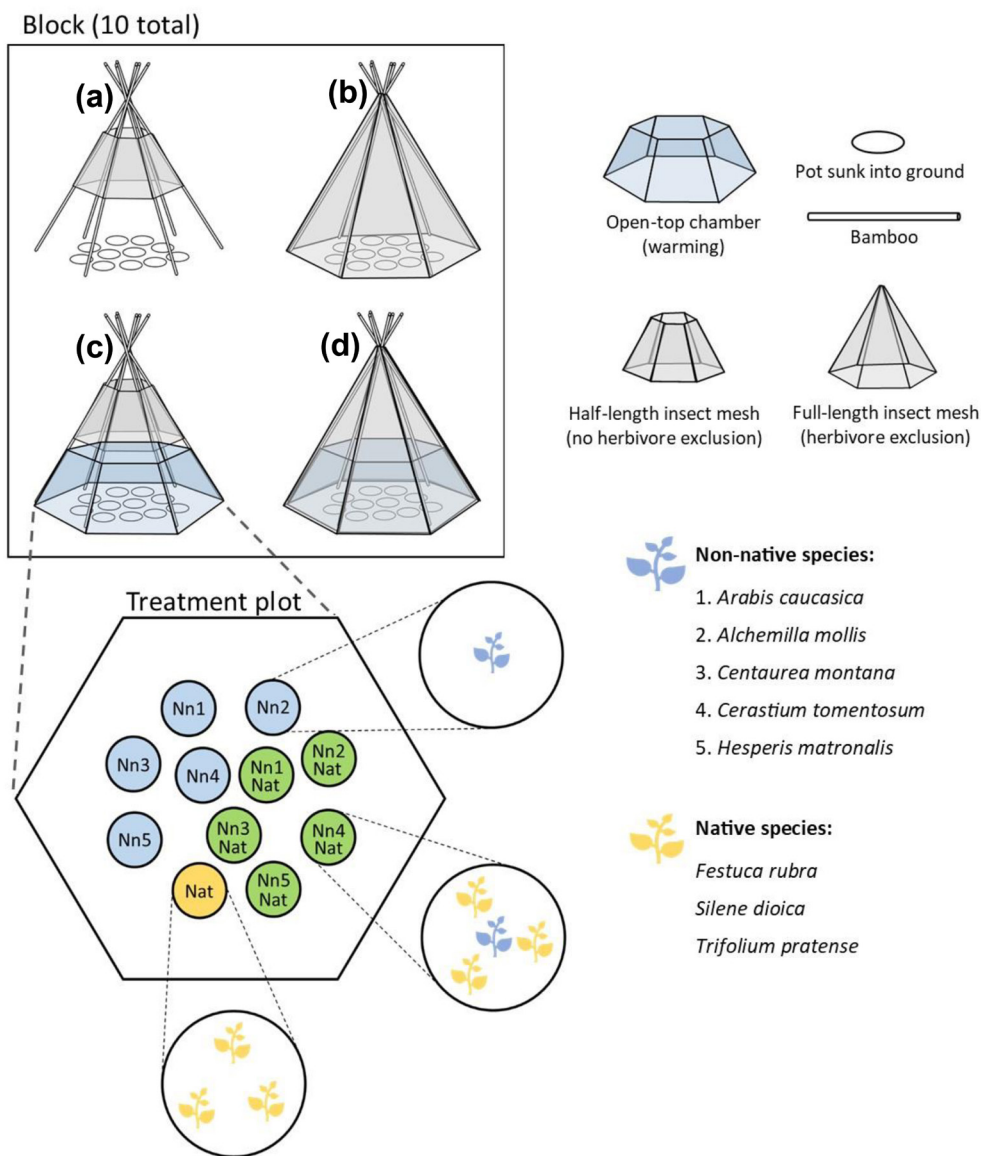


Figure 1. Experimental layout of common-garden experiment. Ten 'block' replicates each contain four treatment 'plots'. Control (a) is ambient and contains only a half mesh cover; herbivore exclusion (b) is ambient and has a full mesh cover; warming (c) has an OTC to increase air temperature and a half mesh cover; warming and exclusion (d) has an OTC and full mesh cover. Half covers were used to account for potential effects of mesh on light, wind and precipitation levels. Each treatment plot contained 11 pots, represented by coloured circles, each containing either one of five non-native species, one of five non-native species with three native species, or three native species alone, totalling 440 pots and 1120 plants across the experiment. NB pot types (non-native, non-native with native competition and native only) were randomly distributed within treatment plots.

non-native plant: number of leaves, number of leaves where over 10% of leaf was damaged by herbivory, the proportion of each damaged leaf missing due to herbivory, plant height (cm; measured from the soil to the highest point of the plant as it lay naturally), length of the largest leaf (mm), and width of the largest leaf (mm). Experiment pots were sunk into the soil within the raised bed replicate blocks so the top of the pot was level with the soil surface to 1) reduce the risk of the pot soil reaching unrealistically high or low temperatures, 2) reduce the risk of the substrate drying out, and 3) increase the volume of space for aboveground plant growth within experimental plots. We randomly positioned

pots within each plot. Finally, we placed temperature loggers within the soil close to the centre of each plot (between sunken pots) to determine whether the experimental warming treatment worked as intended (i.e. whether and to what degree air and soil temperatures within OTCs reached higher temperatures than in non-OTC plots). TMS-4 dataloggers measure soil moisture and temperature at 6 cm below the soil surface, and air temperature at 2 and 15 cm above the surface (Wild et al. 2019). One TMS-4 was placed within each of the four treatment plots for five randomly chosen replicate blocks and set to measure temperatures every 15 min. HOBO 64K Pendant dataloggers, which measure soil temperature only,

were placed within each of the four treatment plots of the remaining five replicate blocks, at a depth of around 6 cm, and set to measure soil temperature every hour. A further eight HOBO loggers were distributed so that two replicate blocks contained both TMS-4 and HOBO loggers. For full set-up see the Supporting information.

Data collection

The experiment ran from 17 June to 17 August 2022. We carried out watering on one occasion two weeks after the experimental start date. At the end of the experiment, we took the following measurements of all non-native plants: height (cm, measured as length from soil surface to highest point of plant), proportion leaves with herbivory (out of all leaves if plant had fewer than 50 leaves in total, and out of a haphazardly chosen subset of 50 leaves if the plant had more than 50 in total), length of the largest leaf (mm), width of the largest leaf (mm), presence/absence of chewing or leaf mining damage across whole plant, number of flowers, surface area of largest leaf, and dry biomass of largest leaf. To measure the surface area of the largest leaf, we removed the largest leaf from the plant and photographed the flat leaf (held in place between white paper below and a glass sheet above, with a piece of 1 mm² graph paper in view for scale). We calculated leaf area from the images using 'ImageJ' and the 'Fiji' plug-in (Schindelin et al. 2012, Schneider et al. 2012). We excluded missing leaf parts due to herbivory from area measurements, because there was no way to accurately predict the full area of the leaf as if it was undamaged. We measured biomass of the largest leaf by placing each leaf in an envelope and drying them within a drying oven at 60°C for 48 h. We then measured weight in grams to four decimal places. We calculated specific leaf area (SLA) by dividing leaf area (mm²) by leaf weight (g). For the native plants *S. dioica* and *T. pratense*, the proportion of leaves with herbivory was measured as a random subset of up to twelve leaves for the entire plant because leaflets of trifoliolate *T. pratense* leaves were treated as separate leaves and time constraints prevented selection of up to fifty leaves for native plants. No herbivory measurements were made of the grass *F. rubra*. Finally, we measured total aboveground biomass of all native and non-native plants by cutting all plants at the soil surface and drying at 60°C for 72 h prior to weighing (in grams to the nearest 0.01 g). Hereafter, aboveground biomass will be referred to as biomass.

Data analysis

Different modelling techniques were carried out in the following analyses but all were validated using the R package 'DHARMA' (Hartig 2021), and any significant interactions between predictor variables were investigated using the R package 'emmeans' (Russell 2021).

Testing the warming effect of OTCs

We needed to determine whether the OTCs had successfully increased temperatures within warming treatments.

We downloaded data from the dataloggers resulting in four separate temperature measures (three measurements at -6, +2 and +15 cm relative to soil surface for TMS-4 dataloggers; one measurement (roughly -3 cm) for HOBO dataloggers). Dataloggers within the control plots for two replicates recorded temperatures at least 6°C warmer than all other recorded temperatures which was likely due to datalogger malfunctions, so these data were not considered. For each of the remaining dataloggers, we calculated the mean temperature for each of the four measures across the entire experimental timeframe (17 June–17 August). We then used a linear mixed effects model in the R package 'glmmTMB' (Brooks et al. 2017) to analyse temperature measures across treatments. Mean temperature across the entire experimental timeframe (for a given soil surface depth/data logger) was used as a response variable and treatment type (control, exclusion, warming, warming+exclusion) as a fixed effect with replicate block number (1–10) as a random effect to account for potential spatial patterns in temperature across the experiment. Temperature differences were also inspected graphically by plotting the daily temperature difference between comparable dataloggers in each block (control vs warming; herbivore exclusion vs warming+herbivore exclusion) (Supporting information). We also downloaded soil moisture data from TMS4 dataloggers and calculated the mean moisture (measured using time-domain transmission (TDT) method with raw TDT data as units (Wild et al. 2019)) across the entire experimental timeframe for each datalogger. Linear mixed effects models were used to determine whether soil moisture was affected by treatment, using mean soil moisture as a response variable, treatment as a fixed effect and replicate block number (1–10) as a random effect.

The warming treatments did increase soil and air temperatures, and the increase was greater for warming than for warming+exclusion treatments (Supporting information). The largest warming effect was for soil 6 cm below the surface where mean temperature of the entire experimental timeframe was increased by an average of 0.91°C (±0.18°C SE) in the warming and 0.74°C (±0.18°C SE) in the warming+exclusion treatment plots compared to control plots (Supporting information). HOBO dataloggers showed an additional increase of 0.29°C for exclusion plots compared to control plots. When plotted, the mean daily difference between warming and control plots, and between warming+exclusion and exclusion plots, was mostly positive but did decrease gradually throughout the summer for all datalogger measurements (Supporting information). There was no difference in mean soil moisture levels across the entire experimental period among treatments (Supporting information).

Testing the effectiveness of herbivore exclusion treatments

To determine whether the exclusion mesh covers were successful in excluding herbivores and reducing herbivory rates, we used a binomial generalised linear mixed model in the R package 'lme4' (Bates et al. 2015). Herbivory was analysed as the proportion of sampled leaves with damage. Competition

(non-native plants grown either alone or with native plants) and treatment (control, exclusion, warming, warming + exclusion) were included as both additive effects and as two-way interactions and transplant type (seed-grown or collected seedlings) was included as an additive effect only. Species was treated as a random effect to estimate overall herbivory differences among treatments, on average across all non-native plant species. Replicate block number (1–10) was an additional random effect.

Herbivory levels were lower in exclusion and warming + exclusion plots compared to controls (mean proportion of leaves damaged was 0.22 in control plots compared with 0.11 each for both exclusion and warming + exclusion; $p < 0.01$ for both), and higher in warming plots. Despite the occurrence of some herbivory in exclusion and warming + exclusion plots, we will continue to refer to these plots as 'exclusion' rather than 'reduction' for ease. There was only weak evidence of lower herbivory levels on non-native plants with native competition ($p = 0.06$) compared to plants without competition, which was more pronounced in warming + exclusion plots (Supporting information). There was no effect of plant origin (seed grown or wild-collected seedlings) on herbivory levels ($p = 0.38$).

Analysing the effect of treatments on non-native and native plants

The following linear mixed effects models were all fitted using 'lme4' (Bates et al. 2015). Separate models were created for each non-native species to determine how each was affected individually by warming, exclusion and competition, and in each model plant performance was represented by one of three measurements as response variables: total plant biomass (square-root transformed), SLA (natural log or square-root transformed) or plant height. We included warming and exclusion in the model as two fixed effects (warming or no warming, exclusion or no exclusion) to assess whether the effects of warming on plant performance were dependent on exclusion of herbivores. We also included competition with native species as a third fixed effect. These three variables were treated as additive terms, but we also included two-way interactions between each pair of variables and a three-way interaction between all three variables. To account for the initial size of plants at the beginning of the experiment, we added length of the largest leaf at the time of planting as an additive term only. For *C. montana*, an additive term of plant origin (seed grown or wild-growing) was included as too few seeds germinated in the greenhouse and plants were supplemented with wild-growing ramets. Replicate block was added as a random effect.

We also created models to investigate treatment effect on native plant biomass. Combined biomass of the native community was the response variable. We included warming and herbivore exclusion as fixed effects. We also included a third fixed effect for competition, with six levels representing no competition with non-native species (native community alone) or competition with each one of the five non-native species. This allowed us to investigate the effects

of competition, and specifically which non-native species had the largest competitive ability. Replicate number (1–10) was added as a random effect. All data handling was completed in R ver. 3.6.1 (www.r-project.org).

Results

All results in the following sections are back-transformed to original units and the reported effects of treatments are compared with plants grown under control conditions (no competition, ambient temperatures, and with no herbivore exclusion). Results are summarised in Fig. 2 and full model summaries can be found in the Supporting information.

Effect of warming on non-native species performance

There was strong evidence that warming resulted in increased biomass for *A. mollis* and *H. matronalis*, with weaker evidence for *A. caucasica* (average increase of 1.48, 15.42, and 4.50 g, respectively; $p = 0.02$, < 0.01 and 0.06 , Fig. 3). Plant height increased under warming for all five non-native species (average increase of 9.20, 9.45, 14.89, 14.03, and 21.16 cm for *A. caucasica*, *A. mollis*, *C. montana*, *C. tomentosum* and *H. matronalis*, respectively; $p < 0.05$ for all). SLA was not affected by warming for any species.

Effect of herbivore exclusion on non-native species performance

There was no effect of herbivore exclusion on the biomass or SLA of any species. Plant height increased under herbivore exclusion for three non-native species (*A. caucasica*, *A. mollis* and *H. matronalis*; average increase of 7.11, 5.46 and 20.50 cm, respectively; $p < 0.05$ for all).

Effect of competition with native plants on non-native species performance

Three of the non-native species (*A. caucasica*, *A. mollis* and *C. tomentosum*) had lower biomass on average when grown with versus without the native species, indicating native competitive effects (average reduction of 4.90, 3.86 and 5.33 g, respectively; $p < 0.01$). *Alchemilla mollis* also experienced reduced height under competition (average reduction of 7.46 cm; $p < 0.01$; Fig. 4). There was weak evidence ($p = 0.07$) that SLA of *A. caucasica* was reduced under competition with native plants.

Interactive effects of warming, herbivore exclusion and competition

Interactions between competition, warming and exclusion were observed in *A. mollis*; there was strong evidence that plants increased both biomass and height more in warmed plots without competition than with competition. The increase in both biomass and height in warmed plots was also greater

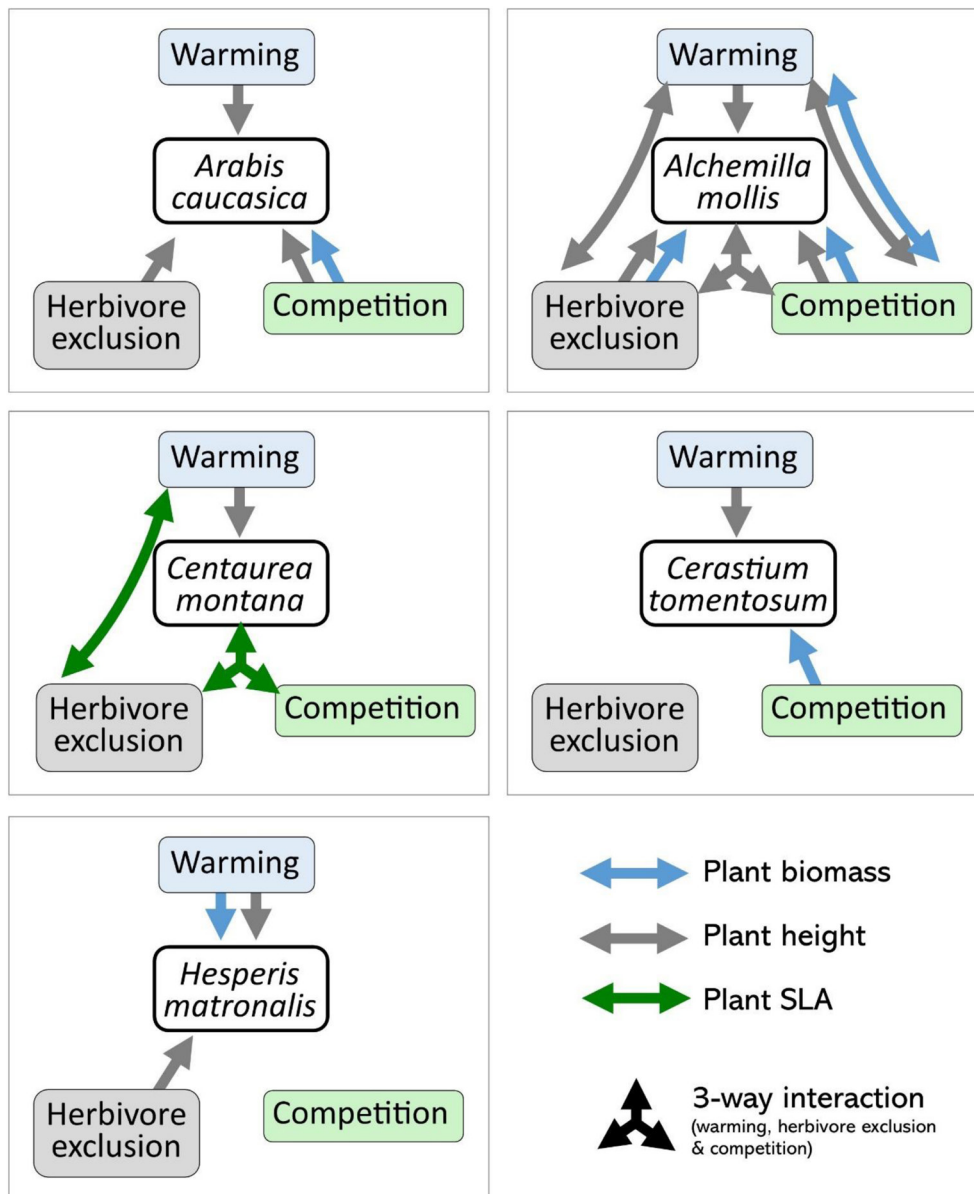


Figure 2. Summary of the effects of each treatment type (warming, herbivore exclusion, competition with a native community) on five non-native plants. Arrows represent significant effect of each treatment, colour coded by the functional trait affected (biomass, height or specific leaf area (SLA)). Arrows between treatments indicate that those treatments had a two-way interactive effect on plant functional traits. Three-way interaction symbol indicates that all three treatment types interacted; details on the manner of these interactions can be found in the Supporting Information.

without the herbivore exclusion treatment than with the exclusion treatment, though evidence for this greater increase of biomass was weak ($p=0.07$). Finally, when herbivores were not excluded the increase in height from ambient to warmed plots was greater for plants without competition. When herbivores were excluded, however, the opposite trend was shown where the increase in height from ambient to warmed plots was greater for plants with competition (Supporting information).

Centaurea montana also showed evidence of interactions between competition, exclusion and warming. Under the herbivore exclusion treatment, plants with no competition had a greater SLA in warmed than ambient plots, but without the

herbivore exclusion treatment, plants with no competition had a smaller SLA under warmed plots (Supporting information).

Native species performance

There was no evidence of warming or herbivore exclusion affecting the total biomass of native species. The only effect of competition on native species was competition with *C. montana*, which resulted in reduced community biomass ($p < 0.01$). Competition with other species did not affect biomass of native species compared to native species grown without competition (Fig. 5, Supporting information).

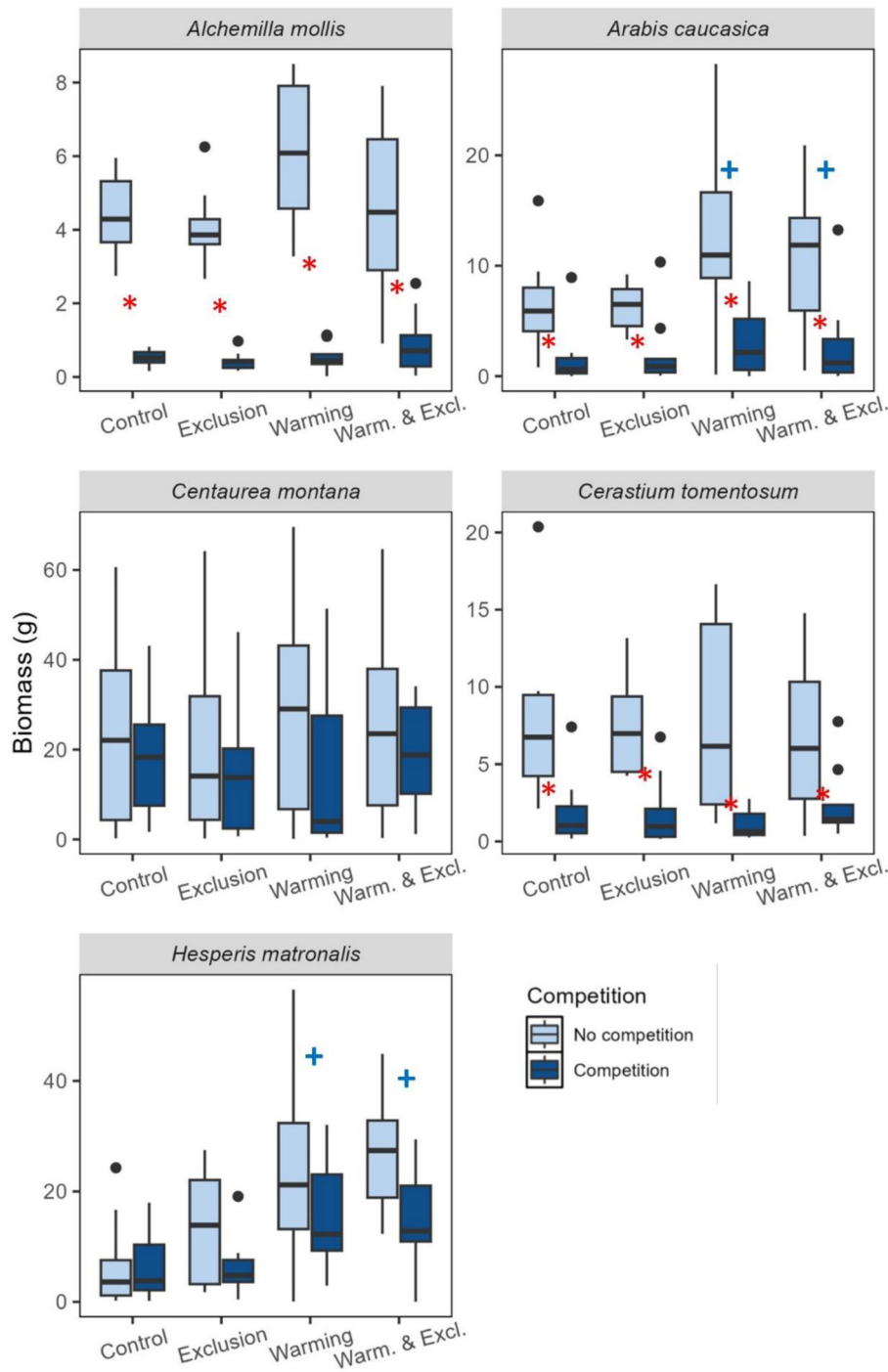


Figure 3. Biomass of each non-native species across each treatment type and with/without native competition. On x-axis, 'Exclusion' refers to herbivore exclusion. Red asterisk represents significant reduction in biomass for plants with native competition compared to those without competition. Blue crosses represent significant increase in biomass for plants in warmed plots compared to controls.

Discussion

In this common-garden experiment, we investigated the combined effects of warming, herbivore exclusion and plant competition on five invasive non-native species which are well-adapted to a high-latitude climate. We found strong

evidence that warming increases plant performance (biomass and height) for non-native species, that herbivore exclusion results in increased non-native plant height and that, unsurprisingly, competition with native species reduces non-native plant biomass. The native species community, however, showed no response to warming or

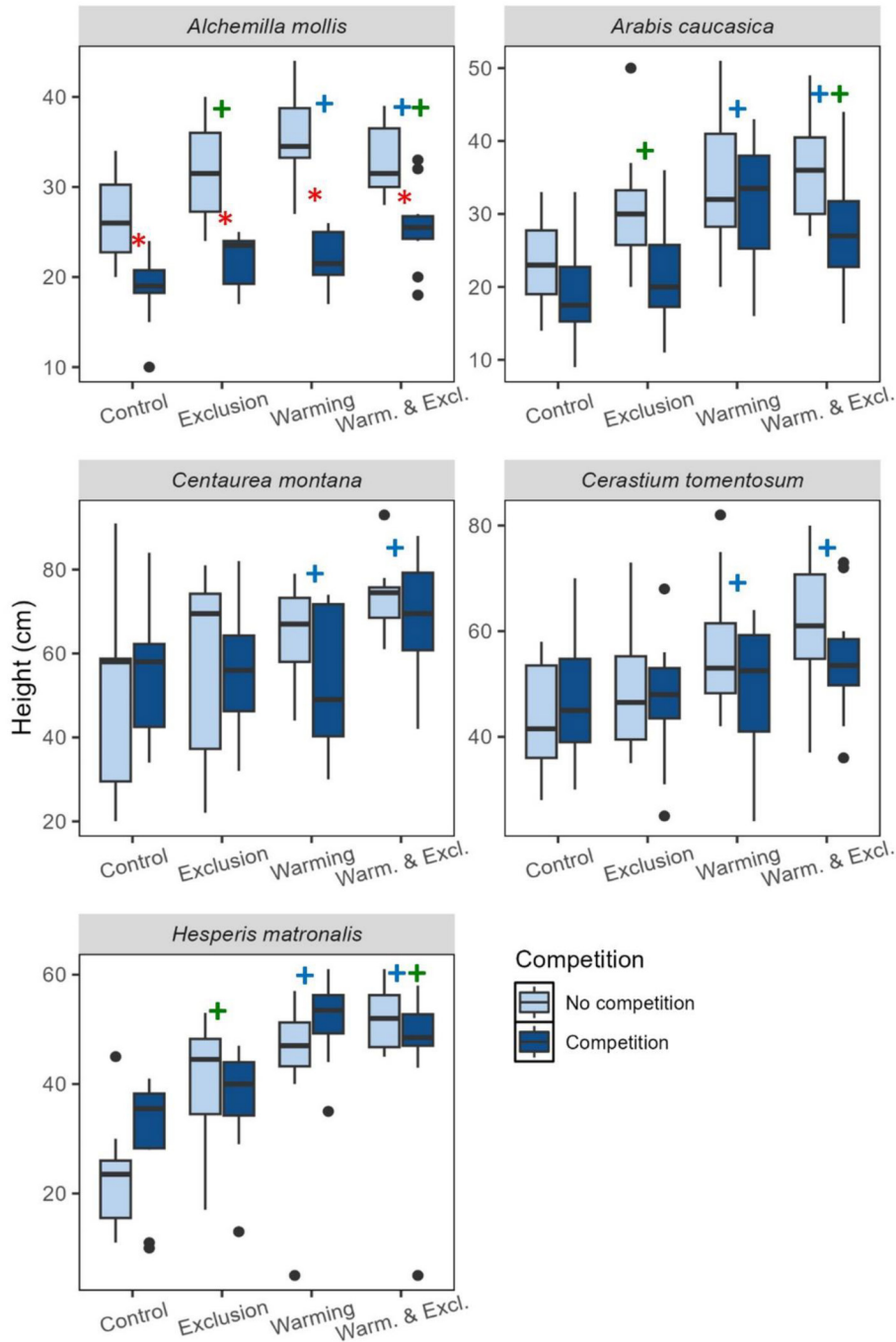


Figure 4. Height of each non-native species across each treatment type and with/without native competition. On x-axis, ‘Exclusion’ refers to herbivore exclusion. Red asterisk represents statistically significant reduction in height for plants with native competition compared to those without competition. Blue crosses represent statistically significant increase in height for plants in warmed plots compared to controls, and green crosses represent statistically significant increase in height for plants with excluded herbivores compared with controls.

herbivore exclusion and was only affected by competition with the non-native species *C. montana*. In the following discussion, we discuss the implications of our findings for understanding 1) how climate change will affect non-native plant performance, and how non-native plant performance might be mediated by 2) herbivory and 3) competition with native plant species.

Effects of climate change

All non-native plants showed an increase in height, whereas only two species (and to a weaker extent a third species) showed strong evidence of increased biomass and no species showed an increase in SLA under warming. This corresponds with assemblage-level predictions by Petersen et al.

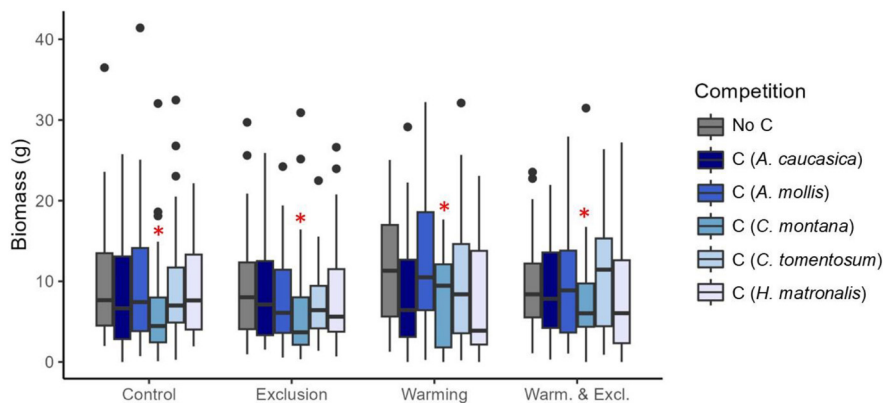


Figure 5. Biomass of native species communities in each treatment type and either in competition with each non-native species or alone (No C). In legend C = competition. Red asterisk indicates where competition significantly reduced biomass compared to control groups (No C).

(2022) that plants will become taller in Norway under climate change. In terms of experimental warming, this trend was also observed by Bjorkman et al. (2018) who found that over multiple locations in the Arctic tundra, plant height responded strongly to warming but SLA was not affected, and Walker et al. (2006) who found that height responded rapidly to warming, again in tundra ecosystems. While our experimental study was not set in tundra, we still observed an effect of warming on height. This result indicates there may be a more pervasive effect of warming on plant height beyond species found in tundra.

Beyond Norway, warming increased height and biomass of plants in the Qinghai-Tibetan Plateau (Zhang et al. 2015) and in a common-garden experiment in Belgium (De Frenne et al. 2011), however, these studies placed warming chambers upon areas of natural landscape and therefore observed these trends within native communities. In contrast, biomass of the native species community as a whole in this experiment did not respond to warming and increased biomass trends were only observed for two non-native species, *A. mollis* and *H. matronalis*. These two non-native plants may be more phenotypically plastic than the native species, fitting with the idea that plasticity promotes establishment of some non-native plants in a wide range of climates (Richards et al. 2006). A study by He et al. (2012b) lends support to this idea, wherein experimental warming of congeneric non-native and native plants grown together had a greater positive effect on non-native than native biomass. The species *A. mollis* and *H. matronalis*, and to a lesser extent *A. caucasica*, showed not only increased height but also increased biomass under warming. All three species are documented to displace native plants (Artsdatabanken 2023), and our findings suggest this impact will be exacerbated by greater growth under a warming climate.

Effects of herbivory

Herbivory of non-native plants was reduced in herbivore exclusion plots which corresponded to increased performance in terms of greater height (but not biomass) of three non-native species. This result contrasts with the broadly held expectation that non-native plants should suffer relatively little from

natural enemies like herbivores (Keane and Crawley 2002). However, non-native species may still suffer herbivory from generalists, and therefore benefit from their exclusion in numbers. We did not measure height of native plants, but like non-native plants, the biomass of native plants did not differ between herbivore exclusion and control treatments. This contrasts with the results of experiments by Geppert et al. (2021) who used herbivore exclusion cages in a large experiment, and by Dawson et al. (2014) who excluded herbivores experimentally by applying insecticides. In both studies, excluding herbivores increased the biomass of both native and non-native species. Taken together, these and our own results suggest that generalist herbivores may in fact constrain non-native plant growth, at least as much as for native comparator plants, resulting in little to no competitive advantage over native plant species. However, it is difficult to draw generalities among species given their idiosyncratic responses to treatments. For example, *A. mollis* showed an increase in height in response to the herbivory exclusion treatment only without warming and competition. Thus, the growth of some non-native species may be less constrained by herbivores in a future warmer climate, but only in the absence of competing natives.

Competition between native and non-native species

Our experimental design allowed us to observe both the impact of a native community on non-native plant performance (competition response of non-natives), and the impact of a non-native plant on a native community (competition effect of non-natives). Unsurprisingly, competition with native species reduced the biomass of three non-native species. One particularly interesting observation, however, was the interaction between competition and warming on the performance of *A. mollis*, where presence of native competition reduced the positive effects of warming on biomass and height. This, in addition to the trend discussed above where non-native plant performance was sometimes lower when herbivores were not excluded, suggests that performance of at least some non-native species under current and future temperatures may well be constrained by competing plants and herbivores in Norwegian ecosystems.

Centaurea montana and *Hesperis matronalis* were unaffected by competition with native species, showing no difference in biomass, SLA or height between plants with and without competition. In addition, *C. montana* was the only non-native species which negatively impacted native plant community performance. This strong competitive ability suggests that populations of *C. montana* could suppress native plant diversity at local scales in its invaded range. However, with the exception of *C. montana*, there was no overall competitive effect of non-native species on native community biomass. This contrasts with multiple lines of evidence that non-native plants outcompete and suppress native species (Mack et al. 2000, Stinson et al. 2006, Lee et al. 2021). For example, a meta-analysis by Vilà and Weiner (2004) found that non-native plants have a greater impact on native plants than vice versa, and that native species are more productive when grown alone than with non-native competitors. In this experiment, we designed the competition treatment primarily to investigate the response of non-native plants to native competition, rather than to measure the competitive effect of non-native plants on natives. The addition of one extra (non-native) plant may therefore have had only a negligible competition effect shared among the three native plants, while the response to competition from three native plants is bound to be greater when compared to non-native plants grown alone. Nonetheless, competitive effects on the native community biomass were detectable for the largest and tallest non-native plant overall *C. montana*.

In addition to limited evidence for competitive effects of non-native plants on native plants, we found no evidence for an interaction between warming and the competitive effect of non-native species on native species, despite observing greater plant performance (biomass) for only non-native plants. This result agrees with a warming study by Verlinden et al. (2013), who found that warming had no effect on the competitive balance of native and non-native plants grown in pairs, even though biomass increased for some species. In contrast, warming increased the competitive ability of a non-native plant *Centaurea maculosa* but not its growth (He et al. 2012b). Differences in competitive ability among non-native species might result from growth conditions and intrinsic differences in plant structure and growth. For example, *A. caucasica* and *C. tomentosum* are low-growing, carpet-forming species that frequently grow in shallow, calcareous soils (Artsdatabanken 2023, Supporting information) and therefore may not have been well adapted to the conditions within this experiment where they were grown in deep, nutrient-rich soils. In contrast, *C. montana* has larger leaves and more upright, thicker stems, and, like *A. mollis* and *H. matronalis*, mostly grows in deep meadow soils (Artsdatabanken 2023, Supporting information). *Centaurea montana* was therefore in more optimal growing conditions than *A. caucasica* and *C. tomentosum* when exposed to native competition during this experiment, which may help to explain why *C. montana* alone had such a large competitive effect.

There were few interactive effects between treatment types for non-native species except *A. mollis*, which experienced

two-way interactive effects between warming and herbivore exclusion and warming and competition and three-way interactive effects between all treatment types (warming, herbivore exclusion and competition). We are therefore unable to make observations about how these effects may interact to impact plant performance generally; however, *A. mollis* is categorised as a 'very high risk' species according to the Norwegian Biodiversity Information Centre (Artsdatabanken 2023), with a high rate of spread that includes movement into areas with many red-listed native species, making it one of the most invasive plants in Norway. Responses of this species to changing conditions are therefore of particular importance in order to understand how to manage its populations in the future. Furthermore, *A. mollis* has many 'generalist' traits such as exhibiting a combination of all three ecological strategies in the competitor, stress-tolerator, ruderal (CSR) theory proposed by Grime (1979) (Klotz and Kühn 2002) and growing in a range of US Department of Agriculture (USDA) hardiness zones (Prism Climate Group 2005, Supporting information). This means that, although our experiment only included five non-native species, the observations made for *A. mollis* may be more widely applicable to other similar species.

Limitations of the experimental design

The OTCs used in this experiment increased the average summer temperature by 0.6–0.9°C (Supporting information) which was slightly less than the documented temperature increase by OTCs of 1–3°C (Molau and Mølgaard 1996). However, the effects of OTCs on plant growth have been found to vary depending on context: Welshofer (2017) found that the effect of OTCs on non-native plants varied with latitude and Cowles et al. (2018) found that the effect of OTCs on plant communities differed across landscape types and precipitation levels. Although the results of our experiment show similar trends to other studies which employed OTCs (Walker et al. 2006, de Frenne et al. 2011, Zhang et al. 2015), it is important to acknowledge that the location and climate of this experiment may influence the warming effects. We should also highlight that as the growing season progressed, the warming effect of OTCs declined (Supporting information), likely because of the cooling effect of plant biomass (Zhang et al. 2013). This is an unavoidable consequence but the experiment was terminated at a point when a warming effect was still detectable for most of the preceding experimental period. OTCs remain a simple and effective method for artificially warming experimental plots and continue to be widely used to simulate climate change.

In this common-garden experiment, herbivore exclusion was carried out by placing fine mesh covers (Fig. 1) as an alternative to using insecticide spray. Despite levels of herbivory being lower in exclusion plots, however, herbivore damage was still observed in reasonably high amounts at the end of the experimental time-frame despite the exclusion mesh covers. Slugs were frequently observed in pots and are likely responsible for most of this. We can therefore only view this

treatment as a reduction and not an exclusion of herbivores, and our responses may therefore not be as strong as if we had fully excluded herbivores from these plots. Furthermore, we did not identify the herbivores present in both exclusion and control plots so were unable to determine if they were specialists or generalists. Nonetheless, the main effect we did observe suggests that growth and success of non-native plants may be constrained by herbivores.

Conclusions

This is the first experiment to investigate the interactive effects between warming, herbivore exclusion and native plant competition on non-native plants. Identifying the response of non-native, invasive plant species to warming is of particular importance in regions like Norway where 1) there are currently a large number of non-native plants species and 2) the climate is changing at a faster rate than at lower latitudes. In addition, the potential for biotic factors to mediate non-native plants' response to warming is vital in understanding the threat of invasive plant species to native ecosystems in the future.

Our study has focused mainly on non-native plant species and further work may therefore need to investigate more the impact of warming on herbivore populations and on native plant communities. This will allow us to understand the mechanisms behind the effects of, and interactions between, warming, herbivory and competition on non-native plants in our experiment.

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Author contributions

Katy Ivison: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Vibekke Vange:** Conceptualization (equal); Data curation (equal); Methodology (equal); Resources (lead); Writing – review and editing (equal). **James M. Speed:** Conceptualization (equal); Data curation (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Wayne Dawson:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.866t1g20w> (Ivison et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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