

PLANT TRAIT AND COMMUNITY RESPONSES TO EXPERIMENTAL CLIMATE
CHANGE

By

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ABSTRACT

Climate change is affecting all ecosystems across the globe. These effects can range from small scale changes in an individual plant's leaf size up to large scale shifts in species distributions. Climate change experiments have uncovered many of these changes in plant traits and plant community properties, but we still lack a complete understanding of how these climate change stressors, such as warming and drought, will affect plants across the globe. Furthermore, we know that plant responses to climate change can be context dependent, given that numerous studies have shown conflicting stress responses for a single trait. For example, warming may either decrease or increase leaf size depending on multiple contexts, such as the amount of warming applied, the abiotic conditions in the natural environment, or the presence and type of biotic interactors. Given that many plant trait and plant community property responses to climate change are context-dependent and haven't yet been well defined, this dissertation aims to unravel some of the complexities defining these responses.

In Chapter 1, we apply in situ warming and drought to an early successional plant community. With this chapter, we measure plant volatile organic compound (VOC) emissions to determine how climate change may impact plant communication and stress protection via their chemical emissions. In Chapter 2, we apply long-term in situ warming and herbivory reduction treatments to two unique early successional plant communities in Michigan, USA. To determine plant responses to warming and herbivory reduction between these environments, we measured several different plant traits and community properties in each of the 7 years of the experiment. Finally, in Chapter 3, we investigate how various environmental, experimental, and plant-level contexts define plant responses to warming via a global meta-analysis of passive experimental warming studies.

Overall, this dissertation uncovers how numerous plant traits and plant community properties respond to climate warming and drought and determines how various contexts, local to global, contribute to plant responses to warming.

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Introduction

Anthropogenic climate change represents one of the most pressing challenges facing scientists over the next century. According to the Intergovernmental Panel on Climate Change, the best estimate of climate warming for 2081-2100, relative to 1850-1900, spans a range from 1.4 to 4.4 °C for global mean annual temperature, depending on the greenhouse gas emissions scenario (IPCC, 2021). Alongside these increases in temperature, we can expect concurrent heatwaves and drought to become more frequent in many parts of the world (IPCC, 2021).

While virtually all ecosystems across the globe will be affected by these changes (Parmesan & Hanley, 2015), it can be hard to draw broad conclusions on ecosystem responses to climate change due to the numerous, nuanced contexts that define ecosystem structure and function. However, some ecological trends appear to hold true across spatial scales; for example, plant green-up and flowering are occurring earlier with warming temperatures, and this trend has been documented across the globe (Cleland et al., 2007; Parmesan & Yohe, 2003; Piao et al., 2019). Although we know this broad, global trend in phenological shifts is occurring, local-scale contexts are still important in defining the magnitude, and potentially even the direction, of plant responses to climate change within their ecological communities. Experimental climate change studies have demonstrated numerous different plant trait and plant community property responses to warming, and while some common trends are seen (such as for phenology), there are some obvious conflicts in results between studies. For example, Descombes et al. 2020 found warming increased plant specific leaf area (SLA), while Hudson et al. 2011 found that warming either decreased SLA or had no effect. These conflicting results demonstrate the context dependency of plant responses to climate change. Local-scale contexts can include factors such as the presence, abundance, and type of biotic interactors, microclimate effects, plant species types, and local disturbances (Dobson et al., 2020; Lemoine et al., 2017; Sousa, 1984; Zarnetske et al., 2012).

In Chapter 1, we uncover how both warming and drought affect the emission of volatile organic compounds (VOCs) for a common species in early successional communities in the Midwest, *Solidago altissima*. Plant VOCs are airborne chemicals emitted from all plant organs and are important mediators in plant interactions with the environment (Loreto et al., 2014; Tumlinson, 2014). Specific VOCs can aid plants in stress protection, as well as communicate eminent stressors to other plants in the environment (Paré & Tumlinson, 1999; Peñuelas &

Llusià, 2003; Sharkey et al., 2007; Unsicker et al., 2009). To study stress effects on emissions, we manipulate climate warming using open-top chambers (OTCs), a passive warming method that can be applied to plant communities in situ (Marion et al., 1997; Welshofer et al., 2018), as well as rainout shelters to block precipitation and create drought conditions for the plant community. We find that the effects of drought on VOC emissions appear to override the effects of warming. For example, the composition of emitted VOCs differs between plants in drought (drought and warming + drought) and non-drought (ambient and warming) treatments, but does not differ between warming treatments. We also highlight specific compounds that either significantly increase or decrease in abundance due to the warming and/or drought treatments, which points to potential important stress-induced changes in emissions that may influence plant communication and stress protection, and therefore, plant fitness.

Chapter 1 highlights a trait (VOCs) not as commonly measured in ecological studies, often due to the difficulty in measuring and analyzing traits such as chemical emissions (MacDougall et al., 2022; Materić et al., 2015). In order to further determine climate stress effects on plants, Chapter 2 investigates how the interaction of climate warming and insect herbivory affects multiple plant traits and community properties at local scales. In this chapter, we again use OTCs to apply warming to plants in situ. We also manipulate the presence of biotic interactors by applying an insecticide, leading to a fully factorial experiment with warming, ambient temperatures, insect herbivory, and reduced insect herbivory treatments. The experiment is replicated in two early successional plant communities in Michigan, USA, and spans seven years. We find that the individual effects of warming on plant traits were more common than interactive warming and herbivory effects. We also discuss variation in plant responses between the two experimental sites and across years, pointing to the need for long-term warming experiments that are replicated across various ecosystems. While the effects of warming in these experiments outweigh the effects of herbivory, the effects of herbivory were still present, pointing to the need to consider biotic interactors alongside abiotic effects in plant responses to warming.

As previously discussed, we know that numerous contexts can contribute to how plants respond to warming. These can include broad-scale environmental contexts, such as the latitude at which a plant resides, down to specific plant-level contexts, such as a plant's functional group (De Frenne et al., 2011; Dormann & Woodin, 2002; Liancourt et al., 2013). While Chapter 2

highlights how multiple traits respond to warming stress, it is limited to two plant communities in the same region. With Chapter 3, we investigate global contexts that contribute to variation in how plants and their communities respond to warming. To do this, we conduct a meta-analysis on OTC studies across the globe to determine: 1. How do plant traits and plant community properties differ in their responses to warming, and 2. What contexts contribute to variation in these responses? We define contexts as either environmental, experimental, or plant-level, which spans broad to individual scales. We find that some contexts explain more variation than others for some trait types; for example, reproductive plant traits are more affected by latitudinal gradients than other trait types. We end this chapter by recommending: 1. Ecologists need to carefully consider the contexts defining the results found in their warming study, 2. More studies are needed that include varying species types (e.g., native and non-native species), and 3. Long-term, coordinated experiments across varying ecosystems are necessary for us to mechanistically understand how plant communities respond to climate warming.

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CHAPTER 1: Climate warming and drought effects on volatile organic compound emissions from *Solidago altissima*

ABSTRACT

Plant volatile organic compound (VOC) emissions are important mediators for plant interactions with biotic and abiotic factors in the environment. Stress-induced changes in VOC emissions can be caused by factors associated with climate change, such as warming or drought. However, we currently lack an understanding of how warming and drought stress affects plants in their natural environment, as well as how warming and drought may interact to synergistically affect plant VOC emissions. To fill these knowledge gaps, we measured VOC emissions from *Solidago altissima* in an early successional plant community under four climate treatments: ambient control, warmed, drought, and warmed + drought. Treatments were applied in situ using open-top chambers for warming and rainout shelters for drought. We find that drought treatments (drought and warmed + drought) have a stronger effect on VOC emissions compared to non-drought treatments (ambient and warmed). We also find that while the overall abundance of VOCs did not differ between treatments, there were specific compounds associated with one or more climate treatments. For example, diisopropyl adipate was more abundant in the drought and warmed + drought treatments, whereas p-cymene was more abundant in the ambient and warmed treatments. Our study shows that in goldenrod, drought may have a stronger effect than warming on VOC emissions, but moreover that specific compounds are especially sensitive to certain climate stressors. Additional experimentation is necessary to uncover the mechanisms underlying stress effects on emissions and the functions associated with the affected compounds. By identifying the compounds sensitive to climate stress, we will gain a greater understanding of how plant interactions with their environment may change under a new climate regime.

INTRODUCTION

Within an environment, plants face numerous, multifaceted interactions with biotic and abiotic factors. Plant emissions of volatile organic compounds (VOCs) are important mediators in these interactions. For example, VOCs can serve as plant growth regulators, pathogen growth inhibitors, defense priming signals, and more (Brilli et al., 2019). However, it is currently unclear how climate change stressors, such as warming and drought, may impact the emission of VOCs for plants. While previous studies have shown that warming and drought can change both the abundance and composition of emitted VOCs (Kreuzwieser et al., 2021; Peñuelas & Llusà,

2003; Sharkey et al., 2007; Sharkey & Singsaas, 1995), these changes can be dependent upon the severity of the stress experienced by the plant (Rissanen et al., 2022) and the species that was sampled (Müller & Junker, 2022), therefore we lack an understanding of how these stressors may impact VOC emissions for many plant species.

The constitutive emission of foliar VOCs can serve as a plant's chemical phenotype, as plant species each emit their own, unique blend of VOCs (Müller & Junker, 2022). VOC emissions may also be stress-induced, in which a stressor in the environment leads to a change in VOC production. These induced VOCs often function as some sort of protective mechanism for the plant; for example, insect herbivory can lead to the production of VOCs that deter herbivores (Morrell & Kessler, 2017; Unsicker et al., 2009) and/or attract natural enemies of herbivores (McCormick et al., 2012; Paré & Tumlinson, 1999; Turlings & Erb, 2018).

Stress-induced changes in VOC production can also occur as a result of abiotic stress, such as warming or drought. Typically, warming leads to an overall increase in foliar VOC production due to increased plant enzymatic activity, increased vapor pressure, and decreased resistance in the diffusion pathway (Peñuelas & Llusà, 2003). Warming may also indirectly increase VOC emissions through increased plant biomass (Kramshøj et al., 2016). Drought can have different effects on VOC emissions, and this difference may be due in part to the severity of the drought experienced by the plant. For example, moderate drought can lead to increased VOC production if limitation in growth leads to increased carbon availability, whereas a more severe drought can reduce photosynthesis and therefore reduce carbon allocation to VOC production (Rissanen et al., 2022). However, there are currently still gaps in our understanding of VOC production under current climate regimes (Yuan et al., 2009), let alone under warmer and drier conditions, therefore we lack complete understanding of these climate stress effects on VOC production.

In addition to changes in overall VOC abundance, the composition of VOCs can also change in response to these stressors. For example, warming can increase the production of isoprene, which may protect plants from heat stress (Sharkey et al., 2007; Sharkey & Singsaas, 1995). Similarly, Kreuzwieser et al. (2021) found that isoprene and monoterpene biosynthesis were maintained despite reduced photosynthesis due to drought, indicating that these compounds may have important functions for stress tolerance, such as quenching reactive oxygen species or stabilizing membranes (Loreto & Velikova, 2001; Peñuelas & Llusà, 2003; Velikova et al.,

2011). Certain compounds or groups of VOCs could experience a reduction in emissions under stress if carbon is partitioned away from the production of those VOCs (Kreuzwieser et al., 2021). In sum, stressors experienced by plants may induce the production of novel compounds that aid in protection, or prevent specific compounds from being produced. By identifying the compounds that are sensitive to climate stress, we will be able to gain a better understanding of how plant emissions may be affected by climate change, which could further affect plant communication and plant-insect interactions.

Numerous studies have investigated warming or drought effects on VOC emissions, but few have studied their combined effects, let alone studying these combined effects in situ (Pierik et al., 2014; Wilschut et al., 2022). It is essential to determine potential interactive effects of warming and drought on emissions because future climate projections show that these stressors will often co-occur (IPCC, 2021). Because emissions are species-specific and highly complex, it can be extremely difficult to generalize how warming and drought may affect VOC production across different environmental and plant-level contexts (Llusà et al., 2006; Staudt et al., 2016). Furthermore, in situ VOC studies are necessary to aid in our understanding of how stressors affect emissions from plants in their natural environment (Pierik et al., 2014; Wilschut et al., 2022).

In this study, our focal study species is tall goldenrod (*Solidago altissima*), which is a native forb in old-field plant communities in the Midwest region of the United States. This species has been previously used in VOC experiments (Howard et al., 2020; Morrell & Kessler, 2017; Shiojiri et al., 2021), but to our knowledge, no studies have investigated warming or drought effects the VOC emissions of this species. *S. altissima* and its close relatives also have known ecological importance for plant community succession and plant-insect interactions (Pisula & Meiners, 2010; Root & Cappuccino, 1992; Uriarte, 2000), making it a good candidate for understanding climate effects on VOC emissions in a natural system. We use an in situ climate change experiment in Michigan, USA to understand how warming, drought, and the combined effects of warming and drought may alter the composition and abundance of VOC emissions for a common species (*S. altissima*) in an early successional community.

METHODS

Study site and species

The climate treatments in this experiment were applied to plants in situ in the Kellogg Biological Station's Long-Term Ecological Research site (KBS-LTER) in Hickory Corners, MI, USA (42.41°N, -85.37°W). This site was under agricultural management until 1989, when management ceased and six replicate fields re-established as early successional plant communities. The fields have been maintained in an early successional stage through annual spring burns since 1997, which prevent woody species colonization. Within the KBS-LTER early successional fields, the most dominant species consist of: tall goldenrod (*Solidago altissima*), red clover (*Trifolium pratense*), timothy grass (*Phleum pratense*), and Kentucky bluegrass (*Poa pratensis*) (Robertson & Hamilton, 2015).

Treatments

Within the KBS-LTER, a large-scale climate manipulation experiment known as the Rain-Exclusion Experiment (REX) began in the summer of 2021. Rainout shelters were placed above the plant community in the six separate early successional field replicates (Fig. S1.1).

Temperature was manipulated in this experiment with the use of open-top chambers (OTCs) built for taller stature plant communities (Welshofer et al., 2018). In June 2021, these chambers were placed on top of the established early successional plant communities in the field replicates to passively increase air temperatures while allowing for natural levels of light, precipitation, and gas exchange to occur (Marion et al., 1997; Welshofer et al., 2018). OTCs remained year-round and were only removed when the annual spring burn occurred. Within REX, the open-top chambers were also nested underneath the rainout shelters to allow for the combination of both warming and drought treatments.

Response variables were measured within 1m² subplots situated under the footprint of each of the four main treatments used in this study (warmed, drought, warmed + drought, and ambient control; Fig. S1.1). Each of the six field replicates contained all four climate treatments (Fig. S1.1). The ambient control subplots used here were open subplots with no treatments applied. MX2202 HOBO data loggers (Onset Computer Corporation, Bourne, MA) were placed in the subplots to determine the effects of our treatments on 1m air temperatures. Soil temperature and moisture in the top 15 cm of soil were monitored in all subplots using Campbell Scientific CS655 probes.

In this experiment, drought treatments were initiated on 25 June 2022. Prior to the initiation of drought, all subplots were watered to ensure the plants began the experiment with equal soil moisture.

Plant headspace collection

From 11 July - 15 July 2022, VOCs were collected from the headspace of *S. altissima* from five of the six fields. We collected VOC samples from one field per day over the course of our 5-day sampling period. At the time of sampling, the plants had been in drought for 17-21 days, depending on the field that was sampled (field 1 = 17 days, field 2 = 18 days, field 3 = 19 days, field 4 = 20 days, field 5 = 21 days).

Five plants within each of the four treatments were sampled each day ($n = 25$ plants per day). Plants with any signs of damage, herbivory, or poor health were not selected for VOC collection. There were very few plants with obvious signs of herbivory or damage, and *S. altissima* is extremely abundant in our experimental subplots, therefore our selection of “healthy” plants was not a biased selection towards the healthiest plants in each subplot. The headspace was defined as the area immediately surrounding the top ~30 leaves from each selected plant. This area was contained within a 35 x 32.5 cm nylon oven bag (Jerina turkey bags). On each day, an empty nylon bag was also sampled to serve as a background air control. The top corner of each nylon bag was fitted with an ORBO coconut charcoal filter to allow clean air to enter the bag during sampling (Fig. S1.2). Air was pulled through the bags for 7 hours each day (0830-1530 h) and onto HayeSep Q VOC traps (volatilecollectiontrap.com) via portable vacuum pumps (IONTIK) at a flow rate of 300 mL/min. Storms on two sampling days cut sampling time to 5 hours for fields 1 and 2 (0830-1330 h), but on all sampling days all treatments in a given field were sampled for the same amount of time.

Once the sampling was complete, the VOC traps were stored in aluminum foil on ice and immediately taken to the lab to be processed. Each trap was eluted with 150 μ L of dichloromethane, which was pushed through the trap using nitrogen gas. One μ L of 500 g/ μ L tetradecane was then added to each sample as an internal standard. VOCs were analyzed with an Agilent 7890A gas chromatogram (GC) fitted with an Agilent VF-5ms column (30 m length, 0.25 mm diameter, 0.25 μ m film) with He as the carrier gas and coupled with an Agilent 5975C mass spectrometer (MS). Samples were injected into the GC/MS with an initial temperature of 225 °C. The temperature program heated the column from 40 °C to 180 °C at a rate of 10

°C/min, then heated at a rate of 40 °C/min until the temperature reached 220 °C, which was held for 10 minutes.

The REX experimental plots are non-destructive, and therefore no plant material can be taken from within the 1m² experimental subplots. As such, we did not harvest plant material post-VOC sampling for a calculation of total biomass sampled. To estimate the biomass sampled per plant, we collected leaves of *S. altissima* from plants immediately outside of each 1m² subplot but still within each treatment. For each treatment, we then fit a linear regression between the collected leaf biomass and leaf length (Table S1.1). Prior to VOC sampling, we marked the top ~30 leaves of the five *S. altissima* individuals in each subplot and recorded the length of each leaf that was to be sampled during VOC sampling. Using our regression equations, we applied each treatment-specific regression to the corresponding measured leaf lengths from the sampled VOC plants in order to estimate total leaf biomass per subplot (Table S1.2). Because the biomass data was estimated on a subplot-level and not an individual plant level, we divided the total biomass per subplot by 5 to estimate total plant biomass per individual (Table S1.2).

Statistical analysis

The temperature and soil moisture data were cleaned and analyzed using R (R Core Team, 2024). We calculated average air temperature, soil temperature, and soil moisture from 11 July - 15 July to match the VOC sampling time frame.

The VOC GC/MS data were first run through the Agilent MassHunter Qualitative Analysis 10.0 program, in which compounds were identified by comparing them to those in the NIST17 (National Institute of Standards and Technology, Gaithersburg, MD) and Adams (Adams, 2007) libraries. All further data cleaning and analysis was conducted using R (R Core Team, 2024). We normalized the data by dividing the abundance of each compound in each sample by the abundance of the internal standard in each sample. After normalizing the data, the abundance of the internal standard was removed from each sample (as its abundance was now equal to 1 across all samples). To remove any background noise from the sampling procedure, the abundance of each compound found in the nylon bag controls was subtracted from the abundances for each sample. Any abundance that became negative after subtraction was replaced with a zero. Caprolactam, which was present due to the nylon oven bags used for sampling, was also removed from each sample. Samples from field 1 were removed prior to analyses due to a

sample processing error ($n = 24$). Samples were also removed prior analyses if they did not contain the internal standard ($n = 1$) or if the sample had abnormally high abundances, which could indicate plant stress from unseen sources such as herbivory ($n = 3$). After sample removal, each climate treatment had $n = 18$ -20 samples.

To standardize compound abundances across treatments, we divided the abundance of each compound in each sample by the plant's estimated biomass and the number of hours sampled. To obtain a final measure of compound abundance/g/hr, we divided each individual plant's VOC abundances by its estimated individual biomass, and then by the total number of hours sampled, which was either 7 or 5 hours.

To test for differences in air temperature, soil temperature, and soil moisture between treatments, we ran a mixed model for each with climate treatment as a fixed effect and field number as a random effect. These mixed models were conducted using the lmer function from the lmerTest package (Kuznetsova et al., 2017), and we tested all pairwise comparisons using the emmeans package (Lenth, 2022).

The compositional differences between climate treatments were investigated using a PERMANOVA (method = Bray-Curtis, permutations = 999, block = field replicate) via the adonis2 function in the R vegan package (Oskanen et al., 2022). We then ran pairwise comparisons for all climate treatments using the pairwise.adonis2 function. We visualized these compositional differences using a PCoA with Bray-Curtis distances using the vegan package. To test for an effect of the climate treatments on the abundance of VOCs emitted, we ran a mixed effect model using the lmer function from the lmerTest package in R (Kuznetsova et al., 2017). For the mixed effect model, VOC abundances were transformed via a cubed root transformation to ensure the data fit the assumptions of normality, and field number was included as a random effect.

To test for specific indicator compounds between treatments (i.e., compounds associated with specific climate treatments), we used the multiplatt function (permutations = 999, block = field replicate, max.order = 3) from the indicpecies R package (Cáceres & Legendre, 2009). The statistical output from multiplatt provides an indicator value ("stat") as the test statistic, which measures the association between a species (in our case, a compound) and a group; this statistic is associated with a p-value. The output also provides the specificity ("A") and sensitivity ("B") of that compound to given climate treatments (Table S1.3). For example, $A = 1.0$, $B = 0.3$ would

demonstrate that that compound was only found in a given climate treatment, but not all replicates of that treatment. Conversely, $A = 0.3$, $B = 1.0$ would demonstrate that that compound was found in all replicates of that treatment, but not solely found within that treatment.

In an attempt to better understand the classification of the 29 compounds identified in the indicator species analyses, we searched known chemical databases for information on each compound (Table S1.4). The databases we included in our search were PubChem (Kim et al. 2023), Pherobase (El-Sayed, 2024), mVOC 4.0 (Lemfack et al., 2018), and the plant-associated VOC database (PVD; Shao et al., 2024). Compounds were cross-searched between these databases using their PubChem CID number and the name of the compound.

RESULTS

Abiotic measurements

Warmed treatments (warmed and warmed + drought) began to experience warmer temperatures than non-warmed treatments (ambient and drought) in June (Fig. S1.3). Air temperatures during the VOC sampling period (11 July - 15 July, 07:00-19:00) in the warmed + drought treatment were ~ 2.5 °C warmer than air temperatures in the ambient ($t = -4.61$, $p < 0.001$), warmed ($t = -3.91$, $p = 0.001$), and drought ($t = -5.29$, $p < 0.001$) treatments (Fig. 1.1A). The warmed treatment had lower soil temperatures than drought ($t = 2.82$, $p = 0.02$) and warmed + drought ($t = 3.13$, $p = 0.01$), whereas the ambient treatment had lower soil temperatures than drought ($t = 2.49$, $p = 0.06$) (Fig. 1.2B). All treatments differed from each other in terms of soil moisture, with the ambient and warmed treatments having the highest levels of soil moisture (Fig. 1.1C).

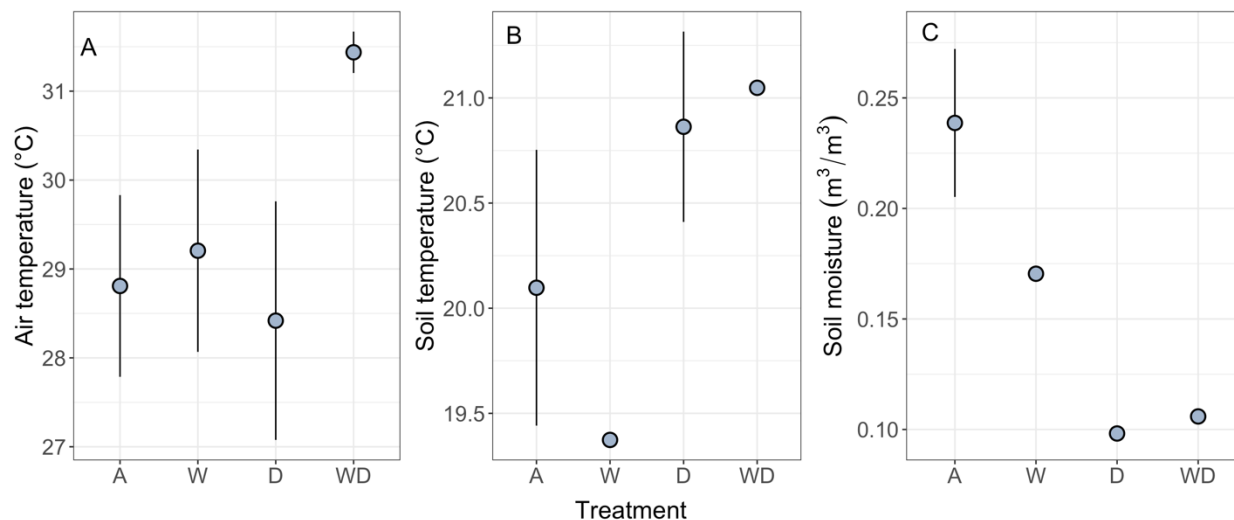


Figure 1.1. A: Air temperatures at 1 m above soil level (°C), B: soil temperatures integrated across the top 15 cm (°C), and C: soil moisture across the top 15 cm (m³/m³) in all climate treatments (A = ambient, W = warmed, D = drought, WD = warmed + drought) from 11 July - 15 July during daytime hours (07:00-19:00). The points and error bars represent mean $\pm$ SE (Air temperature: n = 4 for all; Soil temperature and moisture: n = 3 ambient, n = 4 drought, n = 1 warmed, n = 1 warmed + drought).

VOC composition and abundance

The composition of VOCs in the ambient and warmed treatments differed significantly from the composition of VOCs in the drought (ambient: $F_{1,37} = 1.67$, $p = 0.04$; warmed: $F_{1,37} = 1.81$, $p = 0.04$) and warmed + drought (ambient: $F_{1,35} = 1.85$, $p = 0.03$; warmed: $F_{1,35} = 1.83$, $p = 0.04$) treatments (Fig. 1.2). The composition did not differ between ambient and warmed ($F_{1,35} = 0.83$, $p = 0.55$) or drought and warmed + drought ($F_{1,37} = 0.69$, $p = 0.73$) treatments (Fig. 1.2).

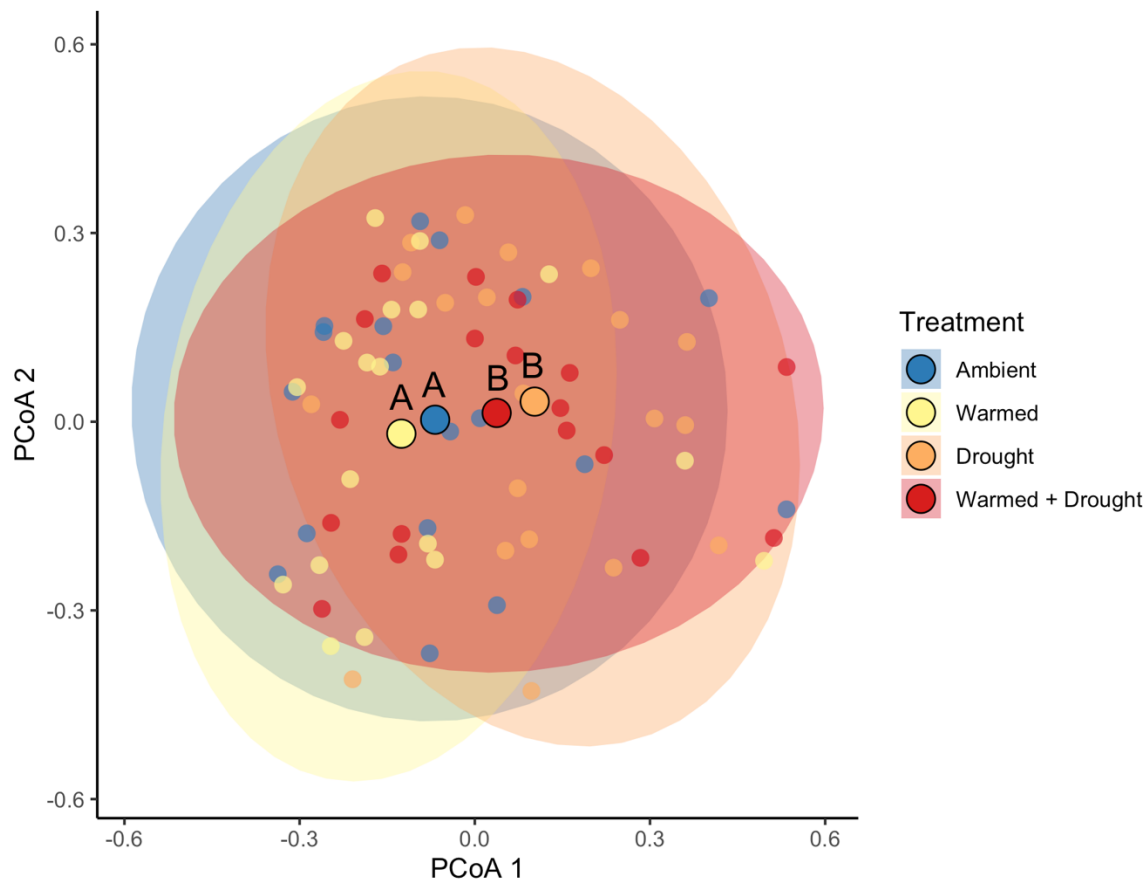


Figure 1.2. PCoA plot using Bray-Curtis dissimilarity for the VOC composition between climate treatments (ambient, warmed, drought, and warmed + drought). Each point represents the composition of an individual plant, and the ellipses represent the 95% confidence interval. The large, outlined point represents the centroid for each climate treatment, and different letters denote statistical differences in VOC composition from a PERMANOVA.

With the indicator species analysis, we found 29 compounds to be significantly associated with one or more climate treatments (Fig. 1.3, Table S1.3). For example, diisopropyl adipate was significantly associated with the drought and warmed + drought treatment groups and was only found within those treatments ($A = 1.00$, $B = 0.34$, $\text{stat} = 0.59$, $p = 0.002$; Table S1.3). Conversely, p-cymene was significantly associated with the ambient and warmed treatment groups ($A = 1.00$, $B = 0.19$, $\text{stat} = 0.44$, $p = 0.03$; Table S1.3). However, we did not find differences in the overall abundance of VOCs emitted among treatments ($F_{3,70} = 0.34$, $p = 0.80$; Fig. S1.4). The classification of these 29 compounds also spanned multiple VOC categories, including ketones, esters, terpenoids, benzenoids, and alcohols (Table S1.4).

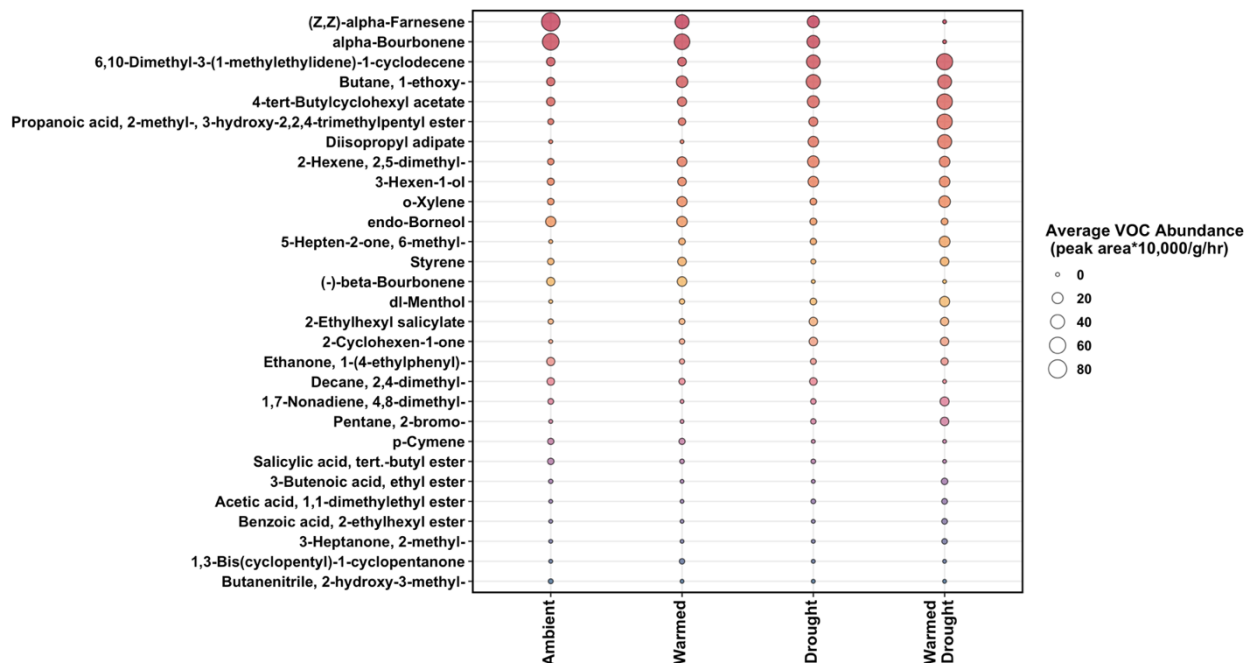


Figure 1.3. Bubble plot showing the abundance of specific VOCs between each climate treatment. These compounds were selected based on their significant association with at least one climate treatment based on indicator species analysis (Table S1.3). Larger bubbles represent a greater abundance of that compound in that treatment; compounds are ordered on the y-axis in terms of decreasing mean abundance.

DISCUSSION

We observed differentiation in VOC composition between the non-drought (ambient and warmed) and drought (drought and warmed + drought) treatment groups. Based on this differentiation, the overall composition of VOCs in *S. altissima* appears to be more affected by drought than warming. We base this conclusion on the fact that there was separation between non-drought and drought treatments, but not between non-warmed (ambient and drought) and warmed (warmed and warmed + drought) treatments (Fig. 1.2).

Drought may be affecting VOC production more than warming if it is a stronger stressor than the warming treatment; Trowbridge et al. (2019) also found that drought appears to override the effects of warming on emissions. During our sampling period, the drought treatments had lower soil moisture and increased temperatures compared to non-drought treatments (Fig. 1.1). However, only the warmed + drought treatment demonstrated increased air temperatures, whereas our warmed treatment was no different from the ambient or drought treatments in terms of air temperature. The lack of warming in our warmed-only treatment, specifically during our

sampling period, may have led to a lack of warming effect on VOC production. However, we do know that the warmed treatment increased air temperatures prior to our sampling period (Fig. S1.5), but this warming effect may not have carried over into affecting VOC production during our 5-day sampling period.

We also initiated the drought ~3 weeks prior to VOC collection, whereas the plants had been warmed for several months leading up to our study. The drought stress was therefore a more novel stress for the plants and could have led to a strong initial stress response (Franks et al., 2014). Because the plants had been experiencing warmer temperatures for several months leading up to sampling, the warming stress may have caused an initial response that we did not capture due to our measurements being collected after several months of warming (Kristensen et al., 2020).

However, although the PERMANOVA demonstrated significant differences between the composition of non-drought and drought treatments, the PCoA shows notable overlap between climate treatments (Fig. 1.2). This demonstrates that the climate treatments may not lead to large, pronounced differentiation in VOC blends, rather that the composition of VOCs may change in more nuanced ways, with a few key compounds being enhanced or suppressed. The indicator species analysis found compounds that were significantly associated with one or more climate treatments. These compounds may serve a stress-protective function for the plants; for example, compounds significantly associated with the drought treatments may aid the plant during drought stress. Alternatively, the compounds associated with specific treatments may be those that were retained during stress; for example, compounds associated with the ambient and warmed treatments may be compounds that were suppressed during drought stress (i.e., during drought, carbon was partitioned away from producing these compounds). Although we can know which compounds were affected by the climate treatments, further experimentation is necessary to determine the specific functions of these compounds.

Furthermore, we saw that the overall abundance of VOCs did not differ between treatments (Fig. S1.4). While we hypothesized that the overall abundance of VOCs would increase under warming, we may not be seeing overall differences in abundances due to the nuanced effects of these climate stressors on specific compounds. Some compounds or groups of compounds may be enhanced, while others are suppressed, leading to no overall net change in abundances between treatments.

For the majority of the 29 compounds (16 out of 29) identified in the indicator species analyses, information on the chemical classification was not available in any database (Table S1.4). For those compounds that did have classification information, we found that they spanned a broad range of VOC categories, which demonstrates that climate stress may affect multiple VOC types equally rather than mainly affecting a specific type of VOCs. However, further classification for the compounds currently lacking it would allow us to more fully determine how climate stress affects these broad VOC categories. Furthermore, many of the same compounds were missing information across all four databases, highlighting the gap in knowledge for the plant VOCs we identified in this study. Nonetheless, these databases highlight the promise of synthesizing VOC information across resources and studies, and future VOC studies should prioritize their use and contribute to this growing body of knowledge.

Overall, we found effects of both warming and drought on the emission of *S. altissima* VOCs, with specific compounds being more affected than others. The affected compounds may serve as stress-protectants for the plants, either directly or indirectly. For example, the compounds could directly assist plants by scavenging for reactive oxygen species produced under stress (Loreto & Velikova, 2001; Peñuelas & Llusà, 2003), stabilizing thylakoid membranes (Velikova et al., 2011), or by cooling the area surrounding the plant (Shallcross & Monks, 2000). In terms of indirect protection, specific compounds could serve as signals to nearby plants that a stressor is imminent in the environment (Ninkovic et al., 2021). For example, species that are more stress-sensitive may emit VOCs to warn plants in their surrounding environment of an oncoming stressor. These stress signals may be more beneficial for cases of strong, short-lived stressors, such as drought, because drought-sensitive species could warn plants of oncoming lack of water. However, due to climate warming occurring gradually over time, warming-induced stress signals may not be as beneficial for plant fitness, but these remaining questions have yet to be explored in the literature. Because it is difficult to generalize climate effects on emissions, more coordinated climate change experiments are necessary to unravel the mechanisms underlying warming and drought effects on VOC production and emission.

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APPENDIX

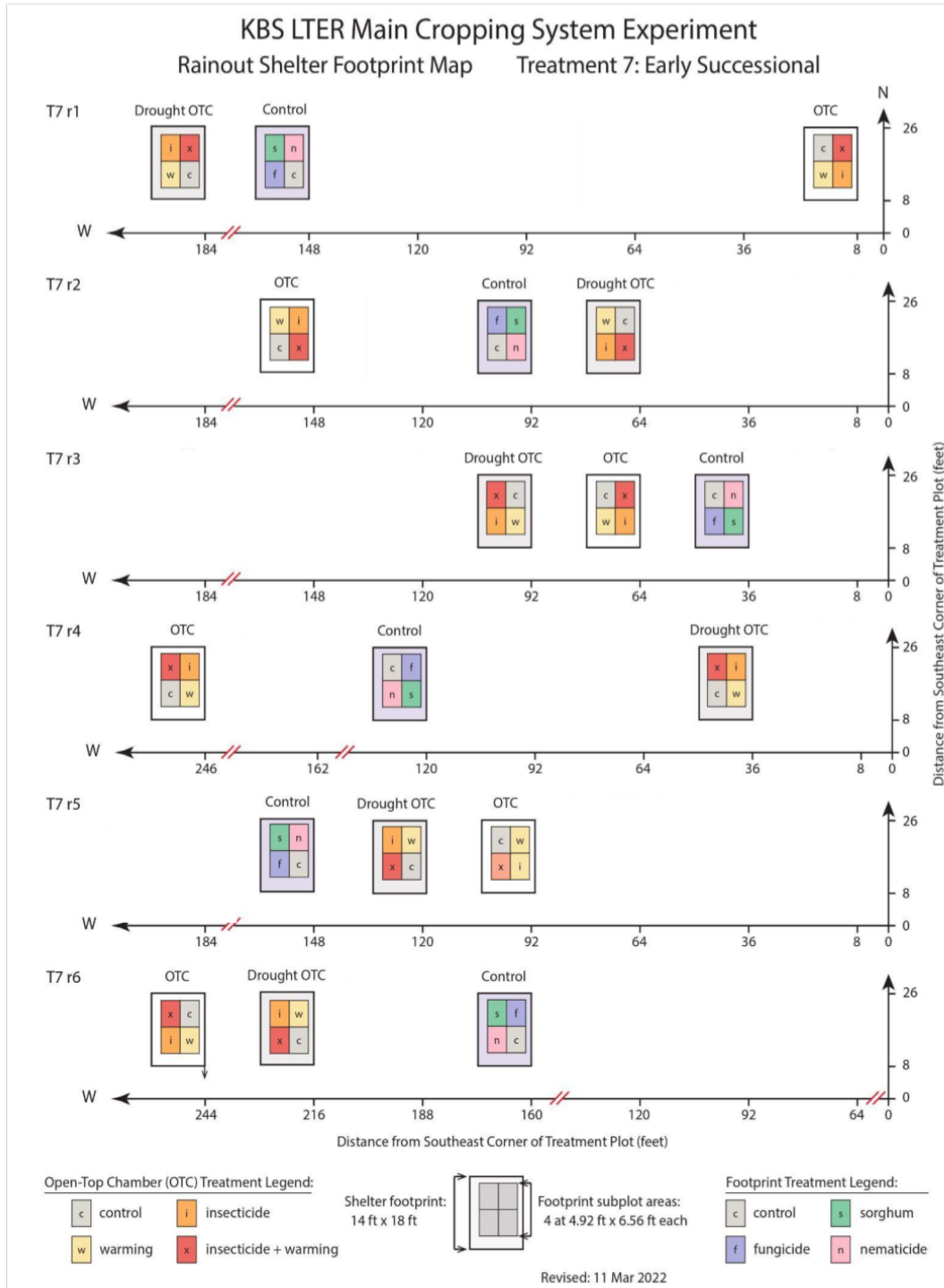


Figure S1.1. Experimental design of the climate treatments in the REX at the KBS-LTER. Each row represents the layout of a field replicate (r1-r6), with the climate treatments randomly dispersed throughout each field. The insecticide, fungicide, sorghum, and

Figure S1.1 (cont'd)

nematicide treatments were not used in our experiment. For our purposes, OTC control = ambient, OTC warming = warmed, drought OTC control = drought, drought OTC warming = warmed + drought. Figure credit: Jane Schuette.

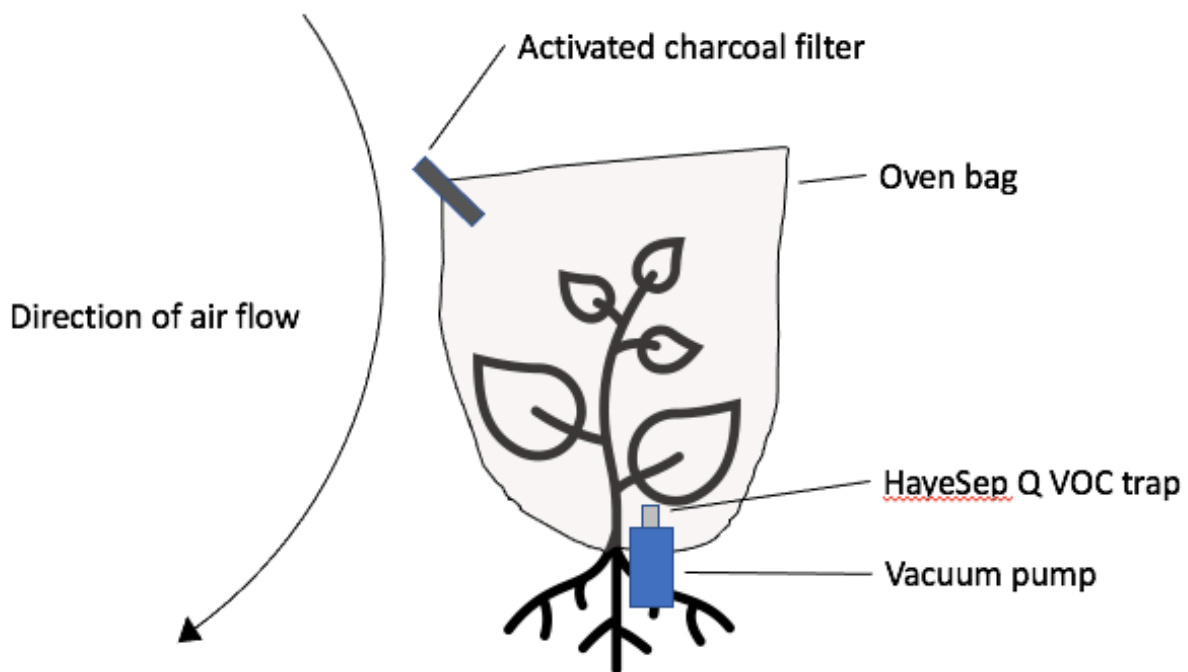


Figure S1.2. Diagram of plant headspace VOC collection. Nylon oven bags contained the top 30 leaves of each plant, with an ORBO charcoal filter fitted to the top corner of the bag to pull clean air through. Vacuum pumps pulled air from the plant headspace onto HayeSep Q VOC traps.

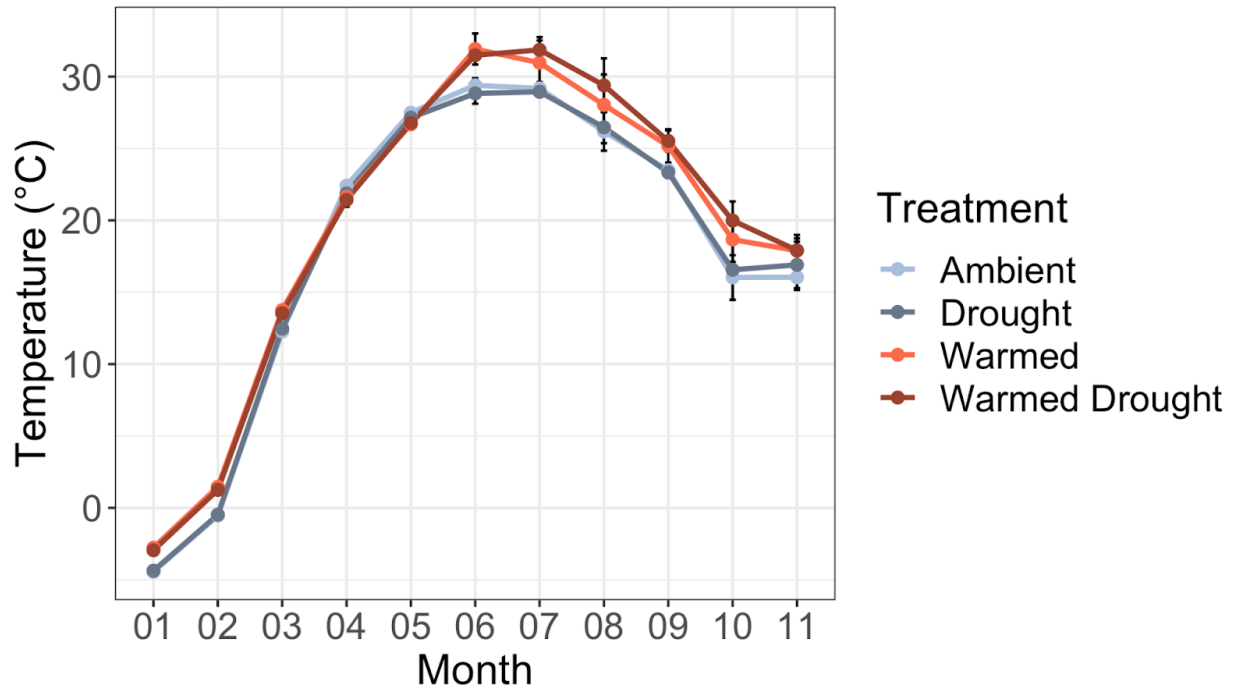


Figure S1.3. Average 1m air temperatures (°C) during daytime hours (07:00-19:00) for each climate treatment (ambient, drought, warmed, and warmed drought) for each month of 2022. Points represent means $\pm$ standard error ($n = 6$ ambient and warmed, $n = 5$ drought and warmed drought).

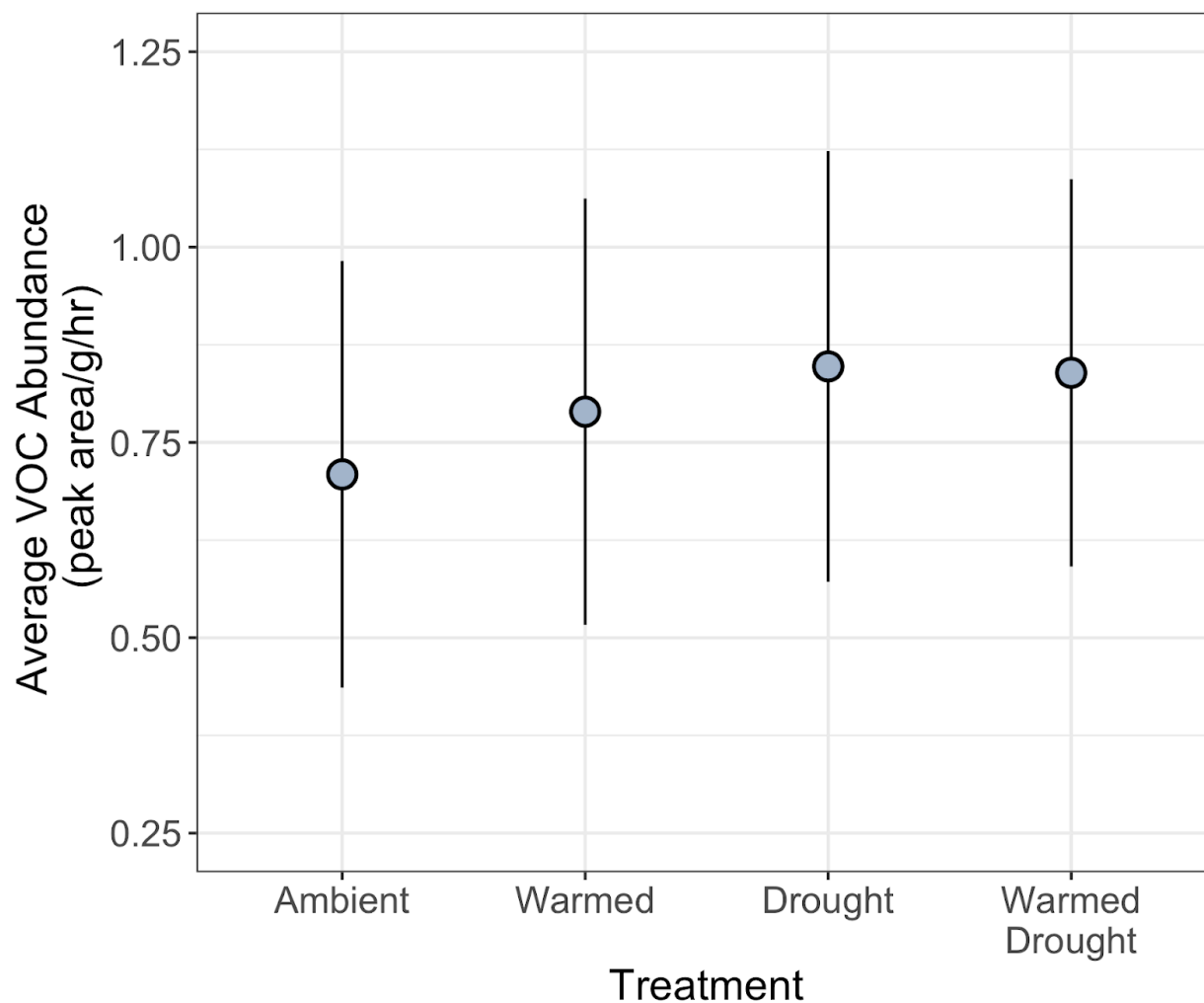


Figure S1.4. Average VOC abundance (peak area/g/hour) in the ambient, warmed, drought, and warmed + drought treatments. Points represent the mean $\pm$ the 95% confidence interval (ambient, warmed, and warmed + drought: $n = 18$, drought: $n = 20$).

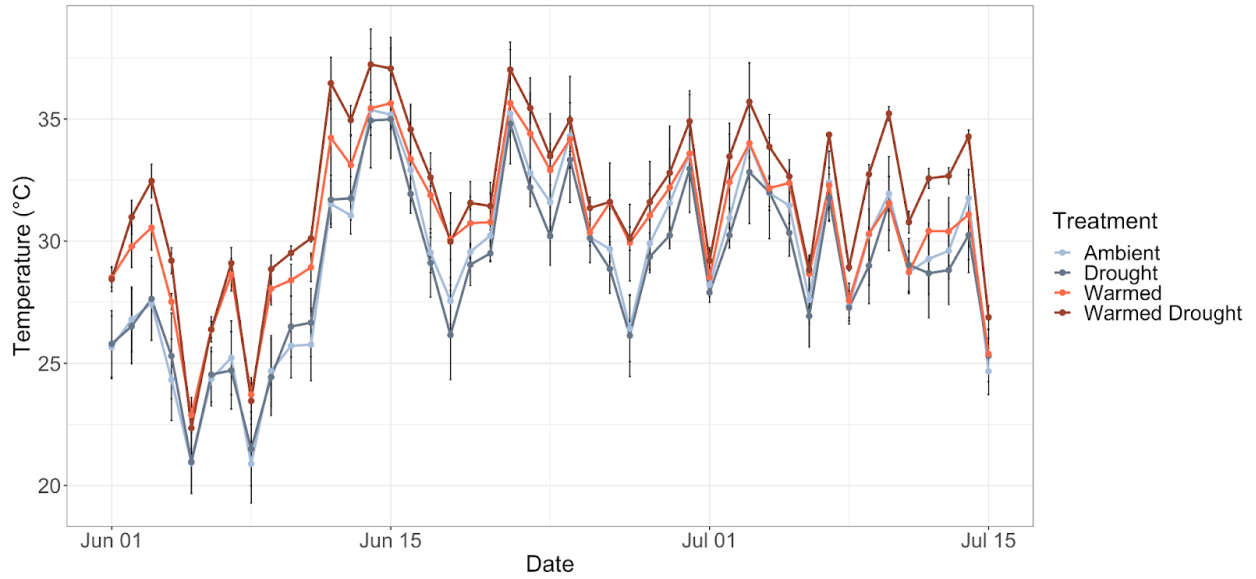


Figure S1.5. Average daily 1m air temperatures (°C) during daytime hours (07:00-19:00) in the ambient, drought, warmed, and warmed drought treatments from June 1- July 15 2022. Points represent means $\pm$ standard error ($n = 4$ for all treatments).

Table S1.1. Regression equations between *Solidago altissima* leaf length (cm) and leaf weight (g) for leaves collected from each of the climate treatments (n ≈ 60 per treatment). For any given leaf length (x), the equation calculates an estimated leaf weight (y).

Treatment	Equation
Ambient	$y = 0.0217x - 0.0589$
Warmed	$y = 0.0235x - 0.0654$
Drought	$y = 0.0192x - 0.0458$
Warmed & Drought	$y = 0.0221x - 0.0653$

Table S1.2. Average individual plant biomass (g) per field replicate. Averages are based on five plants measured per field replicate.

Treatment	Field replicate	Average biomass per replicate (g)	Standard deviation (g)
Ambient	2	3.52	0.97
	3	2.52	0.36
	4	2.31	0.48
	5	2.61	0.44
Drought	2	2.30	0.42
	3	2.59	0.60
	4	2.09	0.25
	5	2.34	0.33
Warmed	2	3.11	0.41
	3	2.57	0.40
	4	3.15	0.22
	5	2.36	0.22
Warmed Drought	2	2.55	0.50
	3	2.78	0.79
	4	1.55	0.12
	5	1.94	0.38

Table S1.3. Indicator compounds associated with one or more climate treatments. ‘Stat’ represents the indicator value for that compound and group. Value ‘A’ represents the specificity of the compound as an indicator of the group, while value ‘B’ represents the sensitivity of the compound as an indicator. A=1.0, B=0.3 would demonstrate that that compound was only found in that specific group, but not all replicates of that group. Conversely, A=0.3, B=1.0 would demonstrate that that compound was found in all replicates of that group, but not solely found within that group. Formula: `multipatt(ab, voc_transpose$Treatment, max.order=3, control = how(nperm=999, blocks=voc_transpose$Rep))`.

Compound	Group	A	B	Stat	P-value
Ethanone, 1-(4-ethylphenyl)-	Ambient	0.52	0.50	0.51	0.028
Salicylic acid, tert.-butyl ester	Ambient	0.84	0.28	0.48	0.003
Butanenitrile, 2-hydroxy-3-methyl-	Ambient	1.00	0.17	0.41	0.014
1,3-Bis(cyclopentyl)-1-cyclopentanone	Warmed	1.00	0.22	0.47	0.005
Propanoic acid, 2-methyl-, 3-hydroxy-2,2,4-trimethylpentyl ester	Warmed Drought	0.75	0.50	0.61	0.001
1,7-Nonadiene, 4,8-dimethyl-	Warmed Drought	0.82	0.39	0.57	0.001
5-Hepten-2-one, 6-methyl-	Warmed Drought	0.78	0.33	0.51	0.004
dl-Menthol	Warmed Drought	0.80	0.28	0.47	0.007
Pentane, 2-bromo-	Warmed Drought	0.90	0.22	0.45	0.004
3-Heptanone, 2-methyl-	Warmed Drought	1.00	0.17	0.41	0.045
Benzoic acid, 2-ethylhexyl ester	Warmed Drought	1.00	0.17	0.41	0.044
3-Butenoic acid, ethyl ester	Warmed Drought	0.97	0.17	0.40	0.049
Acetic acid, 1,1-dimethylethyl ester	Warmed Drought	0.83	0.17	0.37	0.028
Decane, 2,4-dimethyl-	Ambient & Drought	0.83	0.37	0.55	0.015
endo-Borneol	Ambient & Warmed	0.83	0.33	0.53	0.015
(Z,Z)-alpha-Farnesene	Ambient & Warmed	0.82	0.33	0.52	0.029
p-Cymene	Ambient & Warmed	1.00	0.19	0.44	0.027
(-)-beta-Bourbonene	Ambient & Warmed	1.00	0.19	0.44	0.050

Table S1.3 (cont'd)

4-tert-Butylcyclohexyl acetate	Drought & Warmed Drought	0.80	0.61	0.70	0.006
6,10-Dimethyl-3-(1-methylethylidene)-1-cyclodecene	Drought & Warmed Drought	0.85	0.47	0.63	0.024
2-Ethylhexyl salicylate	Drought & Warmed Drought	0.87	0.42	0.61	0.006
Diisopropyl adipate	Drought & Warmed Drought	1.00	0.34	0.59	0.002
2-Cyclohexen-1-one	Drought & Warmed Drought	0.94	0.26	0.50	0.007
o-Xylene	Warmed & Warmed Drought	0.87	0.42	0.60	0.001
Styrene	Warmed & Warmed Drought	0.85	0.42	0.60	0.011
alpha-Bourbonene	Ambient & Drought & Warmed	1.00	0.43	0.66	0.005
2-Hexene, 2,5-dimethyl-	Drought & Warmed & Warmed Drought	0.96	0.52	0.70	0.002
3-Hexen-1-ol	Drought & Warmed & Warmed Drought	0.92	0.50	0.68	0.048
Butane, 1-ethoxy-	Drought & Warmed & Warmed Drought	0.93	0.48	0.67	0.026

Table S1.4. Indicator compounds and their associated chemical classification. The databases include PubChem (Kim et al. 2023), Pherobase (El-Sayed, 2024), mVOC 4.0 (Lemfack et al., 2018), and the plant-associated VOC database (PVD; Shao et al., 2024). The “Final” column combines the classifications from the prior four databases into one final chemical classification determination.

Compound	Pub-Chem CID	PubChem	Phero-base	mVOC 4.0	PVD	Final
Ethanone, 1-(4-ethylphenyl)-	13642			Ketone	Ketone	Ketone
Salicylic acid, tert.-butyl ester	11424 104					
Butanenitrile, 2-hydroxy-3-methyl-	11126 188					
1,3-Bis(cyclopentyl)-1-cyclopentanone	55856 6					
Propanoic acid, 2-methyl-, 3-hydroxy-2,2,4-trimethylpentyl ester	6490			Ester		Ester
1,7-Nonadiene, 4,8-dimethyl-	53495 6					
5-Hepten-2-one, 6-methyl-	9862	Ketone	Ketone	Ketone	Ketone	Ketone
dl-Menthol	1254			Terpene	Terpenoid	Terpenoid
Pentane, 2-bromo-	7890					
3-Heptanone, 2-methyl-	25611					
Benzoic acid, 2-ethylhexyl ester	94310				Ester	Ester
3-Butenoic acid, ethyl ester	74172					
Acetic acid, 1,1-dimethylethyl ester	10908	Esters				Ester
Decane, 2,4-dimethyl-	52035 7	Aliphatic				
endo-Borneol	64685	Alcohols and Polyols			Terpenoid	Terpenoid

Table S1.4 (cont'd)

(Z,Z)-alpha-Farnesene	53173 20					
p-Cymene	7463	Isoprenoid, monoterpene		Terpene	Terpenoid	Terpene
(-)-beta-Bourbonene	62566	Isoprenoid, sesquiterpene		Terpene	Sesqui- terpenoid	Terpene
4-tert-Butylcyclohexyl acetate	36081					
6,10-Dimethyl-3-(1-methylethylidene)-1-cyclodecene	53674 23					
2-Ethylhexyl salicylate	8364					
Diisopropyl adipate	23368					
2-Cyclohexen-1-one	13594	Ketone	Ketone	Ketone		Ketone
o-Xylene	7237			Benzenoid	Benzenoid	Benzenoid
Styrene	7501			Benzenoid	Benzenoid	Benzenoid
alpha-Bourbonene	53081 6					
2-Hexene, 2,5-dimethyl-	18853					
3-Hexen-1-ol	52845 03	Fatty alcohol		Alcohol	Alcohol	Alcohol
Butane, 1-ethoxy-	12355					

CHAPTER 2: Plant community responses to the individual and interactive effects of warming and herbivory across multiple years

The work presented in this chapter is part of the publication:

Young, M. L.*, Dobson, K. C.*, Hammond, M. & Zarnetske, P. L. (2024) Plant community responses to the individual and interactive effects of warming and herbivory across multiple years. *Ecology*. <https://doi.org/10.1002/ecy.4441>. This work is licensed under CC BY 4.0. To view a copy of this license, visit <https://creativecommons.org/licenses/by/4.0/>. Supplemental figures, tables, and sections can be found in the published version of this chapter.

*Moriah Young and Kara Dobson are co-first authors

Individual contribution: Kara Dobson analyzed air and soil temperatures, plant green-up, leaf herbivory, leaf traits (SLA, C, N), and biomass. Kara Dobson and Moriah Young contributed equally to conceptualization of the manuscript and writing.

ABSTRACT

Anthropogenic climate warming affects plant communities by changing community structure and function. Studies on climate warming have primarily focused on individual effects of warming, but the interactive effects of warming with biotic factors could be at least as important in community responses to climate change. In addition, climate change experiments spanning multiple years are necessary to capture interannual variability and detect the influence of these effects within ecological communities. Our study explores the individual and interactive effects of warming and insect herbivory on plant traits and community responses within a 7-year warming and herbivory manipulation experiment in two early successional plant communities in Michigan, USA. We find stronger support for the individual effects of both warming and herbivory on multiple plant morphological and phenological traits; only the timing of plant green-up and seed set demonstrated an interactive effect between warming and herbivory. With herbivory, warming advanced green-up, but with reduced herbivory, there was no significant effect of warming. In contrast, warming increased plant biomass, but the effect of warming on biomass did not depend upon the level of insect herbivores. We found that these treatments had stronger effects in some years compared to others, highlighting the need for multi-year experiments. This study demonstrates that warming and herbivory can have strong direct effects on plant communities, but that their interactive effects are limited in these early successional systems. Because the strength and direction of these effects can vary by ecological context, it is

still advisable to include levels of biotic interactions, multiple traits and years, and community type when studying climate change effects on plants and their communities.

INTRODUCTION

Anthropogenic climate warming is projected to increase global surface temperatures by 1.0-5.7°C by 2100 (IPCC 2021). Climate warming studies in plant communities have primarily focused on the direct, individual effects of warming, including changes in the timing of phenological events and community structure and function (Parmesan 2006; Parmesan and Yohe 2003; Peñuelas and Filella 2001; Renner and Zohner 2018; Root et al. 2003; Walther et al. 2002). However, the interactive effects of warming with biotic factors could also be important in how these communities respond to climate change. For example, warming can affect insect herbivores' preferences and feeding patterns through changes in leaf chemistry and increased insect metabolic rates, and these warming-induced changes in feeding patterns affect the amount of herbivory experienced by plants (Hamann et al. 2021; Pinheiro et al. 2016; Welshofer et al. 2018; Kharouba and Yang 2021). Changes in herbivory levels can furthermore affect plants by altering their chemical composition, productivity, and phenology (Lemoine et al. 2017; Post and Pedersen 2008; Ritchie et al. 1998; Welshofer et al. 2018a). In this case, the plants are indirectly affected by warming, mediated through changes in insect herbivory (Post 2013; Parmesan 2006; Zarnetske et al. 2012; Blois et al. 2013). Many such interactive effects, however, are not well understood (Post 2013; Parmesan 2006; Zarnetske et al. 2012; Blois et al. 2013).

Some of the most commonly observed consequences of climate change are phenological shifts. Shifts in phenology may alter biotic interactions if they alter the relative activity periods of interacting partners. For example, Liu et al. (2011) found that under ambient conditions, gentian flowers typically bloom after the peak density of an insect herbivore. However, experimental warming advanced gentian flowering and delayed the emergence of the herbivore, leading to increased overlap between the two species. These phenological shifts, combined with increased herbivore densities and reduced densities of an alternate host plant, resulted in 100-fold greater damage to gentian flowers and fruits in warmed plots compared to ambient plots.

There can be substantial variation within and among species in the magnitude and direction of warming effects (Sherry et al. 2007; Primack et al. 2009; Youngflesh et al. 2021). Species unable to shift their phenology sufficiently in response to warming may experience negative fitness effects, potentially leading to decreased abundances or even local

extinction (Willis et al. 2008). It is unknown whether the association between propensity for phenological shifts and extinction suggested by Willis et al. (2008) is driven by the direct effects of warming or indirect effects mediated through temporal mismatches with pollinators, herbivores, or competitors. Interacting organisms can also have their own, separate direct effects on plant phenology. For example, herbivory itself has been found to delay phenology, likely due to plants redirecting resources to repair tissue damage (Lemoine et al. 2017; Welshofer et al. 2018a).

Plant leaf traits, including morphological characteristics and chemical composition, are important cues that herbivores use to find quality food sources. Specific leaf area (SLA), which is the ratio of total leaf area to total leaf dry mass, is an important trait that can reflect whole plant growth (Liu et al. 2017). Warming treatments have been shown to have variable effects on SLA (Descombes et al. 2020; Hudson et al. 2011), but insect herbivores have been found to prefer plants whose leaves have smaller SLA (Dostálek et al. 2020; Pereira et al. 2020). Leaf palatability to herbivores has also been found to be positively correlated with N content and negatively correlated with C content (Schädler et al. 2003). Warming treatments have been found to decrease leaf contents of both C and N (Hudson et al. 2011; Yang et al. 2011). If there are warming-induced reductions in plant food quality, herbivores may need to consume greater quantities of plant material in order to meet nutritional demands (Hamann et al. 2021; Welshofer et al. 2018a). Paleontological records also document increased herbivory during periods of global warming in past geological times (Pinheiro et al. 2016). Herbivory itself can influence foliar C and N content, as insects may prefer to eat nutrient rich leaf tissue, leading to declines in overall nutrient content for plants (Ritchie et al. 1998).

In terms of plant community composition, experimental warming treatments in alpine systems and temperate grasslands show reductions in species evenness and richness, with up to 25% of species lost, although the magnitude and the direction of diversity effects varies regionally (Morecroft et al. 2009; Elmendorf et al. 2012; White et al. 2014). Experimental warming may also lead to complex changes in community composition, as some species increase in abundance while other species decline (Welshofer et al. 2018a; de Valpine and Harte 2001; Morecroft et al. 2009; Li et al. 2011; Rudgers et al. 2014). For example, Wangchuk et al. (2021) demonstrated that experimental warming treatments decrease overall plant diversity and richness through the promotion of grass species.

The interaction between climate warming and herbivory can mediate the impact of warming on plant community composition. In particular, herbivory can reduce the impacts of warming on plant diversity and richness (Kaarlejärvi et al. 2017; Post 2013). Even in the absence of warming, herbivory can affect plant community composition by reducing dominant species and increasing light availability at ground level, therefore helping to maintain plant richness and diversity (Brown and Gange 1989; Post 2013; Post and Pedersen 2008; Mortensen et al. 2018; Price et al. 2022; Borer et al. 2014; Koerner et al. 2018).

Experimental warming treatments have also been found to increase community productivity via increased plant biomass (Wangchuk et al. 2021), but this increase can be dependent upon plant functional type (Lin et al. 2010). Other studies have noted that warming treatments may cause decreases in biomass, potentially due to strong competition for resources under conditions of high stress (De Boeck et al. 2008). Furthermore, herbivory on plants has been found to have contrasting effects on plant biomass due to herbivores having varying preferences for certain species over others (Post and Pedersen 2008).

The relative influence of the individual and interactive effects of abiotic and biotic factors can be assessed via experimentally manipulating both climate and the presence or abundance of interacting species. However, of the 126 studies on in-situ warming experiments with open top chambers reviewed by Dobson and Zarnetske (2024), only 14 (11%) included a treatment involving species interactions, and only 57 (45%) spanned more than 3 years. In this study, we explored these individual and interactive effects by manipulating temperature and insect herbivory, separately and in combination, for 7 years in two early successional plant communities. We tracked the plant communities' responses to our experimental manipulations by measuring leaf herbivory, phenology (green-up, flowering, flowering duration, and seed set), plant composition, biomass, and leaf traits (SLA, C, N). We hypothesized that:

1. Warmed plots would have greater amounts of insect herbivory than ambient plots (Hamann et al. 2021; Pinheiro et al. 2016; Welshofer et al. 2018a).
2. Warmed plots would experience earlier green-up and flowering, delayed seed set, and a longer flowering duration, especially under reduced herbivory (Peñuelas and Filella 2001; Walther et al. 2002; Lemoine et al. 2017; Welshofer et al. 2018a; Zhou et al. 2022).
3. Warmed plots would have increased percent cover but lower plant species richness and diversity when compared to ambient plots (Elmendorf et al. 2012; Morecroft et al. 2009;

Wangchuk et al. 2021; White et al. 2014). The effects of warming would be lessened with herbivory because herbivores can decrease percent cover while increasing plant species richness and diversity by reducing dominant species (Brown and Gange 1992; Kaarlejärvi et al. 2017; Post 2013; Wangchuk et al. 2021; Post and Pedersen 2008; Brown and Gange 1989; Ritchie et al. 1998).

4. Warmed plots would have higher plant biomass, higher SLA, and lower foliar C and N content (Descombes et al. 2020; Lin, Xia, and Wan 2010; Yang et al. 2011), especially with herbivory (Post and Pedersen 2008; Ritchie et al. 1998).

METHODS

Site Description

The study system consists of sites in two early successional plant communities in Michigan, USA, separated by 354 km and approximately three degrees latitude. The southern site, located at Kellogg Biological Station's Long-Term Ecological Research Site (KBS-LTER, 42.41°N, 85.37°W), was previously an agricultural field and is now dominated by *Solidago canadensis*, *Poaceae* spp., and *Hieracium* spp. (Appendix S1: Table S1). The mean annual temperature and precipitation in Kalamazoo County, where KBS is located, are 9.33°C and 975.4 mm (30 year means, PRISM Climate Group; Appendix S1: Fig. S1).

The northern site, located at the University of Michigan Biological Station (UMBS, 45.56°N, 84.71°W), is within an old forest clearing that was clear-cut in 1994 and is now dominated by *Centaurea stoebe*, *Pteridium aquilinum*, and *Carex pensylvanica* (Appendix S1: Table S1). The mean annual temperature and precipitation in Emmet County, where UMBS is located, are 6.42°C and 770.7 mm (30 year means, PRISM Climate Group; Appendix S1: Fig. S1).

Experimental Design

At each site, twenty-four 1m x 1m plots are contained within a 25m x 36m x 3m fence that prevents herbivory by deer. Each 1m² plot is contained within a 3m x 3m buffer zone, and all plots are separated by at least 4m to minimize potential shading from the open-top chambers (OTCs). The experiments were established in the spring of 2015 and consist of a fully factorial design with warming and insect herbivore reduction treatments (ambient, warming, reduced herbivory, warming + reduced herbivory; n = 6 per treatment). There were no significant initial

differences in plant composition between the plots within each site in 2015 before treatments were applied (Welshofer et al. 2018a).

Warming was achieved through the use of hexagonal OTCs designed for taller stature plant communities (Welshofer et al. 2018b; Marion et al. 1997; Appendix S1: Fig. S1). OTCs simulate climate warming by passively increasing air temperatures in situ while also allowing for natural levels of precipitation, gas exchange, and solar radiation (Welshofer et al. 2018b; Marion et al. 1997). These chambers remained on the plots year-round and were constructed with clear, UV-transmitting 1/8" Lexan Polycarbonate (ePlastics, San Diego, CA). Insect herbivory was manipulated through insecticide applications throughout the growing season (for details, see Appendix S1: Section S1). Insecticide plots are termed "reduced herbivory", and non-insecticide plots are termed "herbivory" plots.

Data Collection

Abiotic Measurements

Hourly abiotic conditions were recorded at the plot-level at each site using HOBO products (Onset Computer Corporation, Bourne, MA). Three ambient and three warmed plots were equipped with four-channel external U12-008 data loggers that recorded air temperature at 10cm above ground and soil temperature at 5cm below ground. These plots also contained micro station H21-002 data loggers that recorded air temperature at 1m above ground and soil moisture at 5cm below ground. Plastic dish solar shields were installed above each air temperature sensor to mitigate the impact of solar radiation on air temperature readings.

Leaf Herbivory

Leaf herbivory was measured once per season at peak biomass prior to senescence, typically July-August (methods similar to The Herbivory Variability Network 2023). We haphazardly selected four random leaves vertically distributed across the stem of three individuals of each measured species in each plot (Appendix S1: Fig. S2-3). We then visually estimated percent of the leaf eaten (0-100%).

Plant Phenology

Phenology of all plant species within all plots (Appendix S1: Fig. S4-7) was monitored every 3-4 days. The beginning of data collection at each site was determined by the last snow melt of the year in the spring. Phenology consisted of green-up, flowering, flowering duration, and seed set. Green-up was calculated as the date at which a plot reached half of its maximum

percent cover (Appendix S1: Table S2) to account for early season differences in the depth of plant litter, which might affect the detection of plants when they first emerge. A species was recorded as flowering during the period between first flower bud break (anthers exposed) and final flower senescence. Date of first flower was calculated as the average minimum date that a plot recorded a species flowering. The duration of flowering was the number of days between the average date of first flower to the average date of last flower. Seed set was determined when an individual exhibited a mature seed that was ready to be dispersed (pappus/achene, florets dehiscent, etc.), and was calculated as the average minimum date of first occurring seed set per plot.

Plant Community Composition

Percent aerial cover was visually estimated within all 1m² plots as the percentage of the total plot occupied by each species in each plot (0-100%; Appendix S1: Fig. S8). Because each species in each plot could be estimated up to 100% cover, it is possible that the total calculated percent cover of any given plot could exceed 100%. This measurement was taken every 3-4 days through green-up and once a month post green-up.

Leaf Traits (C, N, SLA)

Prior to senescence, green leaves were harvested for measurements of foliar C and N content and specific leaf area (SLA). The species selected for these measurements were commonly found across all plots at each respective site (Appendix S1: Table S3). We chose 3-5 plants of the same species in each plot and harvested 4-5 green, mature leaves with little to no obvious insect damage or disease. The selected leaves were haphazardly selected from the top to the bottom of the plant to be representative of the whole plant. The youngest fully expanded leaf from each individual plant sample was chosen for SLA, while the remaining leaves were stored separately for C and N analysis. SLA leaves were scanned fresh with a LI-COR LI-3000A Portable Leaf Area Meter with conveyor belt LI-3050A at KBS and a LI-COR LI-3100c at UMBS. After SLA leaves were scanned, all leaf samples, including those harvested for C and N analysis, were placed in a drying oven at 60°C for 36-48 hours and subsequently weighed. Combustion analysis was then performed for C and N (see Appendix S1: Section S2).

Plant Community Biomass

In 2021, all aboveground plant biomass was harvested in a 0.20m² area (1 m x 0.20 m) within all 1m² plots at both sites. Plant material was sorted to species, placed in individual paper

bags, dried at 60°C for 3-4 days, and weighed for a final dry biomass weight per species in each plot.

Statistical Analysis

All analyses were conducted using R (R Core Team 2020). All response variables were calculated at the plot level to test for the overall effects of the treatments on the plant community; species-specific effects can be found in the supplement (Appendix S1: Fig. S2-10 and S13-16, Tables S4-19). We tested for the individual and interactive effects of warming level (warmed vs. ambient), herbivory level (herbivory vs. reduced herbivory), and year using linear mixed effects models in R with the package lmerTest (Kuznetsova et al. 2017; R Core Team 2020). Fixed effects included warming level, herbivory level, and year, with interactions between all three factors ($\text{Response variable}_i = \beta_0 + \beta_1\text{warmed} + \beta_2\text{insecticide} + \beta_3\text{year_factor} + \beta_4(\text{warmed} \times \text{insecticide}) + \beta_5(\text{warmed} \times \text{year_factor}) + \beta_6(\text{insecticide} \times \text{year_factor}) + \beta_7(\text{warmed} \times \text{insecticide} \times \text{year_factor}) + \alpha_{\text{plot}[i]} + \epsilon_i; \alpha_{\text{plot}[i]} \sim N(0, \sigma^2_{\alpha})$). To test if species or groups themselves differed for each response variable, we included species, plant origin (native or exotic), or plant growth habit (forb or graminoid) as fixed effects in separate species models ($\text{Response variable}_i = \beta_0 + \beta_1\text{warmed} + \beta_2\text{insecticide} + \beta_3\text{year_factor} + \beta_4(\text{warmed} \times \text{insecticide}) + \beta_5(\text{warmed} \times \text{year_factor}) + \beta_6(\text{insecticide} \times \text{year_factor}) + \beta_7(\text{warmed} \times \text{insecticide} \times \text{year_factor}) + \beta_8\text{species} + \alpha_{\text{plot}[i]} + \epsilon_i; \alpha_{\text{plot}[i]} \sim N(0, \sigma^2_{\alpha})$). Plot number was included as a random effect for all models to account for inherent variation between plots. For leaf herbivory, SLA, C, and N models, individual plant ID was nested within species within plot number and included as a random effect.

To test for evidence of interactive effects for each response variable, we looked for a significant interaction between warming level and herbivory level (Appendix S1: Tables S4-19). If significant, we then tested the pairwise comparisons of all treatments using the emmeans package (Lenth 2022; Appendix S1: Tables S20-32). We also used pairwise comparisons to determine treatment effects for specific years. If there was no significant interaction, we tested for the individual effects of each treatment. We confirmed the data fit the assumption of normality prior to running our models and that there were no outliers with Bonferroni adjusted outlier tests. SLA data were transformed using a cubed root transformation, while percent cover was transformed with natural log transformations. For UMBS, we applied a log transformation to species richness. Leaf herbivory data did not fit the assumptions of normality, as it contained an

excess of zeros and was over dispersed; therefore, we ran a negative binomial hurdle model using the glmmTMB package in R (Brooks et al. 2017; Appendix S1: Tables S19 and S32, Section S3). With this model, we evaluated the probability of a leaf being eaten (a binomial response), and if eaten, the amount of the leaf eaten (a truncated negative binomial response).

Data from 2015 were removed from green-up, first flower, and flowering duration analyses because the OTCs were not in place at that point. For plant composition, we calculated the average percent cover during the month with the greatest recorded percent cover (KBS: August, UMBS: July). We also calculated the average percent cover of forb and graminoid species (functional type) and native and exotic species (origin). Shannon diversity index and species richness were calculated from the plant composition data using the R package *vegan* (Oksanen et al. 2020). UMBS 2021 data were removed from green-up, flowering, seed set, and plant composition analyses due to infrequent data collection in that year.

We were also interested in quantifying the effect of natural temperature variation on our response variables, without consideration of our warming treatment and its effects. Therefore, we quantified the mean temperature in the ambient plots for each site per year. These temperature data were calculated independently for each response variable to match the date ranges of each variable (Appendix S1: Table S2). The models included mean temperature as a fixed effect and plot as a random effect ($\text{Response variable}_i = \beta_0 + \beta_1 \text{MeanTemperature} + \alpha_{\text{plot}[i]} + \epsilon_i; \alpha_{\text{plot}[i]} \sim N(0, \sigma^2_a)$). We did not include natural temperature variation models for SLA or biomass because we did not have at least 5 years of data compared to the other response variables. We also did not include natural temperature variation models for plant origin and plant functional type percent cover, nor species diversity metrics because we believed the overall percent cover results encompassed these metrics.

We compared hourly site-level warmed and ambient temperatures at 1m and 10cm above ground and at 5cm below ground, and soil moisture at 5cm below ground. We removed large outliers from the hourly data that were likely due to sensor malfunctions (e.g., temperatures recorded as $> 49^\circ\text{C}$ or $< -30^\circ\text{C}$). We tested for the effects of the OTCs on hourly temperature and moisture data using Welch's two sample t-tests. At KBS, 2021 data from one set of paired sensors was removed due to a sensor malfunction, and 2021 data was removed at UMBS for one set of paired sensors due to a wasp nest covering the sensor. For 2018, 10cm air temperature and 5cm soil temperature data were removed at KBS due to sensor malfunctions.

RESULTS

Abiotic Measurements

From 2016-2021, the OTCs increased 1m air temperatures by an average of 1.9°C at KBS ($t_{66223} = -27.2$, $p < 0.001$) and 3.0°C at UMBS ($t_{68232} = -40.2$, $p < 0.001$) during daytime hours in the growing season (07:00-19:00, April-August; Fig. 2.1a,b). The amount warmed by the chambers varied within and among years, but OTCs were consistently warmer than ambient plots at 1m (Appendix S1: Tables S33-34). Air temperatures at 10cm in the OTCs were 0.6°C cooler than ambient at KBS ($t_{18939} = 5.1$, $p < 0.001$; Fig. 2.1a). In contrast, OTCs at UMBS were 1.8°C warmer than ambient plots at 10cm ($t_{68289} = -21.6$, $p < 0.001$; Fig. 2.1b). Slight winter warming was also achieved, with chambers warming by 0.6°C at KBS ($t_{49539} = -9.7$, $p < 0.001$) and 0.6°C at UMBS ($t_{52242} = -10.2$, $p < 0.001$) from November-February. From 2016-2021, OTC soil temperatures at 5cm belowground were 0.8°C cooler ($t_{38051} = 14.8$, $p < 0.001$) and 0.9°C warmer ($t_{68371} = -16.0$, $p < 0.001$) than ambient at KBS and UMBS, respectively, from April-August during daytime hours (07:00-19:00; Fig. 2.1c,d). We found only small effects of warming on soil moisture at 5cm, as moisture levels only decreased by 1% ($t_{66885} = 20.7$, $p < 0.001$) and 0.4% ($t_{67023} = 9.9$, $p < 0.001$) in the OTCs at KBS and UMBS, respectively (Appendix S1: Fig. S17).

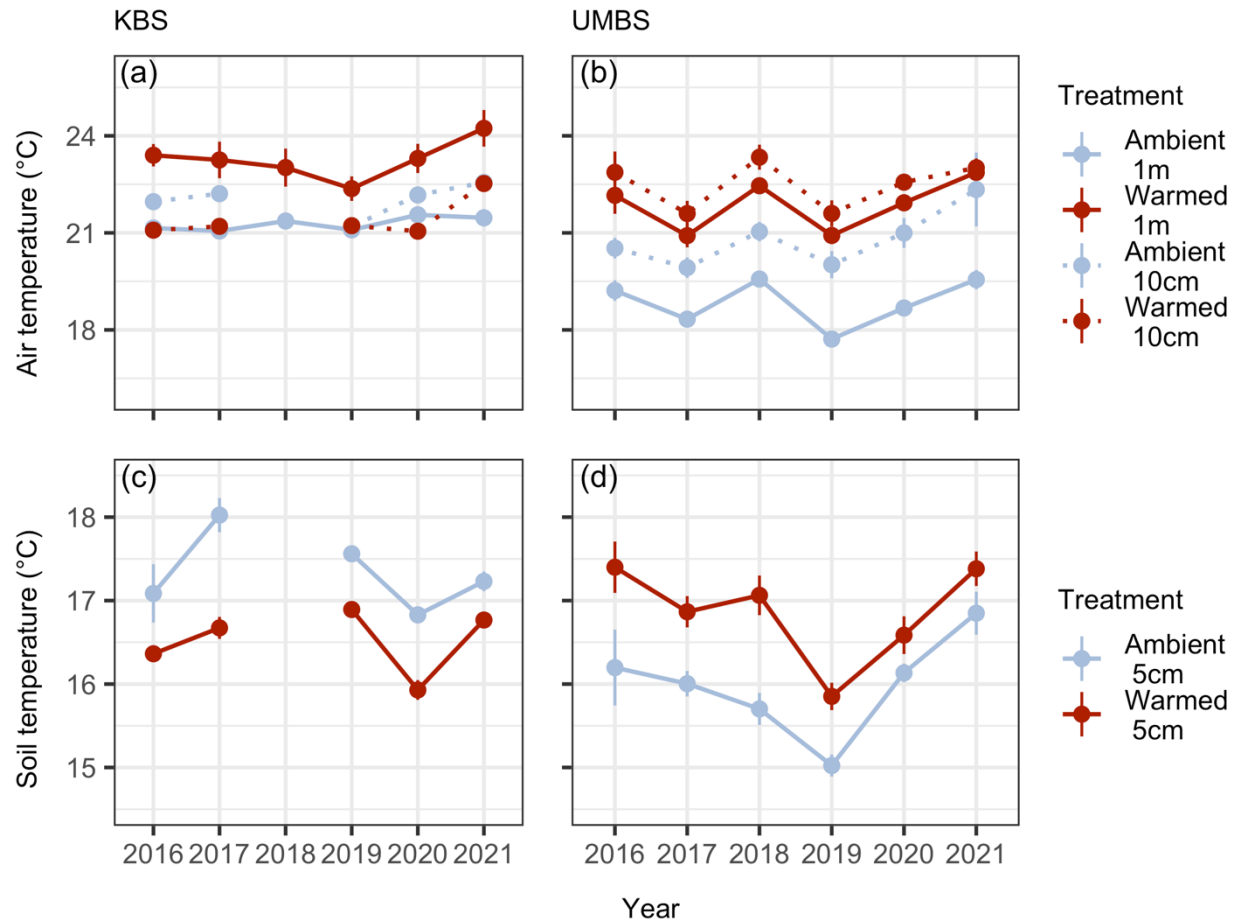


Figure 2.1. Average daytime growing season temperatures (April-August, 07:00-19:00) at 1m (solid line) and 10cm (dotted line) above ground level and 5cm below ground in warmed and ambient plots at KBS (a,c) and UMBS (b,d) . Values are the mean $\pm$ standard error of the three temperature sensors for each treatment (n=3). KBS 10cm air temperature data has one sensor (n=1), UMBS 2021 data has two sensors (n=2), and there is no 2018 10cm air temperature and 5cm soil temperature data at KBS due to sensor malfunctions.

Leaf Herbivory

At both KBS and UMBS, the herbivory reduction treatment was effective at reducing both the probability that a plant was eaten and the amount of leaf area eaten (Fig. 2.2). The treatment appeared to be especially effective at UMBS, as that site contained more years with significant differences between herbivory and reduced herbivory treatments (Appendix S1: Table S32). We also found that warmed plants at UMBS typically had a greater probability of being eaten, as well as a slight increase in the amount eaten by herbivores (Fig. 2.2b,d; Appendix S1: Tables S19 and S32). For example, regardless of herbivory treatment, warming increased the

probability of a plant being eaten by 0.10-0.20 in 2018 at UMBS (herbivory: $z = 4.12$, $p < 0.001$, reduced herbivory: $z = 3.89$, $p < 0.001$; Appendix S1: Table S32). However, at KBS, we did not find a clear trend of warming effects on the probability of being eaten or the amount eaten by herbivores (Fig. 2.2a,c; Appendix S1: Table S19). Certain plant types (e.g., native species) were more likely to be eaten than their counterparts (e.g., exotic species; Appendix S1: Section S3).

When considering the effect of natural temperature variation on herbivory at KBS, we found a temperature increase from 15 °C to 16 °C increased the probability of a plant being eaten by 0.17 ($z_{2321} = -2.92$, $p = 0.004$) but had no effect on the amount eaten ($z_{2321} = 0.04$, $p = 0.97$; Appendix S1: Fig. S18, Table S19). At UMBS, a temperature increase from 15 °C to 16 °C did not have a significant effect on the probability of a plant being eaten ($z_{2121} = 0.45$, $p = 0.65$), but if eaten, the amount of leaf area eaten decreased by 7.6% ($z_{2121} = -11.0$, $p < 0.001$; Appendix S1: Fig. S18, Table S19).

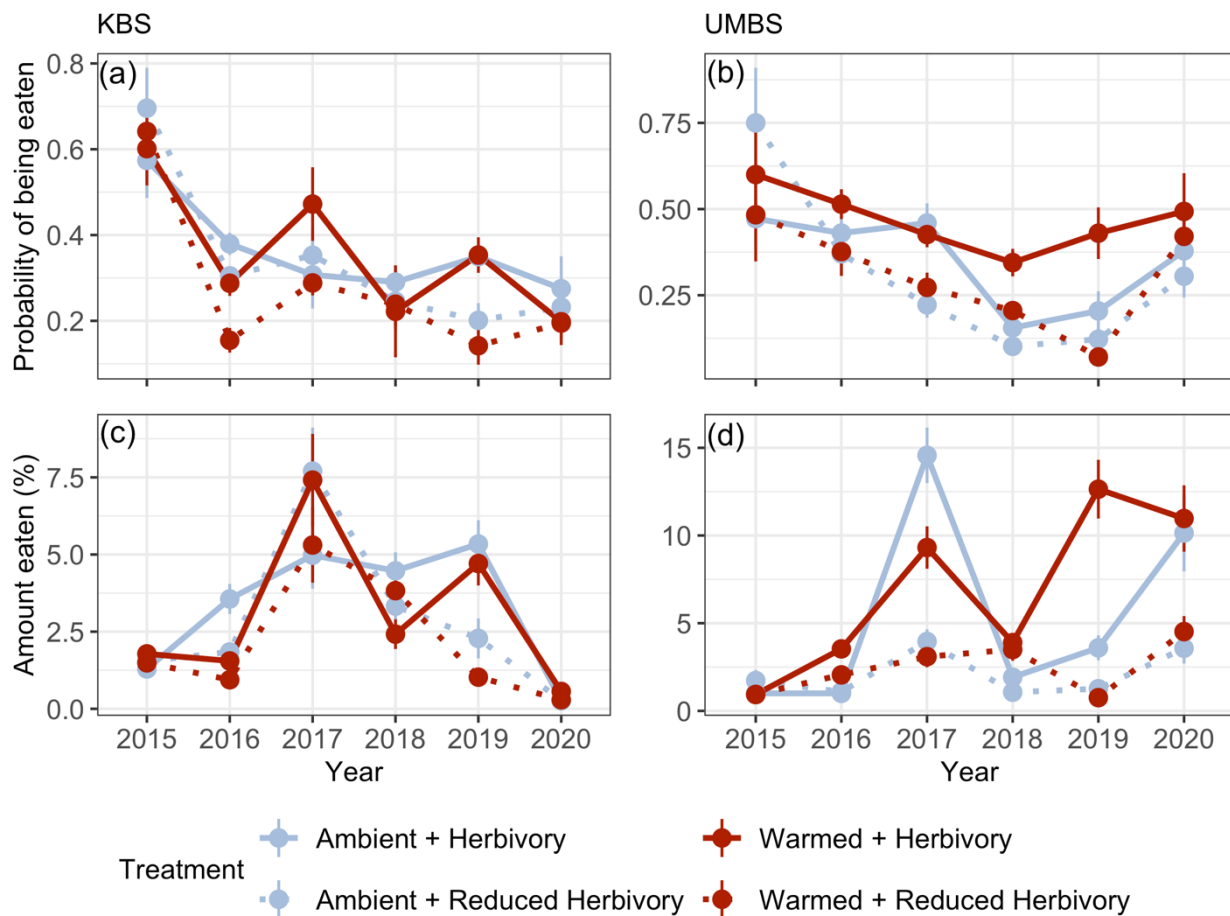


Figure 2.2. a-b: The probability of a plant being eaten between ambient and warmed plots in herbivory and reduced herbivory treatments for each year at KBS and

Figure 2.2 (cont'd)

UMBS. c-d: Average amount of leaf area eaten (%) for plants in ambient and warmed plots in herbivory and reduced herbivory treatments for each year at KBS and UMBS. Points represent means $\pm$ standard error (n=6).

Plant Phenology**Green-up**

At KBS, the effect of warming on green-up depended upon the presence of herbivores (warming x herbivory interaction: $F_{1,24} = 3.30$, $p = 0.08$; Appendix S1: Table S4). Overall, in plots with herbivores present, warming advanced green-up by 6.7 days ($t_{29} = -2.75$, $p = 0.01$; Fig. 2.3a). However, in plots with reduced herbivory, warming did not have a significant effect on green-up ($t_{29} = -0.42$, $p = 0.68$; Fig. 2.3a; Appendix S1: Table S20). We also found that herbivory only advanced green-up when plots were warmed ($t_{29} = -2.81$, $p = 0.009$), whereas in ambient plots, there was no significant effect of herbivory on green-up ($t_{29} = -0.45$, $p = 0.66$; Appendix S1: Table S20). There was a stronger effect of warming on green-up in some years compared to others ($F_{5,119} = 3.36$, $p = 0.007$; Appendix S1: Table S4). For example, warming led to the advancement of green-up by 7 days in 2017 ($t_{171} = 1.76$, $p = 0.08$) and 15 days in 2021 ($t_{172} = 3.68$, $p < 0.001$; Appendix S1: Table S20).

At UMBS, the effect of warming and herbivory on green-up differed between years (warming x herbivory x year interaction: $F_{4,96} = 4.63$, $p = 0.002$; Appendix S1: Table S4). For example, in 2016, herbivory advanced green-up by 18.5 days, but only in ambient plots ($t_{131} = -4.18$, $p < 0.001$); there was no significant effect of herbivory on green-up in warmed plots that year ($t_{131} = 1.26$, $p = 0.21$; Fig. 2.3b; Appendix S1: Table S20). However, most years did not demonstrate a significant warming or herbivory effect on green-up (Appendix S1: Table S20). We did not find significant evidence that natural temperature variation affected green-up at KBS ($F_{1,71} = 0.97$, $p = 0.33$; Appendix S1: Fig. S19, Table S4). At UMBS, however, for each unit increase in ambient temperature, green-up advanced by 5.2 days ($F_{1,48} = 17.8$, $p < 0.001$; Appendix S1: Fig. S19, Table S4).

Flowering

At KBS, the effect of warming on the date of first flower depended on the year ($F_{5,118} = 4.68$, $p = 0.001$; Appendix S1: Table S5). Warming advanced flowering by 7-10 days in 2017, 2018, 2019, and 2021, but did not have a significant effect in 2016 or 2020 (Fig. 2.3c; Appendix

S1: Table S21). There was no significant effect of herbivory on date of first flower ($F_{1,24} = 0.99$, $p = 0.33$). At UMBS, there was no significant effect of warming ($F_{1,24} = 0.31$, $p = 0.58$; Fig. 2.3d) or reduced herbivory ($F_{1,24} = <0.001$, $p = 0.99$; Fig. 2.3d) on the date of first flower. Natural temperature variation did not significantly affect the date of first flower at KBS ($F_{1,99} = 1.64$, $p = 0.20$; Appendix S1: Fig. S20). However, at UMBS, for each unit increase in ambient temperature, date of first flower advanced by 2.2 days ($F_{1,80} = 8.01$, $p = 0.006$; Appendix S1: Fig. S20). There was no significant effect of any treatment on the duration of flowering (Appendix S1: Section S4).

Seed Set

At KBS, the effect of warming on the date of first seed set depended on the year ($F_{6,138} = 5.27$, $p = 0.002$; Appendix S1: Table S7). Warming delayed seed set by 21 days in 2015 ($t_{191} = -4.75$, $p < 0.0001$) and 8 days in 2019 ($t_{186} = -2.08$, $p = 0.04$), but did not have a significant effect in other years (Fig. 2.3g; Appendix S1: Table S22). The effect of warming also depended on the presence of herbivores (warming x herbivory interaction: $F_{1,24} = 4.43$, $p = 0.05$; Appendix S1: Table S7). Warming delayed seed set by 8.7 days in reduced herbivory plots ($t_{29} = -3.25$, $p = 0.003$; Appendix S1: Table S22), but had no significant effect in plots with herbivory present ($t_{29} = -1.44$, $p = 0.60$). Similarly, reduced herbivory delayed seed set by 5.9 days in warmed plots ($t_{29} = -2.21$, $p = 0.04$; Appendix S1: Table S22), but had no significant effect in ambient plots ($t_{29} = 0.50$, $p = 0.62$). At UMBS, there was an interactive effect of warming and herbivory on date of seed set for some years (warming x herbivory x year interaction: $F_{4,96} = 3.95$, $p = 0.01$; Appendix S1: Table S7). For example, in 2019 and 2020, warming advanced seed set in reduced herbivory plots (Fig. 2.3h; Appendix S1: Table S22). When considering the effect of natural temperature variation on the date of first seed set at KBS, we found that for each unit increase in temperature, the date of first seed set was delayed by 4.2 days ($F_{1,100} = 7.55$, $p = 0.007$; Appendix S1: Fig. S22). At UMBS, for each unit increase in ambient temperature, date of first seed set advanced by 2.2 days ($F_{1,88} = 10.7$, $p = 0.002$; Appendix S1: Fig. S22).

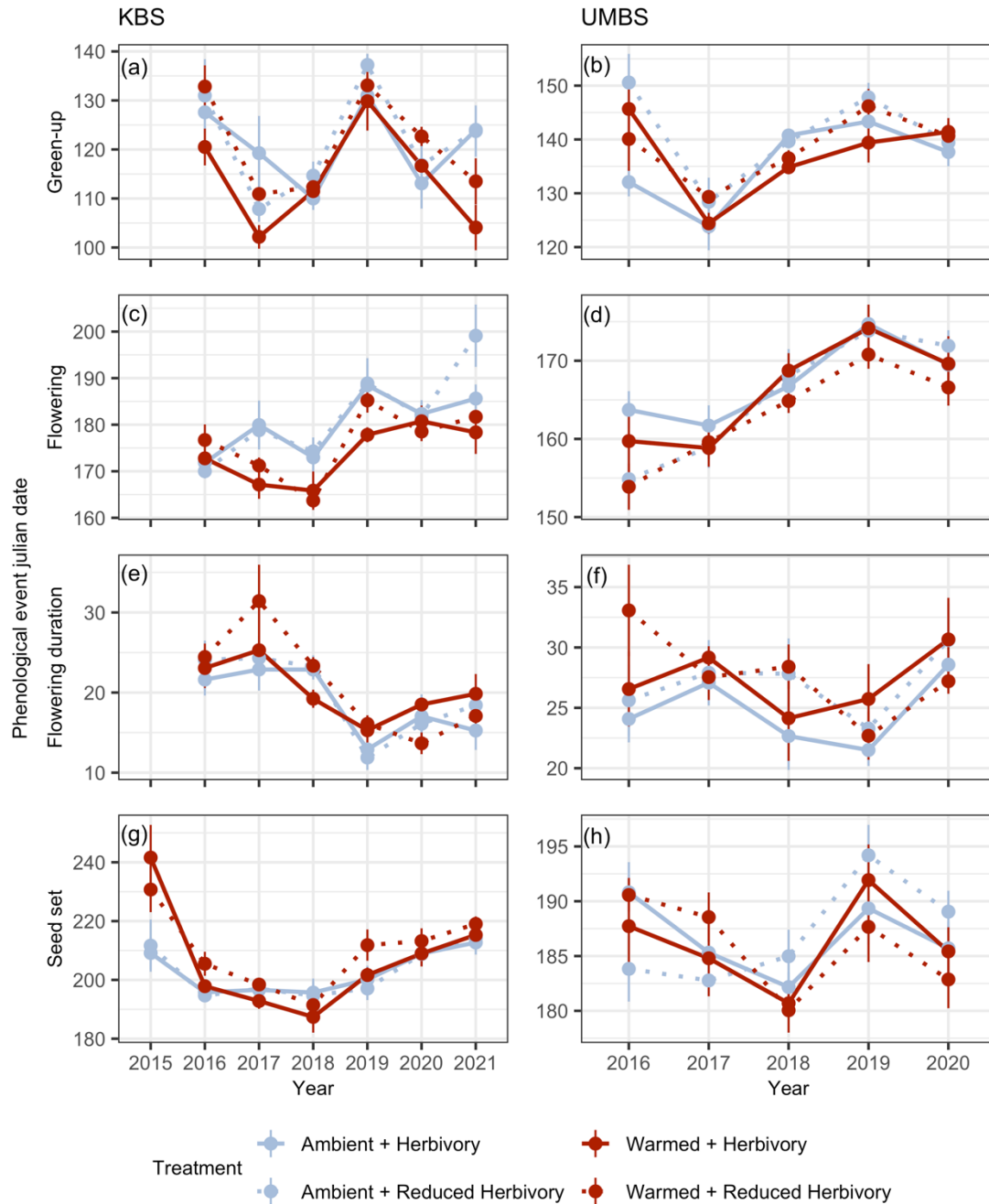


Figure 2.3. Green-up (a-b), flowering (c-d), flowering duration (e-f), and seed set (g-h) between warmed and ambient plots in herbivory and herbivory reduction treatments for each year at KBS and UMBS. 2015 data were removed for green-up, flowering, and flowering duration at KBS due to the chambers being built early that summer. Points represent means $\pm$ standard error (n=6).

Plant Community Composition

Percent Cover

At KBS, the effect of warming on percent cover depended on year ($F_{6,140} = 2.94$, $p = 0.01$; Appendix S1: Table S8). In particular, there was a significant increase in percent cover in 2020 and 2021 in warmed plots (Appendix S1: Table S23). Warmed plots had 1.4 times the percent cover of ambient plots in 2020 ($t_{175} = -2.1$, $p = 0.03$) and 1.6 times the percent cover of ambient plots in 2021 ($t_{175} = -2.18$, $p = 0.001$; Fig. 2.4a; Appendix S1: Table S23). Depending on the year, reduced herbivory positively affected percent cover ($F_{6,140} = 3.21$, $p = 0.01$). For example, the reduced herbivory treatment had 1.4 times the percent cover of the herbivory treatment in 2021 ($t_{167} = -2.32$, $p = 0.02$), but this was the only year where a significant effect of reduced herbivory was found (Appendix S1: Table S23). Depending on the year, warming increased all four plant “types” (forb, graminoid, native, exotic; Appendix S1: Tables S9-12, Sections S5-6). At UMBS, neither warming ($F_{1,24} = 1.71$, $p = 0.20$) nor reduced herbivory ($F_{1,24} = 1.46$, $p = 0.24$; Fig. 2.4b) had a significant effect on percent cover. Natural temperature variation did not significantly affect percent cover at KBS ($F_{1,57} = 0.21$, $p = 0.65$; Appendix S1: Fig. S23). At UMBS, for each unit increase in ambient temperature, percent cover increased by 0.06% ($F_{1,48} = 17.36$, $p < 0.001$; Appendix S1: Fig. S23).

Plant Diversity

At KBS, warming decreased species richness by an average of 1.0 species over the study period ($F_{1,24} = 12.89$, $p < 0.001$; Fig. 2.4c). Reduced herbivory did not significantly affect species richness overall ($F_{1,24} = 0.01$, $p = 0.92$); instead, the effect depended on the year ($F_{6,140} = 4.07$, $p = 0.001$; Fig. 2.4c; Appendix S1: Table S13). Only in 2016 did reduced herbivory positively affect plant species richness ($t_{121} = -2.52$, $p = 0.01$; Appendix S1: Table S28). At UMBS, there was no significant effect of warming ($F_{1,24} = 0.52$, $p = 0.48$) or reduced herbivory ($F_{1,24} = 0.21$, $p = 0.65$; Fig. 2.4d; Appendix S1: Table S13) on species richness. For both sites, neither warming nor reduced herbivory significantly affected Shannon diversity over the study period (Appendix S1: Fig. S11, Tables S14 and S29, Section S7).

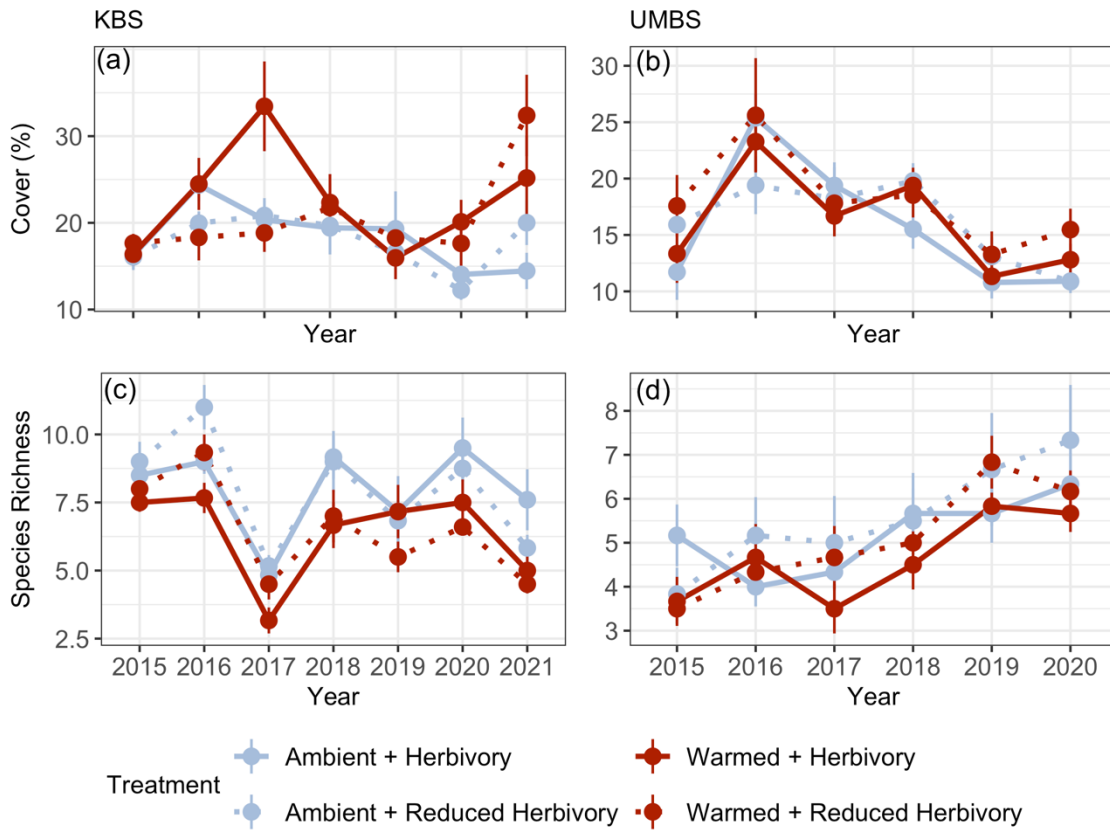


Figure 2.4. Average percent cover (a-b) and species richness (c-d) in warmed and ambient plots between herbivory and reduced herbivory treatments at KBS and UMBS. Points represent means $\pm$ standard error (n=6).

Leaf Traits (C, N, SLA)

At KBS, herbivory decreased nitrogen content across the two representative species by 0.10% ($F_{1,38} = 3.84$, $p = 0.06$; Appendix S1: Fig. S12, Table S16). Only in 2021 did warming significantly decrease N content ($t_{87} = 2.10$, $p = 0.04$; Appendix S1: Table S31). At UMBS, warming only significantly decreased N content in 2018 ($t_{29} = 1.99$, $p = 0.06$; Appendix S1: Table S31). There was no significant effect of herbivory reduction on N content ($F_{1,43} = 0.53$, $p = 0.47$). When considering the effect of natural temperature variation on nitrogen content, increasing ambient temperatures increased N content by 0.11% at KBS ($F_{1,183} = 2.96$, $p = 0.09$) and by 0.43% at UMBS ($F_{1,202} = 163$, $p < 0.001$; Appendix S1: Fig. S25). There was no significant effect of any treatment on leaf C content (Appendix S1: Section S8).

Warming led to an average increase in SLA of 11.2 cm²/g across the six representative species at KBS ($F_{1,116} = 4.52$, $p = 0.04$; Appendix S1: Fig. S12), but there was no significant overall effect of herbivory reduction ($F_{1,116} = 0.45$, $p = 0.50$; Appendix S1: Fig. S12, Table S17).

SLA also increased over time ($F_{2,56} = 244$, $p < 0.001$), with the highest SLA found in 2021 in the warmed and reduced herbivory treatment (Appendix S1: Fig. S12). At UMBS, neither warming ($F_{1,88} = 0.002$, $p = 0.97$) nor herbivory reduction ($F_{1,88} = 0.026$, $p = 0.87$) had a significant effect on SLA, but SLA did decrease over time ($F_{2,756} = 23.8$, $p < 0.001$; Appendix S1: Fig. S12).

Biomass

At KBS, both warming and herbivory affected total plant biomass. Warming increased biomass by 30g/0.20m² ($F_{1,19} = 7.38$, $p = 0.014$; Fig. 2.5a), whereas herbivory decreased biomass by 25g/0.20m² ($F_{1,19} = 5.88$, $p = 0.026$; Fig. 2.5a; Appendix S1: Table S18). However, we did not find that the effect of warming varied significantly based on the presence or absence of herbivores ($F_{1,19} = 0.26$, $p = 0.62$). At UMBS, neither warming ($F_{1,20} = 0.002$, $p = 0.97$) or herbivory reduction ($F_{1,20} = 0.82$, $p = 0.38$) had a significant effect on biomass (Fig. 2.5b).

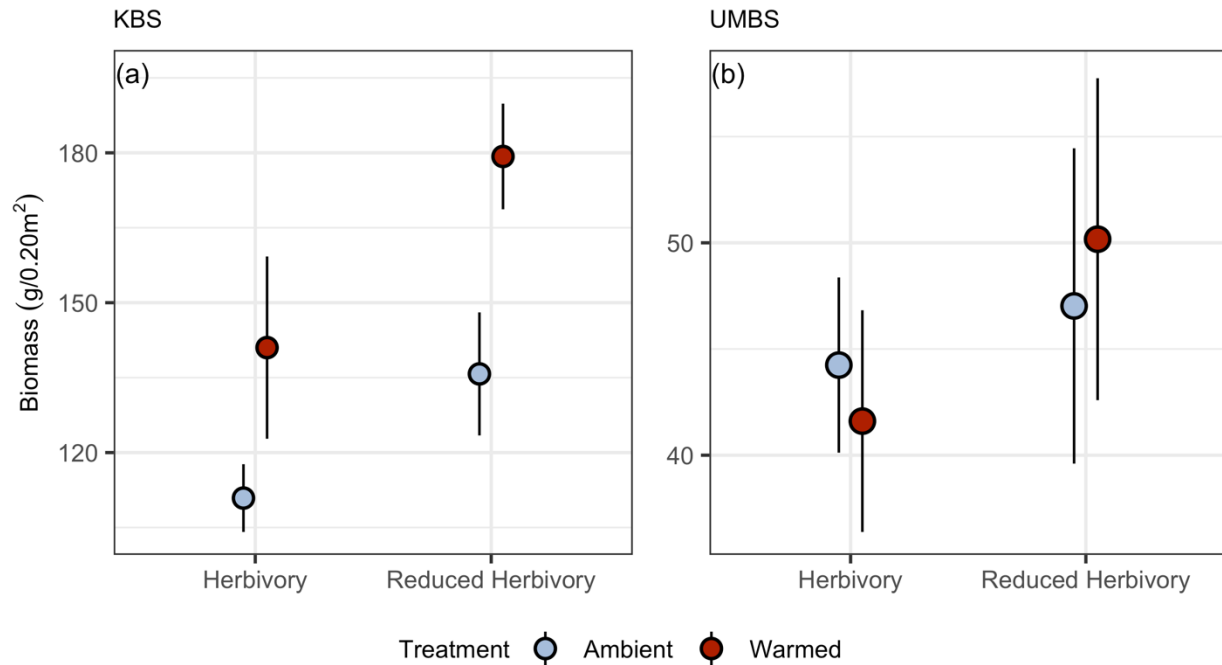


Figure 2.5. Plant biomass (g/0.20m²) in 2021 for plants in warmed and ambient plots in herbivory and reduced herbivory treatments at KBS (a) and UMBS (b). Points represent means $\pm$ standard error (n=6).

DISCUSSION

In this multi-year experiment, we found that plant responses to warming are largely driven by the separate effects of warming and herbivory. We found little evidence for herbivore-mediated interactive effects on plant traits and community composition. Plants were more

responsive to the warming treatment at our southern site, KBS. Warming ultimately led to increased plant productivity and shifts in phenology and composition; in warmed plots at KBS, we found greater percent cover, increased biomass and SLA, earlier green-up and flowering, delayed seed-set, and reduced species richness. Aside from lack of support for strong interactive effects, our findings generally support our hypotheses and align with past warming studies (Karimi et al. 2021; Wangchuk et al. 2021).

Previous studies have noted a positive effect of warming on percent cover, specifically with warming more strongly promoting the growth of exotic species and graminoids (Wangchuk et al. 2021; Willis et al. 2010), and often a coincident reduction in species richness due to fewer species benefiting from warmer conditions (Morecroft et al. 2009; Elmendorf et al. 2012; White et al. 2014). Those findings demonstrate that future plant communities may be dominated by more exotic and graminoid species, and fewer native and forb species. In support of Hypothesis #3, we also found that warming reduced species richness (Fig. 2.4c), however, depending on the year at KBS, both native and exotic species and both graminoid and forb species increased under warming (Appendix S1: Fig. S9-10). Therefore, in this system, exotic and graminoid species may not outcompete native and forb species under a new climate regime. Nonetheless, more research is needed on the effects of warming on these competitive interactions, as some species may benefit more than others (De Boeck et al. 2008), and these responses are likely more nuanced than broad exotic vs. native or forb vs. graminoid responses to warming. We did not find evidence that insect herbivory significantly mediated these outcomes, although herbivory did reduce percent cover and species richness in some years (Appendix S1: Fig. S9-10).

Plant biomass at KBS was affected by both warming and herbivory reduction, but not their interaction. While warming increased plant biomass, herbivory reduced it (Fig. 2.5a); this finding supports our Hypothesis #4. This suggests that herbivory may ameliorate warming effects on plant growth (Post and Pederson, 2008), especially in systems where herbivory also increases under warmer conditions (Hamann et al. 2021). The increased plant productivity in the OTCs at KBS may have also shaded our temperature sensors, hence leading to cooler 10cm air temperatures and 5cm soil temperatures in the OTC plots (Fig. 2.1a,b).

The expansion of the growing season, due to advanced green-up and delayed seed set, may explain why plant productivity increased in warmed plots at KBS. We found support for

Hypothesis #2 that warming will lead to earlier green-up, flowering, and delayed seed set at KBS (Fig. 2.3). Interestingly, warming did not lead to significantly longer flowering duration (Fig. 2.3e,f). In contrast, we saw the opposite effect of warming on seed set in some years at UMBS, where warming led to an advancement of the date of first seed set (Fig. 2.3h). Because warming did not advance green-up or delay seed set at UMBS, and therefore did not expand the growing season, this might explain why there was no significant warming effect on biomass at that site (Fig. 2.5b).

For green-up and seed set, we did find evidence for interactive effects between warming and herbivory. In general, there was potential for herbivory to advance green-up, but the effects of herbivory depended upon the site and warming treatment. At KBS, there was a strong effect of herbivory on green-up, but only in warmed plots (Fig. 2.3a). In contrast, at UMBS, herbivory only affected green-up in ambient plots (Fig. 2.3b). We also found that herbivory has the potential to alleviate the effects of warming on seed set at KBS; warming only delayed seed set in reduced herbivory plots, demonstrating that herbivory may be buffering the effect of warming on seed set. These findings contribute to an existing body of evidence that warming alters phenology (Peñuelas and Filella 2001; Walther et al. 2002; Zhou et al. 2022), however, here we show that these particular phenological responses to warming depend upon the level of biotic interactions with insect herbivores. The opposing effects of herbivory on green-up at KBS vs. UMBS may be due to underlying differences in species types and environmental conditions between the sites, which is discussed in more depth below. The support for Hypothesis #2 suggests that the timing of plant life cycle events may change with climate change, and this change has the potential to alter community dynamics and plant interactions with other organisms (Liu et al. 2011).

In support of Hypotheses #4, warming increased SLA and herbivory decreased N content for plants at KBS (Appendix S1: Fig. S12). Interestingly, although warming decreased N content, we did not find a concurrent warming effect on leaf herbivory at KBS (Fig. 2.2a,c). However, at UMBS, warming increased the probability of a plant being eaten, which supports Hypothesis #1 (Fig. 2.2b), but warming ultimately did not affect leaf traits. Typically, we would expect decreased N content to lead to increased herbivory because insects require more leaf material to meet nutritional needs (Hamann et al. 2021). Our ability to capture plant responses to herbivory may have been limited by our method of measuring herbivory. For example, we only

measured chewing damage on leaves for herbivory, leaving out herbivory by sap sucking and stem boring insects. Other forms of herbivory might lead to differing results when compared to outcomes due to insect-specific herbivory (Lebbink et al. 2023). Moreover, certain plant types (i.e., native plants and forbs) were more likely to be eaten than their counterparts (i.e., exotic plants and graminoids) (Appendix S1: Section S3). Other factors such as plant size, plant defenses, and plant relatedness can also affect herbivory levels (The Herbivory Variability Network 2023). The differential effects of warming on different plant types suggests that some plants may be more vulnerable to herbivory under climate change, which could lead to overall changes in community composition (Sherry et al. 2007; Primack et al. 2009; Youngflesh et al. 2021). While we did not measure insect abundance and presence in this experiment, future studies would benefit from monitoring the insect community alongside the plant community to better link changes in herbivore presence with their effects on plants.

The results of our models using natural temperature variation as a continuous explanatory variable sometimes differed from our results using our warming treatment as a categorical explanatory variable (warmed vs. ambient). For example, our warming treatment models show that experimental warming had no significant effect on green-up and flowering at UMBS (Fig. 2.3), while greater natural temperatures advanced both green-up and flowering at UMBS (Appendix S1: Fig. S19-20). These models may differ because naturally warmer years increase temperatures at the whole community level, whereas our warming treatments warm at the plot level and likely have a larger effect on sessile organisms. Warming at the community-level warms not just the plant community, but also affects the organisms that interact with that community, including primary and secondary consumers and plant species outside of a 1m² plot. Because natural temperature variation affects communities in different ways than warming treatments, the results of climate change experiments may differ from potential future climate warming.

Throughout our analyses, we noted the high amount of both yearly and species-specific variability in plant responses to both of our treatments. This inherent variation demonstrates the importance of conducting longer-term climate studies on plant communities. For example, it may take many years for the composition of plant communities to respond to a change (Bahlai et al. 2021; Cusser et al. 2021; Dickson and Gross 2013). Dickson and Gross (2013) found N addition caused an increase in aboveground productivity within a few years, but it required 14 years for

plant species richness to decrease. In our study, we also found that some response variables required multiple years to demonstrate a response; for example, we only found a treatment effect on percent cover in the final two years of the experiment (Fig. 2.4a). Although our treatments were in place for seven consecutive years, we recognize that an even longer duration experiment may yield stronger plant compositional responses to warming and reduced herbivory and may be necessary to uncover the interactive effects of warming and herbivory.

We also saw that plants at the southern site (KBS) were more responsive to warming than at the northern site (UMBS). We expected the more northern site to have greater sensitivity to climate changes (Prev  y et al. 2017), however, other site contexts like plant community and soil type also play a role. In particular, the plant community differences between the sites may explain why the northern site was not as responsive to warming compared to the southern site. The most common species at UMBS is an exotic forb (*Centaurea stoebe*) (Appendix S1: Table S1), which may have a greater tolerance to changing temperatures compared to native species (Hahn et al. 2012). The OTCs also warmed by a much greater amount at UMBS (Fig. 2.1b,d), and these hotter temperatures could have led to plant stress and mitigated any increased growth response to warming, which may explain why plant productivity variables (e.g., biomass, percent cover, SLA) did not change as a result of either the warming or the herbivory reduction treatments. Furthermore, the soil at UMBS differs from the soil at KBS; it is sandier and drier on average (Appendix S1: Fig. S17). Previous studies have noted the importance of soil traits in mediating plant responses to climate change (Bjorkman et al. 2018; Collins et al. 2021; Elmendorf et al. 2012; Wolkovich et al. 2012), therefore the soil type at UMBS may be ameliorating some warming and herbivory effects. Future experiments could identify and test how site contexts contribute to differential responses to warming and herbivory, which would lead to greater understanding of which environmental factors are the most important for determining community responses to warming.

These results may also depend upon our experimental design of using OTCs for warming. While OTCs are a common method for manipulating temperature in plant communities, they are not without their limitations. For example, the structure of the OTCs can limit wind, precipitation, and increase humidity (Hollister et al. 2022; Ettinger et al. 2019). The chambers themselves may also limit dispersal between plots in the community, and therefore could affect

plant composition and herbivory in unintended ways. Despite these potential limitations, OTCs are a well-known and effective method for manipulating the abiotic environment in situ.

Conclusions

Our study demonstrates that warming and herbivory can have strong direct effects on plant communities, but that warming and insect herbivore-mediated interactive effects may be more subtle in these early successional systems. Under current and future climate scenarios, warming is likely to affect biotic interactions alongside plant communities themselves, leading to complex responses to warming. Furthermore, the strength and direction of these effects can vary by ecological context. Thus, it is still beneficial to include levels of biotic interactions, multiple traits, and community type when studying climate change effects on plants and their communities, especially over multiple years. By including these biotic interactions in climate change experiments, we can gain a more holistic understanding of how communities may respond to a changing climate.

Acknowledgements

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CHAPTER 3: A global meta-analysis of passive experimental warming effects on plant traits and community properties

ABSTRACT

In order to predict how plants and their communities will respond to further climate warming, we need to improve our understanding of how plant traits and community properties differ in their responses to warming, as well as what contexts contribute to variation in these responses. To address this knowledge gap, we compiled data from 126 in-situ passive experimental warming studies on 13 different plant trait and community property responses. We then collected metadata from these studies to define 9 different study contexts spanning environmental, experimental, and plant-level scales. We find that some traits decrease when warmed (e.g., aboveground N content), while others increase (e.g., plant biomass). We also identify contexts that contribute to variation in plant responses to warming, such as latitude, but the importance of these contexts varies by the trait or community property. For example, as latitude increases, the effect of warming on reproductive traits becomes stronger, but this latitude-trait relationship did not hold for all traits. Our study demonstrates the importance of carefully designing and interpreting the outcomes of climate change experiments and highlights the need for coordinated warming experiments across varying environmental contexts in order to mechanistically understand and predict plant community responses to climate warming.

INTRODUCTION

In the context of recent anthropogenic climate change (IPCC, 2021), plant traits and plant community properties can be used to understand and predict ecological responses to abiotic stressors, particularly rising temperatures (Díaz et al., 2016; Heilmeyer, 2019; Liu et al., 2021; Soudzilovskaia et al., 2013). Experiments involving warming effects on plants and their communities have provided important insights into these responses. For example, species with high resource input into structural traits (e.g., thick leaves, low specific leaf area (SLA), and high root C content) typically increase in abundance under warmer temperatures due to increases in seed quality and/or forming more buds, allowing them to have increased shoot numbers in the next season (Soudzilovskaia et al. 2013). In terms of community properties, total plant community biomass typically increases under warming due to promotions in plant growth (Lin et al., 2010). Despite these findings, it is unclear how environmental, experimental, and plant-level contexts affect these responses, hindering our ability to predict how plants and their communities

respond to climate change. We aim to help fill this gap through meta-analysis of plant trait and community property responses to in-situ warming.

We focus on plant traits and plant community properties because these are important mediators for plant interactions with their environment (Diaz et al., 2004; Violle et al., 2007) and they can vary across multiple contexts (Gratani, 2014). Plant traits are defined as any morphological, physiological, or phenological (morpho-physio-phenological) feature measurable at the individual level, whereas community properties are defined as emergent features measurable at the community or ecosystem level (e.g., community biomass, percent cover, etc.) (Violle et al., 2007). Furthermore, plant functional traits (PFTs) are defined as morpho-physio-phenological traits which are assumed to impact plant fitness indirectly by affecting plant performance (e.g., plant survival, vegetative biomass, or reproductive output) (Violle et al., 2007). For example, a plant's leaf size may affect plant performance due to the trait's association with photosynthetic capacity (Comstock & Ehleringer, 1990). Though there is debate about the importance and usage of functional traits in ecology (van der Plas et al., 2020), they can provide a meaningful, taxon-independent view of overall community structure and function (Funk et al., 2017; Hagan et al., 2023).

While plant traits and community properties may be useful for predicting overall responses to climate change, traits themselves can also change as a result of climate stressors. For instance, SLA has been seen to increase in response to warming (Descombes et al., 2020). The ability of a single genotype to produce a range of phenotypes as a function of the environment is known as phenotypic plasticity (Bradshaw, 1965; Nicotra et al., 2010). Plasticity in plant traits can assist plants in responding to changes in the environment, such as temperature increases associated with climate change (Gratani, 2014; Matesanz et al., 2010; Nicotra et al., 2010). Due to the potential for plastic trait responses to abiotic stressors, we would ideally first determine the extent of trait plasticity before we can begin to use mean trait values to potentially predict overall community responses to climate change stressors. Evaluating a variety of environmental, experimental, and plant-level contexts can help quantify the potential causes for inter- and intraspecific trait variation, and provide insights into the potential for plastic responses to climate change. For example, Stotz et al. (2021) determined that phenotypic plasticity for five trait types (leaf morphology, physiology, plant allocation, size, and performance) can be associated with both climate (e.g., mean annual temperature) and non-climate (e.g., nutrient

availability) related contexts in the environment. However, while their study looked at overall plant plasticity associations with environmental contexts, they did not consider how climate warming may alter these plastic trait associations. For instance, though traits may be affected by temperature differences across a species' range, how might novel warming stress affect species' traits within their current environment? Remaining questions such as this demonstrate that variation in plant and community responses to warming has not yet been well defined between environmental, experimental and plant-level contexts.

Our focus on in-situ field experiments enables the inclusion of multiple environmental contexts such as latitude, mean annual precipitation and temperature, and species distance from their range edge—all of which can affect plant traits and community properties (Nicotra et al., 2010). By focusing solely on passive warming experiments using open-top chambers (Marion et al., 1997), we limit methodological differences between studies, which can lead to large differences in experimental outcomes (Wolkovich et al., 2012). With these studies, we performed a meta-analysis investigating how 9 different environmental (e.g., latitude), experimental (e.g., length of warming study), and plant-level (e.g., plant functional type) contexts contribute to variation in plant responses to warming. We address two main questions: 1. How does in situ experimental warming affect various plant traits and community properties, and 2. How do different environmental, experimental, and plant-level contexts contribute to variation in plant trait and plant community responses to in-situ warming?

METHODS

Literature search

In total, we identified 126 in-situ passive open top chamber studies around the world (Fig. 3.1, Table S3.1). Our selection began with a comprehensive Scopus database search through Michigan State University conducted on 10 November 2020 using the following search criteria: TITLE-ABS-KEY ("climate change") OR TITLE-ABS-KEY ("climate-change") OR TITLE-ABS-KEY ("climate warm*") OR TITLE-ABS-KEY ("climate-warm*") OR TITLE-ABS-KEY ("global change") OR TITLE-ABS-KEY ("global-change") OR TITLE-ABS-KEY ("globalwarm*") OR TITLE-ABS-KEY ("global-warm*") OR TITLE-ABS-KEY ("global-climate-change") OR TITLE-ABS-KEY ("global-climate-warm") OR TITLE-ABS-KEY ("ITEX") OR TITLE-ABS-KEY ("itex") AND TITLE-ABS-KEY ("experiment"). This search returned 24,516 peer-reviewed papers published between 1971 and 2020 (Fig. S3.1). 13,660

papers were successfully downloaded after removing corrupted or otherwise inaccessible papers. Text mining, via the R package “tm” (Feinerer & Hornik, 2023), was used to search through each of the given papers for any combination of the terms “open-top,” “itex,” “(passive) warming,” and/or “chamber”, resulting in 2,990 papers. The Scopus search was repeated on 5 August 2022 to capture any papers published between 2020-2022 that may contain relevant data, resulting in 8,955 new papers meeting the search criteria (Fig. S3.1). The original 2,990 and additional 8,955 papers were manually screened to check for relevance using the following criteria: (1) the article utilized an open-top chamber design, (2) a field experiment was performed using the open-top chamber, and (3) the experiment was used to determine relevant plant response(s) to elevated temperatures. The original search returned 177 relevant papers and the reconducted 2022 search returned 54 relevant papers for a total of 231 papers.

For data extraction, we chose a subset of relevant plant responses that were most commonly measured in experimental warming studies. These plant response variables included: above- and belowground biomass, above- and belowground nitrogen content, spring phenology, fall phenology, flower lifespan, flower number, fruit number, fruit weight, percent cover, plant growth, and leaf growth. To determine the most commonly measured traits and properties, we recorded each trait that was included as a measured response in the original 177 relevant warming studies. The total number of studies a trait was measured in ranged from 1-49. We determined that a trait present in at least 13 studies was common and included only these common traits in our data collection. We did not collect data on traits that were rarely measured (e.g., water use efficiency, which was measured by one study) due to low replication across studies.

The 231 relevant papers were narrowed down to 126 papers that met the plant response criteria and also contained data we were able to collect (Fig. 3.1, Fig. S3.1, Table S3.1). There were several reasons why a paper may not have contained usable data: not listing plant trait measurements in both warmed and control treatments, not including variation, not including sample size, or not presenting the data in a format in which it was accessible. If we were unable to collect data from the publication, we contacted the lead author of the study to solicit the needed data; 14 of 25 contacted authors responded to our inquiry and provided the requested data.

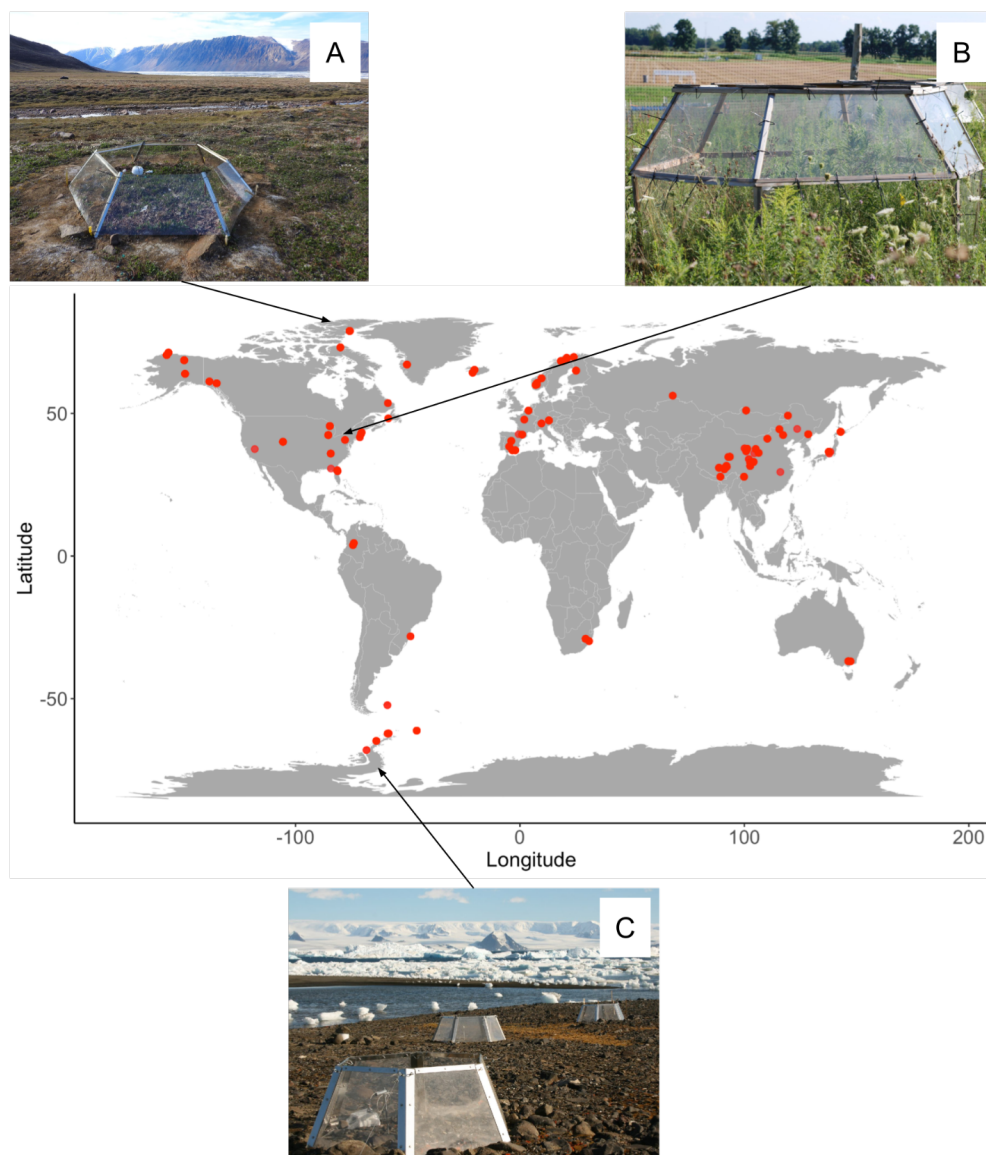


Figure 3.1. Geographic distribution of the 126 studies used in this meta-analysis. Each dot represents the location of one warming experiment; some studies contained >1 warming experiment within the manuscript, therefore studies may have >1 dot. Map lines delineate study areas and do not necessarily depict accepted national boundaries. A: Open-top chamber (OTC) at Alexandra Fiord, Ellesmere Island by Cassandra Elphinstone (CC BY-SA 4.0); B: OTC at Kellogg Biological Station, Michigan by Phoebe Zarnetske; C: OTCs at James Ross Island, Antarctica by Miloš Barták, courtesy of the Czech Polar Reports (with permission).

Free-air concentration enrichment (FACE) experiments were not considered because differences between this method and open-top chambers have been extensively documented (Hendrey & Kimball, 1994; Macháčová, 2010). We also did not include papers utilizing any active warming method, such as heating cables, due to differing experimental designs potentially leading to different experimental outcomes (Wolkovich et al., 2012). Reviews and meta-analyses were excluded due to potential overlap with the primary articles being reviewed in this study. The third criteria for inclusion, which stated that the experiment was used to determine plant response(s) to elevated temperatures, excluded articles utilizing open-top chambers that monitored processes such as CO₂ flux. If a study included a fully factorial design with warming crossed with a secondary stressor (CO₂ increase, herbivory, etc.), we only collected data from the warmed-only and control treatments.

Data collection

For each of the 126 studies, we collected metadata on environmental, experimental, and plant-level contexts. We weren't able to obtain data on each of the data types listed below for all studies, so these data were collected when available.

For each study, we collected data on the following environmental contexts: latitude and longitude, elevation, mean annual precipitation and temperature, and the distance of each species to its northern range edge. Most studies published the latitude and longitude within the manuscript, but if only a general region was given (e.g., the name of a research station), we pulled the coordinates for the centroid of the given region. Absolute latitude was calculated as the absolute value of latitude in order to obtain total degrees away from the equator. Elevation was calculated for each experiment's coordinates using the *elevatr* R package (Hollister et al., 2023). WorldClim mean annual temperature and precipitation was extracted for each coordinate using the *geodata* and *terra* R packages (Hijmans, 2023; Hijmans et al., 2023). We quantified each species' distance from its northern range edge to determine if individuals further from their 'leading edge' had differential responses to warming compared to individuals closer to the edge (Angert et al., 2011). To determine the distance to the northern range edge, we used the GBIF and BIEN R packages (Chamberlain et al., 2024; Maitner et al., 2018) to collect all occurrence records for each species included in our dataset as of June 2023. We used both GBIF and BIEN to ensure a comprehensive search of species' occurrence records. We then determined the maximum recorded latitude for each species, either from GBIF or BIEN, and subtracted the

study latitude for each species from its maximum latitude to determine the distance (in degrees) to that species' northernmost occurrence, as a proxy for the species' northern range edge. The range edge analyses were only performed for species from experiments in the northern hemisphere, as species located in the southern hemisphere may track the climate southward, rather than northward (Angert et al., 2011).

For experimental contexts, we collected: publication number (1-126), publication information (primary author, year published, and journal), start year of the warming experiment, error type recorded (standard error, standard deviation, etc.), timing of warming (year-round or seasonal), site information (if one study contained multiple sites), average amount warmed by the chambers (°C), how average chamber warming was determined (growing season or annual average), and number of years warmed in the study.

For plant-level contexts, we collected: plant traits and community properties measured (Table S3.2), plant family, genus and species, plant functional group (Table S3.3), plant native status in the region of the study (native or non-native), and tissue type measured for aboveground biomass and N content (leaf, shoot, etc.). To standardize species names, we used Plants of the World Online (POWO, 2023) to ensure all species are listed under their currently accepted name. The native status of a species was determined using the species distribution maps on POWO, in which a species was marked as “native” for a study if the experiment resided within the noted native range. Any species outside of the native range on the distribution map was designated as “non-native”. Similarly to Stuble et al. (2021), we grouped some response variables into broader categories of similar plant function (Table S3.2). For example, all early phenophases (e.g., bud break, flowering, etc.) were grouped under “spring phenophases” due to their association with a similar plant function (in this case, the beginning of a life cycle phase). The response variables measured in this study could be categorized as either a plant trait or a community property, as discussed, but some variables could be both a trait and a property. For example, aboveground biomass may have been measured for a single individual of a species, making it a trait, or it may have been summed across multiple individuals/species in a plot, making it a community property. We parse out these differences when we test for differences between plant functional groups, in which we include “total community” as a grouping.

To generate effect sizes for each study's response variables, we extracted the mean, variation, and sample size of a given response variable in warmed and control treatments. Data

were primarily collected from tables and figures, with some data coming from openly available data or the publication text including figure and table captions. Figures were imported into Fiji (Schindelin et al., 2012) for data extraction. To ensure data collection from figures was standardized amongst the three individuals extracting data, each individual independently extracted data from three of the same randomly selected figures to ensure their measurements were similar. After all measurements were completed, we visually compared each figure to its extracted data to ensure that the measurements were accurate for all figures.

Statistical analysis

All analyses were conducted using R (R Core Team, 2024). We first transformed all variation measurements recorded as standard error or 95% confidence intervals to standard deviation to ensure we could calculate effect sizes. Using the metafor R package (Viechtbauer, 2010), we then calculated Hedges' *g* effect sizes to determine the effect of warming on each response variable from each study (Table S3.2). Hedges' *g* is a commonly used effect size in meta-analytic studies, as it standardizes the mean differences between groups while also accounting for uneven group sample sizes (Hedges, 1981). Each study may have multiple effect sizes due to multiple traits being measured across different contexts (e.g., multiple species, different levels of warming, etc.).

To test for potential publication bias, we generated funnel plots of the relationship between effect size and standard error, sampling variance, inverse standard error, and inverse sampling variance. In all plots, we found a standard funnel distribution, indicating an absence of strong publication bias (Fig. S3.2).

All models were conducted using the `rma.mv` function from the metafor R package (Viechtbauer, 2010). We ran an initial random-effects univariate model to test for the effect of warming on each response variable. This initial model contained species nested within site nested within publication number as random effect (Table S3.4). Because metafor does not allow for NAs in random effects, and not all measurements had species-level information, we substituted functional group for species when species-level designations were missing, in order to include all data in models.

We then ran separate random-effects univariate models for each response variable to test if the warming response depended on: absolute latitude, mean annual precipitation, mean annual temperature, species distance from range edge, timing of warming, amount warmed by the

experiment, number of years warmed, plant functional group, and plant native status. These models also contained species nested within site nested within publication number as random effects (Tables S3.5-S3.16). The effect of elevation was not analyzed as we found that latitude and elevation were negatively correlated ($t_{1254} = -27.4$, $p < 0.001$; Fig. S3.3). We also include Holm-corrected comparisons for contexts that contain multiple levels; while the univariate model for each variable tests if each level within a context differs from 0, the Holm-corrected comparisons compare each level to each other. For example, the univariate models for plant native status tests if native and/or non-native species' effect sizes differ from 0, while the Holm-corrected comparison tests if native and non-native species' effect sizes are different from each other.

For models that tested the effects of a grouped variable (e.g., spring phenophases) or grouped plant functional type (e.g., shrubs) on the warming response, we also ran an initial model to ensure that the finer-scale levels within the grouped variable did not affect model outcomes. For example, we tested to see if deciduous and evergreen shrubs differed in their response to warming, and if not, we ran our model with the broader grouping (i.e., shrub). Similarly, for grouped variables, we tested to ensure that each finer-scale trait did not differ from the traits in its grouping. For example, we ensured that height and shoot length did not have opposite responses to warming (e.g., a positive and negative estimate) in order to group them under the broader "growth" trait. We tested for the effects of these finer-scale levels for all variables (Table S3.2) and functional groups (Table S3.3) that contained multiple levels. The models testing for differences between these finer-scale levels can be found in the supplement (Tables S3.17-S3.18). Similarly, because aboveground biomass and N content contained multiple different tissue types that were measured across studies, we ensured that tissue-specific responses to warming were similar for both variables (Table S3.19).

For all models, we limited data to the last year of data collection for each study to avoid temporal pseudoreplication for experiments that followed the same plots over time (Stuble et al., 2021). For two variables (fruit number and percent cover), we found that the models containing all years detected an overall response to warming, whereas our year-limited models did not (Table S3.20). This difference may be due to multi-year experiments containing some years with a warming response, but the effect was lessened when the dataset was reduced to the final year for those experiments.

RESULTS

Plant trait and community property responses

We found that plant traits and community properties differed in their responses to warming (Fig. 3.2, Table S3.4). Aboveground N content decreased in response to warmer temperatures (Hedges' $g = -0.41$, $z_{13} = -4.88$, $p < 0.0001$), and leaves showed a stronger change in N content compared to other measured tissue types (Table S3.19). There was also a marginal negative effect of warming on spring phenophases, meaning spring phenological events occurred earlier when warmed (Hedges' $g = -0.12$, $z_{13} = -1.76$, $p = 0.08$). Aboveground biomass (Hedges' $g = 0.25$, $z_{13} = 3.64$, $p < 0.001$), belowground biomass (Hedges' $g = 0.60$, $z_{13} = 3.73$, $p < 0.001$), fruit weight (Hedges' $g = 0.58$, $z_{13} = 4.04$, $p < 0.0001$), plant growth (Hedges' $g = 0.65$, $z_{13} = 10.0$, $p < 0.0001$), and leaf growth (Hedges' $g = 0.54$, $z_{13} = 8.24$, $p < 0.0001$) all increased in response to warming. For aboveground biomass, total plant biomass showed a stronger warming response compared to specific plant tissues (Table S3.19). All other traits and community properties did not demonstrate an overall effect of warming (Fig. 3.2, Table S3.4).

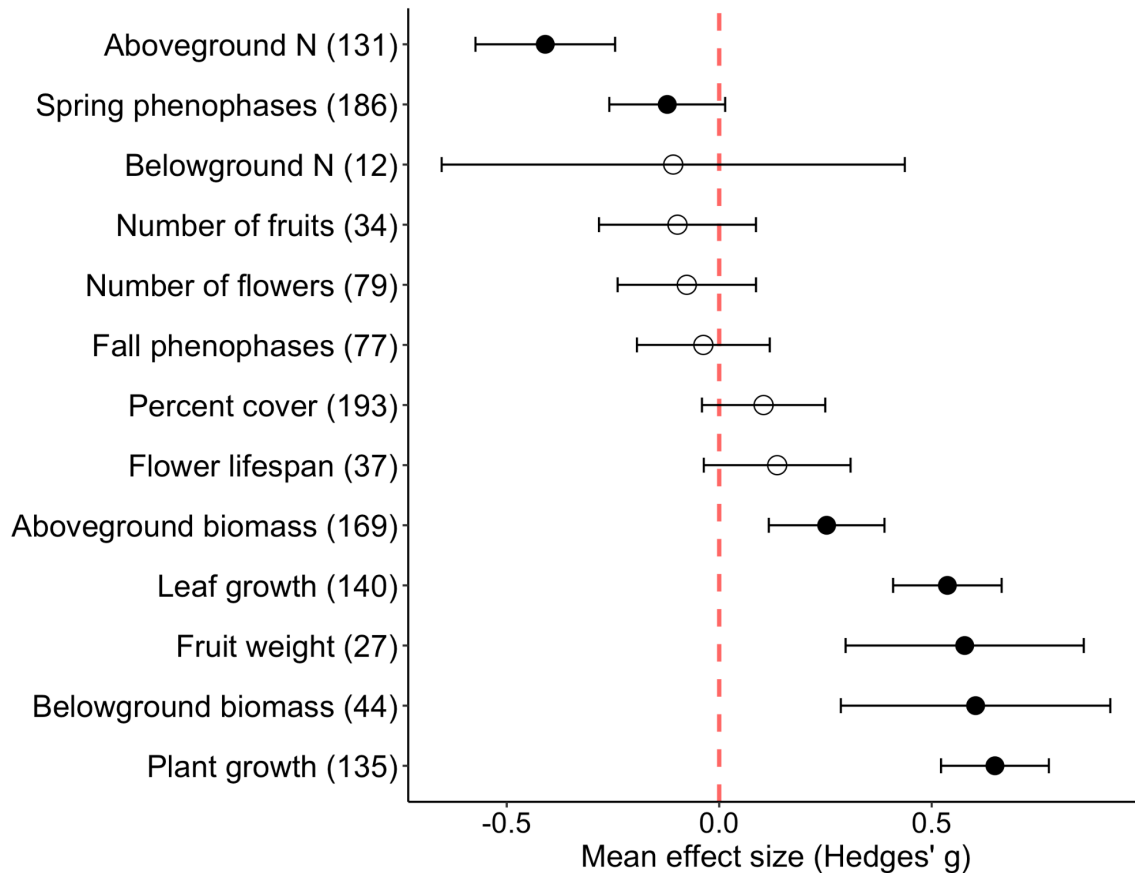


Figure 3.2. Mean Hedges' g effect size for each measured plant trait and community property. Mean values are estimates from the mixed-effects model which accounts for species, site, and publication number. Filled points represent effect sizes that differ (or nearly differ, e.g. spring phenophases) from 0, whereas unfilled points do not differ from 0. Numbers in parentheses next to each trait on the y-axis represent the sample size for that trait, and the points and error bars represent mean $\pm$ 95% confidence intervals.

Environmental contexts

When looking at environmental contexts that contributed to variation in responses to warming, we tested for effects of absolute latitude, mean annual precipitation, mean annual temperature, and species distance from its range edge. As latitude increased, the effect of warming on the number of fruits ($\beta = 0.03$, $z_1 = 1.99$, $p = 0.05$), fruit weight ($\beta = 0.05$, $z_1 = 2.36$, $p = 0.02$), and belowground N content ($\beta = 0.06$, $z_1 = 3.32$, $p < 0.001$) increased (Fig. 3.3, Table S3.5). There was also a marginal increase in the effect of warming on the number of flowers as latitude increased ($\beta = 0.01$, $z_1 = 1.68$, $p = 0.09$). On the other hand, there was a marginal

negative effect of warming on spring phenophases as latitude increased ($\beta = -0.02$, $z_1 = -1.81$, $p = 0.07$).

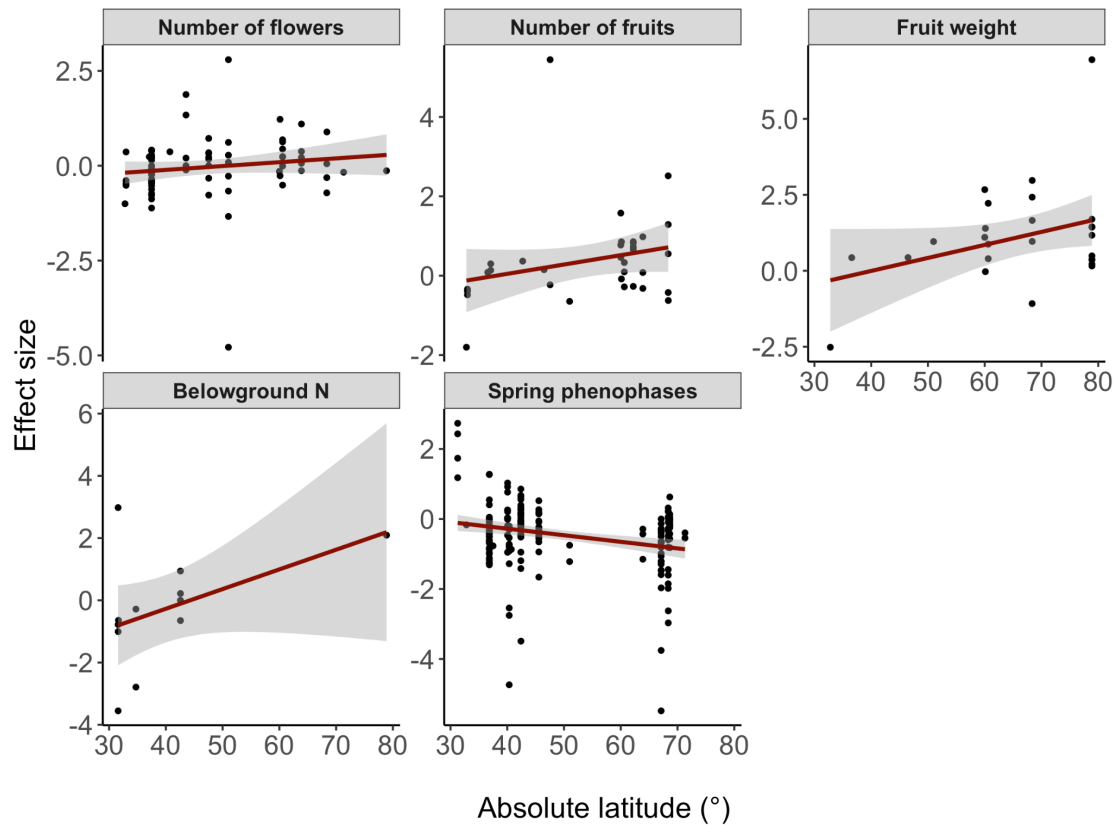


Figure 3.3. The effect of absolute latitude (°) on Hedges' g effect size. Shown are the response variables that demonstrate an effect of latitude; the effect of latitude on all traits and properties, as well as sample sizes, can be found in Table S3.5 and Figure S3.4. Lines represent a linear regression with the shaded region as the 95% confidence interval.

As mean annual precipitation increased, the effect of warming on flower lifespan increased ($\beta = 0.07$, $z_1 = 2.19$, $p = 0.03$; Table S3.6, Fig. S3.5). As a species' distance from its range edge increased (i.e., species become farther away from their northern edge), the effect of warming on plant growth ($\beta = -0.014$, $z_1 = -2.11$, $p = 0.03$) and percent cover ($\beta = -0.036$, $z_1 = -2.40$, $p = 0.02$) became more negative (Table S3.7, Fig. S3.6). Mean annual temperature did not affect any plant traits or community properties (Table S3.8, Fig. S3.7).

Experimental contexts

For experimental contexts, we tested for an effect of the timing of warming, the amount warmed by the experiment, and the number of years warmed. Only when warmed year-round did aboveground biomass (Hedges' $g = 0.65$, $z_2 = 3.29$, $p = 0.001$), belowground biomass (Hedges' g

= 1.06, $z_2 = 2.75$, $p = 0.006$), fruit weight (Hedges' $g = 0.94$, $z_2 = 2.38$, $p = 0.02$), and aboveground N content (Hedges' $g = -0.52$, $z_2 = -3.78$, $p < 0.001$) demonstrate an effect of warming (Fig. 3.4, Table S3.9). In contrast, fall phenology (Hedges' $g = -1.70$, $z_2 = -2.15$, $p = 0.03$) and fruit number (Hedges' $g = 0.63$, $z_2 = 1.78$, $p = 0.08$) only demonstrated a warming effect when warmed seasonally (Fig. 3.4, Table S3.9). Plant growth, leaf growth, and spring phenology demonstrated similar effects of warming, regardless of the timing of warming (Table S3.9, Fig. S3.8). The Holm-corrected comparisons demonstrated differences between year-round and seasonal warming for aboveground biomass and fall phenology (Table S3.10).

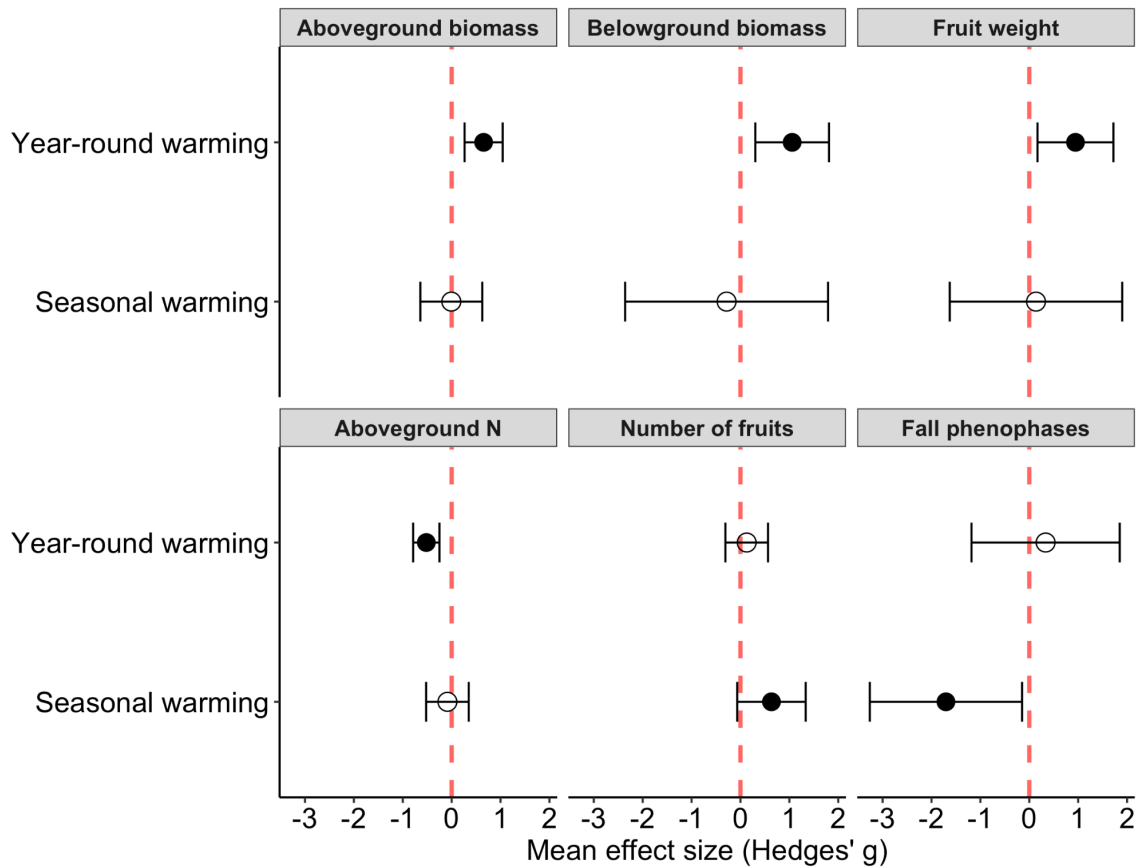


Figure 3.4. The effect of the timing of warming (year-round or seasonal) on mean Hedges' g effect size. Shown are the response variables that demonstrate a difference in Hedges' g based on the timing of warming; the results for all response variables, as well as sample sizes, can be found in Table S3.9 and Figure S3.8. Filled in points represent an effect size different (or nearly differ, e.g. number of fruits) from 0. Mean values are estimates from the mixed-effects model which accounts for species, site, and publication number. Points and error bars represent mean $\pm$ 95% confidence intervals.

Belowground N content demonstrated a response to the amount warmed by the experiment, with warmer temperatures leading to a stronger decrease in belowground N content ($\beta = -0.98$, $z_1 = -1.67$, $p = 0.05$; Fig. S3.9). The amount warmed by the experiment did not affect any other plant traits or community properties (Table S3.11, Fig. S3.9).

As the number of years warmed increased, the effect size for flower lifespan ($\beta = 0.57$, $z_1 = 2.02$, $p = 0.04$) and spring phenophases ($\beta = 0.13$, $z_1 = 1.77$, $p = 0.08$) increased, meaning longer experiments increase the length of flowering and have less pronounced advancement of spring phenophases (Table S3.12, Fig. S3.10). In contrast, increasing the number of years warmed decreased the effect of warming on fruit number ($\beta = -0.23$, $z_1 = -1.95$, $p = 0.05$) and leaf growth ($\beta = -0.03$, $z_1 = -1.83$, $p = 0.07$).

Plant-level contexts

For plant-level contexts, we tested for an effect of plant functional group and plant native status. Graminoids were the most common functional group to experience an effect of warming, with 9 out of 13 traits/properties demonstrating a warming effect on graminoids (Fig. 3.5, Table S3.13). Forbs and shrubs were the second most common functional groups to show an effect of warming for 5 out of 13 traits/properties (Fig. 3.5, Table S3.13). Although bryophytes and lichens were not commonly measured plant types, they appear to have opposing responses compared to vascular plants for some traits. For example, bryophytes (Hedges' $g = -0.46$, $z_7 = -3.34$, $p < 0.001$) and lichens (Hedges' $g = -0.39$, $z_7 = -2.72$, $p = 0.01$) have reduced percent cover when warmed, whereas graminoids (Hedges' $g = 0.22$, $z_7 = 2.34$, $p = 0.02$) and shrubs (Hedges' $g = 0.40$, $z_7 = 3.45$, $p < 0.001$) have increased percent cover (Fig. 3.5, Table S3.13). Holm-corrected comparisons also demonstrated that warming decreased percent cover for bryophytes and lichens when compared to shrubs and graminoids (Table S3.14).

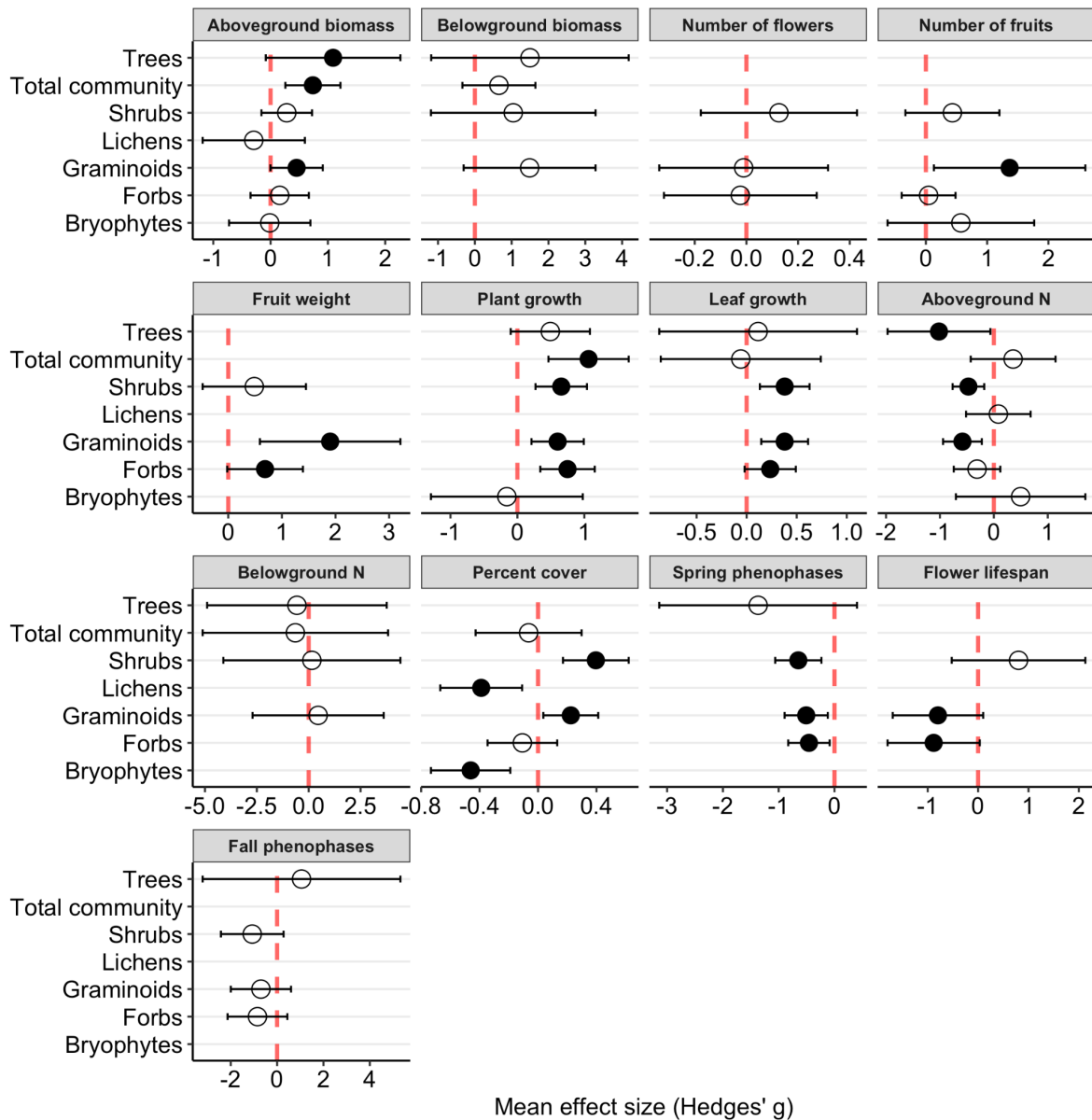


Figure 3.5. The effect of plant functional group on mean Hedges' g effect sizes for each plant trait and community property. Filled points represent effect sizes different or nearly different from 0. Sample sizes can be found in Table S3.13. Mean values are estimates from the mixed-effects model which accounts for species, site, and publication number. Points and error bars represent mean $\pm$ 95% confidence intervals.

Non-native species measurements were uncommon compared to native species measurements (Table S3.15), therefore we limited our results to the traits with a sample size of $n \geq 10$ for both native and non-native species. Native and non-native species showed similar responses to warming for leaf growth (Native: Hedges' $g = 0.33$, $z_2 = 3.82$, $p < 0.001$; Non-

native: Hedges' $g = 0.35$, $z_2 = 2.31$, $p = 0.02$) and spring phenology (Native: Hedges' $g = -0.56$, $z_2 = -3.14$, $p = 0.002$; Non-native: Hedges' $g = -0.53$, $z_2 = -2.55$, $p = 0.01$; Fig. S3.11). For aboveground biomass, native plants were positively affected by warming (Hedges' $g = 0.39$, $z_2 = 2.06$, $p = 0.04$), whereas non-native plants had no response (Hedges' $g = 0.07$, $z_2 = 0.25$, $p = 0.80$; Fig. S3.11). We found differences between native and non-native species for other traits and community properties (Table S3.15), but as stated above, sample sizes were too low for non-native species to allow for meaningful statistics (e.g., aboveground N content had $n = 100$ for native, and $n = 5$ for non-native; Table S3.15). The Holm-corrected comparisons demonstrated differences between native and non-native species for belowground biomass, fruit number, and fruit weight (Table S3.16), however these comparisons contained $n < 10$ non-native measurements.

DISCUSSION

Across 126 studies around the world, we found that some response variables were negatively affected by warming, such as aboveground N content, while other variables, such as plant growth, experienced a positive effect from warming. These results were unsurprising, as the traits and properties measured in this meta-analysis are unique and produced through different processes (e.g., nitrogen content in plants versus biomass production). Consequently, it is logical for a stressor to differentially affect these traits and properties. A variety of environmental, experimental, and plant-level contexts explained these responses to warming, including latitude, the timing of warming, the amount warmed, the length of the warming experiment, and plant functional group.

In terms of environmental contexts, latitude explains much of the variation in some trait and community property responses to warming across studies. As latitude increases, the effect of warming becomes stronger. Depending on the trait type, warming either has a more positive effect at higher latitudes (e.g., number of flowers, number of fruits, and fruit weight), or a more negative effect (e.g., spring phenophases). This demonstrates that plants at higher latitudes may show a more pronounced warming response than plants at lower latitudes. This finding could be attributed to the fact that as climate variability increases, plasticity may also increase (Anderson & Song, 2020). Plants that reside in regions that experience greater variations in temperature, such as plants at higher latitudes, may have stronger thermal tolerances and therefore greater plasticity compared to plants that experience less variation in temperature (Ghalambor et al.,

2006; Janzen, 1967). Therefore, due to greater temperature variability at high latitudes, plants residing in those areas could have greater phenotypic plasticity, and accordingly, more pronounced responses to warming.

Interestingly, many of the traits that experienced an effect of latitude were traits related to reproduction (number of flowers, number of fruits, and fruit weight), demonstrating that reproductive traits may be more susceptible to latitudinal gradient effects than other traits. Unfortunately, there is a strong Northern hemisphere bias in our dataset, which may limit some of our understanding of climate effects across a broad range of latitudes (Hansen & Cramer, 2015).

Plant growth and percent cover demonstrated a more negative effect of warming as species' distances from their northern range edge increased. This shows that species closer to their northern range edge experienced a more positive effect of warming in terms of increased plant growth and percent cover. In contrast, species further away from the range edge experienced lessened or potentially more negative effects of warming (i.e., decreased plant growth and percent cover). Similar to our results for latitude, this effect may also be due to increased climate variability leading to increased plasticity for plants that reside farther north (Ghalambor et al., 2006; Janzen, 1967). However, more research is necessary to uncover how plant traits and community properties may relate to species range shifts and edge expansion with further climate warming. Our use of GBIF and BIEN occurrence records also may not have captured the true northernmost extent, and therefore the leading edge, for some species.

The timing of warming, which is an experimental context, also plays a large role in some plant trait responses to warming. For example, warming only affected aboveground biomass, belowground biomass, fruit weight, and aboveground N content when warming was year-round (Fig. 3.4). In contrast, warming only affected fruit number and fall phenophases when warming was seasonal. The results for belowground biomass and fruit number may not be as meaningful due to low sample sizes with seasonal experiments ($n = 2$ and $n = 9$), compared with larger sample sizes for year-round experiments ($n = 42$ and $n = 25$) (Table S3.9). Interestingly, we also see that fall phenophases have a negative effect size when warmed seasonally, but a slightly positive effect size when warmed year-round. Most climate studies find a delay in fall phenology when plants are warmed (Collins et al., 2021; Peñuelas & Filella, 2001; Walther et al., 2002), shown by a positive effect size in this study. Climate change projections show that winter

warming will be significant (Kreyling et al., 2019), therefore year-round warming experiments may more accurately reflect the effects of climate warming.

Other contexts associated with experimental design, such as the amount warmed by the experiment and the length of the study, affected a few traits and properties. Belowground N content decreased as the amount warmed by the experiment increased; however, the sample size for belowground N in this analysis was somewhat low ($n = 7$; Fig. S3.9). We were surprised to find that no other traits or properties were affected by the amount warmed by the experiment, as the amount warmed ranged from 0.10-4.60 °C. This finding demonstrates that plant responses to warming may be similar across a range of temperatures. On the other hand, certain species or species types may exhibit more pronounced trait changes due to changes in the amount warmed by the experiment, which this multi-species analysis does not capture. The plants in these experiments may have also reached the extent of their plastic capabilities, meaning that even if temperatures were to increase further, a trait may not continue to change if factors in the environment limit its plasticity (Valladares et al., 2007). Furthermore, at extreme temperatures, plants may be limited in their ability to plastically respond due to high amounts of stress (Valladares et al., 2007). However, natural anthropogenic climate change is often associated with other abiotic and biotic changes, such as changes in precipitation regimes (IPCC, 2021) or biotic interactions (Zarnetske et al., 2012). Therefore, increased temperatures coupled with other changes are likely to produce novel plant responses that may not be seen with temperature increases alone (Xu et al., 2013; Young et al., In Review).

In terms of the length of the experiment, we found that long-term experiments led to less pronounced advancement of spring phenology and had increased flower lifespans when compared to short-term experiments (Fig. S3.10). Longer experiments also demonstrated a decreased warming effect on leaf growth and fruit number. Over time, warming stress may not have as strong of an effect on a plant's phenotype if the plastic response is reversible (Kristensen et al., 2020). Plastic responses may be immediate when plants experience novel, rapid stress (Franks et al., 2014), but the effect may lessen over time as the plant(s) adjust to a new regime.

Finally, in terms of plant-level characteristics such as growth form and native status, the results varied based on the trait or property measured. Although there were similar sample sizes in this meta-analysis for graminoids, forbs, and shrubs, graminoids most often demonstrated a warming response (Fig. S3.12, Table S3.13). We found some contrasting results between non-

vascular (bryophytes and lichens) and vascular growth forms, with non-vascular species often being more negatively affected by warming (e.g., decreased percent cover; Fig. 3.5). This finding corroborates other research on this topic (Elmendorf et al., 2012), however, non-vascular species had relatively small sample sizes (ranging from $n = 39$ to 46) compared to other growth forms (graminoids, forbs, shrubs, etc.; ranging from $n = 327$ to 338; Fig. S3.12). Our analyses comparing native and non-native species were hindered by low representation of non-native species in warming studies (Table S3.15). Contrasting responses between plant types may explain why some traits do not exhibit an overall effect of warming. For example, the positive effect of warming on vascular plant percent cover and the negative effect of warming on non-vascular plant percent cover may lead to no change in total community percent cover (Fig. 3.2). These variations in plant responses to warming highlight the importance of considering differences between plant types (e.g., growth forms, provenance, etc.) in climate change studies.

Conclusions

This meta-analysis demonstrates the nuanced responses of plant traits and community properties to climate warming. However, we find some clear relationships that increase understanding of climate warming impacts on plants around the world, and guide future experiments. First, researchers conducting warming experiments should carefully consider their experimental design in the context of interpretation of their results. Seasonal warming studies may not fully capture trait responses to climate warming due to the lack of winter warming in those studies. We recognize that seasonal warming studies may be the only option in locations that receive heavy snowfall, therefore researchers should recognize that the plant responses observed in summer-only warming experiments may be weaker than responses to year-round warming (Sanders-DeMott & Templer, 2017). This finding demonstrates how experimental warming studies may be underpredicting the severity to which climate warming affects plants, which has been corroborated in studies such as Wolkovich et. al. (2012).

Second, more studies are needed that investigate warming effects on different plant types, such as native vs. non-native or vascular vs. non-vascular species. Our study highlights the lack of data on non-native and non-vascular species responses to warming compared to their counterparts (Fig. S3.12, Table S3.15). Studies have demonstrated that under future climate regimes, non-native species may benefit over natives (Zettlemoyer et al., 2019), but more research is needed on this topic to determine specific trait responses that may be beneficial for

population persistence and invasion success. Furthermore, by including varying species types in climate studies, we could gain a stronger understanding of which species may persist or perish under future climate regimes.

Third, researchers should recognize how multiple contexts in the environment may affect the results seen in their warming experiments. For example, results of warming studies at higher latitudes may not be able to be replicated at lower latitudes, due to differences in environmental contexts. It is difficult to generalize plant response to warming due to the many nuanced factors that play a role in determining how traits and properties respond to climate stress. However, warming experiments are still necessary for us to understand the mechanisms that underlie plant responses to climate change. Many efforts are being made to synthesize similar warming experiments across the globe in order to parse apart these plant responses to warming, such as the WaRM Network (Prager et al., 2022). Long-term studies are also essential in aiding our understanding of plant community change over time; networks such as the Long-Term Ecological Research network contain valuable information on community changes over long time scales (Cusser et al., 2021; Knapp et al., 2012). Coordinated experiments such as these are an effective method for mechanistically understanding how varying contexts contribute to warming responses.

In conclusion, warming experiments are necessary for us to be able to test causal relationships between plants and climate. More studies across multiple contexts, including underrepresented regions (e.g., the Southern hemisphere), varying habitat types, and multiple species types would improve our understanding of how plants and communities may respond to climate stress and what contexts are important for defining these responses.

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APPENDIX

Table S3.1. List of the 126 passive in-situ warming studies that data were collected from for this meta-analysis.

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Table S3.2. Plant trait and community property groups and the finer-scale traits and properties contained within those groups. The definition(s) associated with each trait were determined using the information given in the studies that collected that trait. The broader groupings were used in analyses as our response variables.

Group	Contains	Definition(s)
Spring phenophases	Leaf appearance	Date of appearance of leaf or leaf bud
	Leaf expansion	Date of appearance of fully expanded leaf
	Emergence	Date of emergence of vegetation
	Bud break	Date of appearance of flower buds or catkin reaches 1mm
	Flowering	Date of appearance of first open flower, anthers, onset of the stigma, or median date of flowering duration
	Stem elongation	Date of occurrence of stem elongation
Fall phenophases	Senescence	Date of first leaf senescence, total coloration of leaves, or median date of leaf coloration
	Seed set	Date of first stigma withered, ovaries begin to swell, or capsule/seed/fruit maturation date
	Abscission	Date of last flower petal shed or flowers close
Growth	Height	Height of vegetation from ground level to top of plant/canopy, vertical length of most recent growth, or total growth per year
	Shoot length	Total length of plant shoot or length of most recent plant shoot
Leaf growth	SLA	Specific leaf area
	Leaf area	Average area of randomly selected leaves
	Leaf width	Average width of randomly selected leaves
	Leaf length	Average length of randomly selected leaves or leaf elongation rate
Aboveground nitrogen		Nitrogen concentration of aboveground plant parts

Table S3.2 (cont'd)

Belowground nitrogen	Nitrogen concentration of belowground plant parts
Percent cover	Percent of ground covered by plants (0-100) using visual estimates, point-intercept method, grid method, or using image analysis software
Aboveground biomass	Biomass of aboveground plant parts through harvesting plant material, point-frame method, or NDVI
Belowground biomass	Biomass of belowground plant parts through harvesting plant material
Total biomass	Biomass of the total plant (above and belowground) through harvesting plant material
Leaf lifespan	Time interval between leaf budding and leaf senescence
Flower lifespan	Time interval between flower bloom and flower abscission, seed maturation, seed dispersal, or onset of pollen release
Preflower length	Time interval between snowmelt and first flower
Number of flowers	Number of flowers, flower buds, inflorescences, flowering tillers, or catkins
Flower weight	Biomass of flowers or inflorescences
Number of fruits	Number of mature fruits, capsules, seeds, bulbils, flowers with set seeds, or sporophytes
Fruit weight	Biomass of seeds, bulbils, mature fruits, or achenes

Table S3.3. Functional groups and finer-scale groups contained within each grouping. The broader functional groups were used in analyses. “Total community” represents measurements that were conducted at the plant community level, and did not contain finer-scale measurements (i.e., measurements for specific functional types or species).

Functional groups	Contains
Graminoids	Graminoids
Shrubs	Deciduous shrubs Evergreen shrubs
Forbs	Forbs Leguminous forbs
Trees	Deciduous trees Evergreen trees
Lichens	Lichens
Bryophytes	Bryophytes
Pteridophytes	Pteridophytes
Total community	Total plant community

Table S3.4. Meta-analytic multivariate model outputs for the effect of warming on each response variable. Model structure: `rma.mv(yi, vi, mods = ~Var_type_broad-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 169)	0.2528	0.0694	3.6412	0.0003	0.1167	0.3889
Belowground biomass (n = 44)	0.6033	0.1618	3.7294	0.0002	0.2862	0.9203
Flower number (n = 79)	-0.0763	0.0831	-0.9181	0.3586	-0.2391	0.0866
Fruit number (n = 34)	-0.0982	0.0942	-1.0422	0.2973	-0.2829	0.0865
Fruit weight (n = 27)	0.5776	0.1430	4.0400	<0.0001	0.2974	0.8578
Growth (n = 135)	0.6488	0.0647	10.0246	<0.0001	0.5220	0.7757
Leaf growth (n = 140)	0.5369	0.0652	8.2374	<0.0001	0.4091	0.6646
Aboveground nitrogen (n = 131)	-0.4093	0.0838	-4.8837	<0.0001	-0.5735	-0.2450
Belowground nitrogen (n = 12)	-0.1082	0.2780	-0.3893	0.6971	-0.6531	0.4367
Percent cover (n = 193)	0.1044	0.0740	1.4109	0.1583	-0.0406	0.2495
Spring phenophases (n = 186)	-0.1223	0.0696	-1.7582	0.0787	-0.2586	0.0140
Fall phenophases (n = 77)	-0.0373	0.0798	-0.4676	0.6401	-0.1936	0.1190
Flower lifespan (n = 37)	0.1364	0.0881	1.5484	0.1215	-0.0363	0.3091

Test of Moderators: $Q_M = 389.6701$, $df = 13$, $p < 0.0001$

Test of Residual Heterogeneity: $Q_E = 4058.1032$, $df = 1251$, $p < 0.0001$

Table S3.5. Meta-analytic multivariate model outputs testing the influence of latitude on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Latitude, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 169)	-0.0093	0.0110	-0.843	0.3990	-0.0308	0.0123
Belowground biomass (n = 44)	-0.0420	0.0363	-1.156	0.2478	-0.1132	0.0292
Flower number (n = 79)	0.0111	0.0066	1.6831	0.0924	-0.0018	0.0239
Fruit number (n = 34)	0.0261	0.0131	1.9891	0.0467	0.0004	0.0518
Fruit weight (n = 27)	0.0527	0.0224	2.3572	0.0184	0.0089	0.0965
Growth (n = 135)	0.0022	0.0091	0.2418	0.8089	-0.0157	0.0201
Leaf growth (n = 140)	-0.0049	0.0047	-1.040	0.2985	-0.0142	0.0043
Aboveground nitrogen (n = 131)	0.0052	0.0070	0.7421	0.4580	-0.0085	0.0189
Belowground nitrogen (n = 12)	0.0612	0.0184	3.3235	0.0009	0.0251	0.0973
Percent cover (n = 193)	0.0004	0.0030	0.1161	0.9076	-0.0056	0.0063
Spring phenophases (n = 186)	-0.0209	0.0115	-1.814	0.0698	-0.0435	0.0017
Fall phenophases (n = 77)	-0.0544	0.0327	-1.663	0.0964	-0.1184	0.0097
Flower lifespan (n = 37)	0.0035	0.0290	0.1208	0.9039	-0.0533	0.0603

Table S3.6. Meta-analytic multivariate model outputs testing the influence of mean annual precipitation on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Mean_annual_precip, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 169)	0.0024	0.0044	0.5480	0.5837	-0.0062	0.0110
Belowground biomass (n = 44)	0.0121	0.0162	0.7494	0.4536	-0.0196	0.0438
Flower number (n = 79)	0.0037	0.0027	1.3757	0.1689	-0.0016	0.0091
Fruit number (n = 34)	0.0053	0.0058	0.9182	0.3585	-0.0060	0.0166
Fruit weight (n = 27)	0.0083	0.0083	1.0034	0.3157	-0.0080	0.0246
Growth (n = 135)	0.0015	0.0036	0.4040	0.6862	-0.0057	0.0086
Leaf growth (n = 140)	0.0013	0.0021	0.6193	0.5357	-0.0028	0.0054
Aboveground nitrogen (n = 131)	-0.0005	0.0031	-0.1702	0.8649	-0.0066	0.0056
Belowground nitrogen (n = 12)	-0.0041	0.0155	-0.2642	0.7916	-0.0345	0.0263
Percent cover (n = 179)	0.0015	0.0014	1.0738	0.2829	-0.0013	0.0044
Spring phenophases (n = 186)	0.0031	0.0064	0.4854	0.6274	-0.0095	0.0157
Fall phenophases (n = 77)	0.0161	0.0196	0.8211	0.4116	-0.0223	0.0545
Flower lifespan (n = 37)	0.0693	0.0316	2.1920	0.0284	0.0073	0.1313

Table S3.7. Meta-analytic multivariate model outputs testing the influence of species distance from its northern range edge on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Lat_difference, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 96)	0.0021	0.0130	0.1646	0.8693	-0.0234	0.0277
Belowground biomass (n = 14)	-0.0013	0.0728	-0.018	0.9860	-0.1440	0.1414
Flower number (n = 79)	0.0076	0.0077	0.9943	0.3201	-0.0074	0.0227
Fruit number (n = 29)	0.0028	0.0111	0.2558	0.7981	-0.0189	0.0245
Fruit weight (n = 27)	0.0164	0.0432	0.3789	0.7048	-0.0684	0.1011
Growth (n = 108)	-0.0137	0.0065	-2.114	0.0345	-0.0264	-0.0010
Leaf growth (n = 118)	-0.0017	0.0064	-0.263	0.7923	-0.0142	0.0108
Aboveground nitrogen (n = 112)	0.0015	0.0094	0.1625	0.8709	-0.0168	0.0199
Belowground nitrogen (n = 11)	-0.0559	0.0443	-1.263	0.2068	-0.1427	0.0309
Percent cover (n = 57)	-0.0363	0.0152	-2.396	0.0166	-0.0661	-0.0066
Spring phenophases (n = 138)	0.0099	0.0060	1.6570	0.0975	-0.0018	0.0217
Fall phenophases (n = 50)	-0.0035	0.0087	-0.401	0.6885	-0.0206	0.0136
Flower lifespan (n = 35)	0.0099	0.0112	0.8818	0.3779	-0.0121	0.0318

Table S3.8. Meta-analytic multivariate model outputs testing the influence of mean annual temperature on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Mean_annual_temp, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 169)	0.0198	0.0216	0.9145	0.3605	-0.0226	0.0621
Belowground biomass (n = 44)	-0.0223	0.1243	-0.179	0.8579	-0.2659	0.2214
Flower number (n = 79)	0.0076	0.0205	0.3691	0.7120	-0.0326	0.0477
Fruit number (n = 34)	-0.0351	0.0470	-0.746	0.4554	-0.1273	0.0571
Fruit weight (n = 27)	-0.0441	0.0636	-0.693	0.4880	-0.1687	0.0805
Growth (n = 135)	-0.0034	0.0185	-0.185	0.8530	-0.0396	0.0328
Leaf growth (n = 140)	0.0041	0.0098	0.4194	0.6749	-0.0152	0.0234
Aboveground nitrogen (n = 131)	-0.0016	0.0144	-0.109	0.9134	-0.0297	0.0266
Belowground nitrogen (n = 12)	-0.1045	0.0734	-1.424	0.1544	-0.2483	0.0393
Percent cover (n = 179)	-0.0020	0.0068	-0.299	0.7644	-0.0154	0.0113
Spring phenophases (n = 186)	-0.0021	0.0235	-0.091	0.9273	-0.0482	0.0439
Fall phenophases (n = 77)	0.0451	0.0618	0.7293	0.4658	-0.0761	0.1663
Flower lifespan (n = 37)	0.0004	0.0780	0.0056	0.9955	-0.1524	0.1533

Table S3.9. Meta-analytic multivariate model outputs testing the influence of the timing of warming (year-round or seasonal) on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Year_round_warm-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Timing of warming	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass	Year-round (n = 120)	0.6537	0.1988	3.2885	0.0010	0.2641	1.0433
	Seasonal (n = 49)	-0.0072	0.3230	-0.0223	0.9822	-0.6403	0.6259
Belowground biomass	Year-round (n = 42)	1.0570	0.3844	2.7499	0.0060	0.3036	1.8104
	Seasonal (n = 2)	-0.2839	1.0588	-0.2681	0.7886	-2.3590	1.7913
Flower number	Year-round (n = 49)	-0.0315	0.1214	-0.2596	0.7952	-0.2695	0.2064
	Seasonal (n = 30)	0.1012	0.1325	0.7637	0.4450	-0.1586	0.3610
Fruit number	Year-round (n = 25)	0.1273	0.2225	0.5723	0.5671	-0.3087	0.5634
	Seasonal (n = 9)	0.6338	0.3570	1.7752	0.0759	-0.0659	1.3335
Fruit weight	Year-round (n = 24)	0.9447	0.3964	2.3833	0.0172	0.1678	1.7215
	Seasonal (n = 3)	0.1372	0.8999	0.1525	0.8788	-1.6266	1.9010
Growth	Year-round (n = 77)	0.6375	0.1553	4.1041	<0.0001	0.3330	0.9419
	Seasonal (n = 58)	0.7502	0.2126	3.5287	0.0004	0.3335	1.1668
Leaf growth	Year-round (n = 108)	0.3066	0.0891	3.4400	0.0006	0.1319	0.4813
	Seasonal (n = 32)	0.3742	0.1844	2.0289	0.0425	0.0127	0.7356
Aboveground nitrogen	Year-round (n = 105)	-0.5178	0.1372	-3.7806	0.0002	-0.7876	-0.249
	Seasonal (n = 26)	-0.0867	0.2225	-0.3898	0.6967	-0.5227	0.3493
Belowground nitrogen	Year-round (n = 11)	0.0654	0.6041	0.1082	0.9138	-1.1187	1.2494
	Seasonal (n = 1)	-0.6438	1.3042	-0.4936	0.6216	-3.2000	1.9124
Percent cover	Year-round (n = 102)	0.0020	0.0831	0.0245	0.9804	-0.1609	0.1650
	Seasonal (n = 91)	0.0227	0.0749	0.3027	0.7621	-0.1242	0.1696

Table S3.9 (cont'd)

Spring phenophases	Year-round (n = 91)	-0.6886	0.2452	-2.8079	0.0050	-1.1693	-0.208
	Seasonal (n = 95)	-0.4216	0.2485	-1.6966	0.0898	-0.9085	0.0654
Fall phenophases	Year-round (n = 43)	0.3340	0.7735	0.4319	0.6658	-1.1820	1.8501
	Seasonal (n = 34)	-1.7047	0.7946	-2.1453	0.0319	-3.2621	-0.147
Flower lifespan	Year-round (n = 37)				NA		
	Seasonal (n = 0)				NA		

Table S3.10. Holm-corrected comparisons for the effect of the timing of warming (year-round vs. seasonal) on each plant trait. Sample sizes for each measurement can be found in Table S3.9.

Variable	Timing of warming	Estimate	SE	Z-value	P-value
Aboveground biomass	Year-round - Seasonal	0.6609	0.3793	1.742	0.081
Belowground biomass	Year-round - Seasonal	1.341	1.126	1.19	0.234
Flower number	Year-round - Seasonal	-0.1327	0.1797	-0.738	0.460
Fruit number	Year-round - Seasonal	-0.5064	0.4207	-1.204	0.229
Fruit weight	Year-round - Seasonal	0.8075	0.9833	0.821	0.412
Growth	Year-round - Seasonal	-0.1127	0.2223	-0.507	0.612
Leaf growth	Year-round - Seasonal	-0.0676	0.2048	-0.33	0.741
Aboveground nitrogen	Year-round - Seasonal	-0.4320	0.2614	-1.653	0.098
Belowground nitrogen	Year-round - Seasonal	0.7092	1.4373	0.493	0.622
Percent cover	Year-round - Seasonal	-0.0206	0.1119	-0.184	0.854
Spring phenophases	Year-round - Seasonal	-0.2671	0.3261	-0.819	0.413
Fall phenophases	Year-round - Seasonal	2.039	1.109	1.838	0.066
Flower lifespan	Year-round - Seasonal				NA

Table S3.11. Meta-analytic multivariate model outputs testing the influence of amount warmed on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Amount_warmed_C, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 151)	0.1254	0.1738	0.7215	0.4706	-0.2152	0.4660
Belowground biomass (n = 41)	0.0317	0.2638	0.1200	0.9044	-0.4854	0.5488
Flower number (n = 78)	-0.1084	0.0742	-1.460	0.1443	-0.2538	0.0371
Fruit number (n = 31)	0.1043	0.2200	0.4742	0.6353	-0.3268	0.5355
Fruit weight (n = 22)	0.6616	0.4952	1.3360	0.1816	-0.3090	1.6322
Growth (n = 108)	-0.0966	0.1193	-0.810	0.4178	-0.3304	0.1371
Leaf growth (n = 131)	0.0723	0.0930	0.7773	0.4370	-0.1100	0.2547
Aboveground nitrogen (n = 110)	0.0402	0.1260	0.3193	0.7495	-0.2068	0.2872
Belowground nitrogen (n = 11)	-0.9786	0.4976	-1.967	0.0492	-1.9539	-0.0033
Percent cover (n = 139)	0.0071	0.0718	0.0984	0.9216	-0.1337	0.1478
Spring phenophases (n = 179)	-0.1372	0.1448	-0.947	0.3434	-0.4210	0.1466
Fall phenophases (n = 70)	-0.4544	0.6106	-0.744	0.4568	-1.6512	0.7424
Flower lifespan (n = 32)	0.1560	0.1904	0.8193	0.4126	-0.2172	0.5292

Table S3.12. Meta-analytic multivariate model outputs testing the influence of number of years warmed on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Years_warmed, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass (n = 169)	-0.0163	0.0423	-0.386	0.6992	-0.0992	0.0666
Belowground biomass (n = 44)	-0.0503	0.3001	-0.168	0.8668	-0.6385	0.5378
Flower number (n = 79)	-0.0096	0.0519	-0.185	0.8534	-0.1112	0.0921
Fruit number (n = 34)	-0.2346	0.1201	-1.954	0.0507	-0.4699	0.0008
Fruit weight (n = 27)	-0.0079	0.1120	-0.071	0.9438	-0.2274	0.2116
Growth (n = 135)	-0.0151	0.0298	-0.505	0.6133	-0.0734	0.0433
Leaf growth (n = 140)	-0.0276	0.0151	-1.829	0.0674	-0.0572	0.0020
Aboveground nitrogen (n = 131)	0.0276	0.0220	1.2512	0.2109	-0.0156	0.0708
Belowground nitrogen (n = 12)	0.1970	0.3972	0.4961	0.6199	-0.5815	0.9756
Percent cover (n = 193)	-0.0065	0.0097	-0.677	0.4987	-0.0255	0.0124
Spring phenophases (n = 186)	0.1268	0.0716	1.7712	0.0765	-0.0135	0.2670
Fall phenophases (n = 77)	0.0319	0.1993	0.1600	0.8729	-0.3587	0.4225
Flower lifespan (n = 37)	0.5711	0.2832	2.0167	0.0437	0.0161	1.1261

Table S3.13. Meta-analytic multivariate model outputs testing the influence of plant functional type on the effect of warming for each response variable. “Total” represents measurements made on the total plant community. Model structure: `rma.mv(yi, vi, mods = ~Func_group_broad-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Functional type	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass	Bryophyte (n = 9)	-0.0150	0.3621	-0.0413	0.9670	-0.7247	0.6948
	Forb (n = 19)	0.1589	0.2597	0.6120	0.5405	-0.3501	0.6680
	Graminoid (n = 30)	0.4540	0.2329	1.9498	0.0512	-0.0024	0.9104
	Lichen (n = 3)	-0.2938	0.4550	-0.6459	0.5184	-1.1856	0.5979
	Pteridophyte (n = 1)	1.1508	1.0224	1.1256	0.2603	-0.8531	3.1547
	Shrub (n = 55)	0.2817	0.2253	1.2504	0.2111	-0.1599	0.7234
	Tree (n = 18)	1.0902	0.5993	1.8190	0.0689	-0.0845	2.2649
	Total (n = 34)	0.7380	0.2451	3.0106	0.0026	0.2576	1.2185
Belowground biomass	Graminoid (n = 8)	1.4871	0.9137	1.6276	0.1036	-0.3037	3.2778
	Shrub (n = 6)	1.0431	1.1405	0.9146	0.3604	-1.1922	3.2785
	Tree (n = 4)	1.4969	1.3685	1.0938	0.2740	-1.1853	4.1790
	Total (n = 26)	0.6535	0.5060	1.2916	0.1965	-0.3382	1.6451
Flower number	Forb (n = 27)	-0.0236	0.1508	-0.1567	0.8755	-0.3192	0.2719
	Graminoid (n = 32)	-0.0107	0.1667	-0.0643	0.9487	-0.3374	0.3159
	Shrub (n = 20)	0.1258	0.1542	0.8159	0.4145	-0.1764	0.4281
Fruit number	Bryophyte (n = 5)	0.5710	0.6103	0.9356	0.3495	-0.6252	1.7673
	Forb (n = 19)	0.0445	0.2241	0.1984	0.8427	-0.3948	0.4837
	Graminoid (n = 3)	1.3665	0.6304	2.1676	0.0302	0.1309	2.6020
	Shrub (n = 7)	0.4327	0.3911	1.1064	0.2686	-0.3338	1.1992
Fruit weight	Forb (n = 14)	0.6859	0.3604	1.9029	0.0571	-0.0206	1.3923
	Graminoid (n = 3)	1.8999	0.6684	2.8426	0.0045	0.5899	3.2099
	Shrub (n = 10)	0.4854	0.4915	0.9874	0.3234	-0.4780	1.4488
Growth	Bryophyte (n = 3)	-0.1576	0.5786	-0.2723	0.7854	-1.2917	0.9766
	Forb (n = 19)	0.7488	0.2076	3.6074	0.0003	0.3419	1.1556
	Graminoid (n = 32)	0.6011	0.1994	3.0148	0.0026	0.2103	0.9919
	Shrub (n = 38)	0.6550	0.1961	3.3409	0.0008	0.2707	1.0392
	Tree (n = 29)	0.4919	0.3021	1.6284	0.1034	-0.1001	1.0839
	Total (n = 14)	1.0637	0.3059	3.4772	0.0005	0.4641	1.6632

Table S3.13 (cont'd)

Leaf growth	Forb (n = 31)	0.2353	0.1306	1.8014	0.0716	-0.0207	0.4913
	Graminoid (n = 57)	0.3797	0.1193	3.1820	0.0015	0.1458	0.6137
	Shrub (n = 48)	0.3802	0.1265	3.0050	0.0027	0.1322	0.6282
	Tree (n = 1)	0.1148	0.5040	0.2279	0.8198	-0.8730	1.1026
	Total (n = 3)	-0.0586	0.4078	-0.1436	0.8858	-0.8579	0.7407
Aboveground nitrogen	Bryophyte (n = 2)	0.4963	0.6124	0.8103	0.4178	-0.7041	1.6966
	Forb (n = 15)	-0.3122	0.2202	-1.4178	0.1562	-0.7437	0.1194
	Graminoid (n = 29)	-0.5830	0.1833	-3.1799	0.0015	-0.9424	-0.224
	Lichen (n = 11)	0.0831	0.3056	0.2719	0.7857	-0.5159	0.6820
	Shrub (n = 59)	-0.4720	0.1495	-3.1563	0.0016	-0.7651	-0.179
	Tree (n = 8)	-1.0180	0.4865	-2.0926	0.0354	-1.9715	-0.065
	Total (n = 5)	0.3571	0.4010	0.8905	0.3732	-0.4289	1.1432
Belowground nitrogen	Graminoid (n = 3)	0.4537	1.6125	0.2814	0.7784	-2.7067	3.6141
	Shrub (n = 4)	0.1525	2.1766	0.0700	0.9442	-4.1137	4.4186
	Tree (n = 4)	-0.4578	2.2081	-0.2571	0.7971	-4.8956	3.7600
	Total (n = 1)	-0.6438	2.2793	-0.2825	0.7776	-5.1112	3.8236
Percent cover	Bryophyte (n = 27)	-0.4610	0.1382	-3.3350	0.0009	-0.7320	-0.190
	Forb (n = 31)	-0.1072	0.1216	-0.8819	0.3379	-0.3455	0.1311
	Graminoid (n = 55)	0.2241	0.0958	2.3382	0.0194	0.0362	0.4119
	Lichen (n = 25)	-0.3890	0.1429	-2.7220	0.0065	-0.6692	-0.109
	Pteridophyte (n = 3)	0.5014	0.4315	1.1619	0.2453	-0.3444	1.3471
	Shrub (n = 32)	0.3956	0.1147	3.4492	0.0006	0.1708	0.6205
	Total (n = 18)	-0.0646	0.1851	-0.3489	0.7272	-0.4273	0.2981
Spring phenophases	Forb (n = 99)	-0.4575	0.1894	-2.4159	0.0157	-0.8287	-0.086
	Graminoid (n = 47)	-0.5069	0.1975	-2.5664	0.0103	-0.8940	-0.119
	Pteridophyte (n = 1)	-0.0865	0.5145	-0.1682	0.8665	-1.0949	0.9219
	Shrub (n = 35)	-0.6483	0.2112	-3.0699	0.0021	-1.0622	-0.234
	Tree (n = 2)	-1.3683	0.9042	-1.5132	0.1302	-3.1405	0.4040
Fall phenophases	Forb (n = 43)	-0.8473	0.6578	-1.2882	0.1977	-2.1365	0.4419
	Graminoid (n = 23)	-0.6985	0.6631	-1.0533	0.2922	-1.9981	0.6012
	Shrub (n = 8)	-1.0726	0.6898	-1.5550	0.1199	-2.4245	0.2793
	Tree (n = 2)	1.0533	2.1763	0.4840	0.6284	-3.2123	5.3189
Flower lifespan	Forb (n = 16)	-0.8822	0.4669	-1.8895	0.0588	-1.7973	0.0329
	Graminoid (n = 16)	-0.7976	0.4581	-1.7411	0.0817	-1.6954	0.1003
	Shrub (n = 5)	0.8026	0.6766	1.1861	0.2356	-0.5236	2.1287

Table S3.14. Holm-corrected comparisons for the effect of the plant functional type on each plant trait. Sample sizes for each measurement can be found in Table S3.13.

Variable	Plant functional type	Estimate	SE	Z-value	P-value
Aboveground biomass	Forb - Bryophyte	0.1739	0.3901	0.446	1.00
	Graminoid - Bryophyte	0.4690	0.3700	1.268	1.00
	Lichen - Bryophyte	-0.2789	0.4950	-0.563	1.00
	Pteridophyte - Bryophyte	1.1658	1.0633	1.096	1.00
	Shrub - Bryophyte	0.2967	0.3588	0.827	1.00
	Total community - Bryophyte	0.7530	0.3938	1.912	1.00
	Tree - Bryophyte	1.1052	0.7002	1.578	1.00
	Graminoid - Forb	0.2951	0.2318	1.273	1.00
	Lichen - Forb	-0.4528	0.4686	-0.966	1.00
	Pteridophyte - Forb	0.9919	1.0133	0.979	1.00
	Shrub - Forb	0.1228	0.2472	0.497	1.00
	Total community - Forb	0.5791	0.3103	1.866	1.00
	Tree - Forb	0.9313	0.6532	1.426	1.00
	Lichen - Graminoid	-0.7479	0.4501	-1.662	1.00
	Pteridophyte - Graminoid	0.6968	1.0040	0.694	1.00
	Shrub - Graminoid	-0.1723	0.2108	-0.817	1.00
	Total community - Graminoid	0.2840	0.2853	0.996	1.00
	Tree - Graminoid	0.6362	0.6430	0.989	1.00
	Pteridophyte - Lichen	1.4447	1.0942	1.320	1.00
	Shrub - Lichen	0.5756	0.4395	1.310	1.00
	Total community - Lichen	1.0319	0.4735	2.179	0.82
	Tree - Lichen	1.3841	0.7525	1.839	1.00
	Shrub - Pteridophyte	-0.8691	1.0193	-0.853	1.00
	Total community - Pteridophyte	-0.4128	1.0365	-0.398	1.00
	Tree - Pteridophyte	-0.0606	1.1851	-0.051	1.00
	Tree - Pteridophyte	0.4563	0.2822	1.617	1.00
	Total community - Shrub	0.8085	0.6403	1.263	1.00
	Tree - Shrub	0.3522	0.6475	0.544	1.00
	Tree - Total community				
Belowground biomass	Shrub - Graminoid	-0.4440	1.4062	-0.316	1.00
	Total community - Graminoid	-0.8336	1.0425	-0.800	1.00
	Tree - Graminoid	0.0098	1.6454	0.006	1.00
	Total community - Shrub	-0.3896	1.2435	-0.313	1.00
	Tree - Shrub	0.4537	1.7814	0.255	1.00
	Tree - Total Community	0.8434	1.4590	0.578	1.00
Flower number	Graminoid - Forb	0.0129	0.2131	0.061	1.00
	Shrub - Forb	0.1495	0.2119	0.706	1.00
	Shrub - Graminoid	0.1366	0.2228	0.613	1.00

Table S3.14 (cont'd)

Fruit number	Forb - Bryophyte	-0.5266	0.6502	-0.810	1.00
	Graminoid - Bryophyte	0.7954	0.8774	0.907	1.00
	Shrub - Bryophyte	-0.1383	0.7249	-0.191	1.00
	Graminoid - Forb	1.3220	0.6690	1.976	0.289
	Shrub - Forb	0.3882	0.3908	0.993	1.00
	Shrub - Graminoid	-0.9338	0.7419	-1.259	1.00
Fruit weight	Graminoid - Forb	1.2141	0.7014	1.731	0.167
	Shrub - Forb	-0.2005	0.4901	-0.409	0.682
	Shrub - Graminoid	-1.4146	0.6892	-2.052	0.120
Growth	Forb - Bryophyte	0.9063	0.5998	1.511	1.00
	Graminoid - Bryophyte	0.7587	0.5956	1.274	1.00
	Shrub - Bryophyte	0.8126	0.5877	1.383	1.00
	Total community - Bryophyte	1.2212	0.6520	1.873	0.916
	Tree - Bryophyte	0.6495	0.6527	0.995	1.00
	Graminoid - Forb	-0.1476	0.1655	-0.892	1.00
	Shrub - Forb	-0.0938	0.1767	-0.531	1.00
	Total community - Forb	0.3149	0.3568	0.883	1.00
	Tree - Forb	-0.2569	0.3665	-0.701	1.00
	Shrub - Graminoid	0.0539	0.1525	0.535	1.00
	Total community - Graminoid	0.4625	0.3463	1.335	1.00
	Tree - Graminoid	-0.1092	0.3619	-0.302	1.00
	Total community - Shrub	0.4087	0.3504	1.166	1.00
	Tree - Shrub	-0.1631	0.3601	-0.453	1.00
	Tree - Total community	-0.5718	0.4299	-1.330	1.00
Leaf growth	Graminoid - Forb	0.1444	0.1433	1.008	1.00
	Shrub - Forb	0.1445	0.1662	0.872	1.00
	Total community - Forb	-0.2939	0.4282	-0.686	1.00
	Tree - Forb	-0.1205	0.5206	-0.231	1.00
	Shrub - Graminoid	0.0005	0.1603	0.003	1.00
	Total community - Graminoid	-0.4383	0.4249	-1.032	1.00
	Tree - Graminoid	-0.2649	0.5179	-0.511	1.00
	Total community - Shrub	-0.4388	0.4270	-1.028	1.00
	Tree - Shrub	-0.2654	0.5196	-0.511	1.00
	Tree - Total community	0.1734	0.6483	0.267	1.00
Aboveground nitrogen	Forb - Bryophyte	-0.8084	0.6508	1.242	1.00
	Graminoid - Bryophyte	-1.0793	0.6393	-1.688	1.00
	Lichen - Bryophyte	-0.4132	0.6844	-0.604	1.00
	Shrub - Bryophyte	-0.9683	0.6304	-1.536	1.00
	Total community - Bryophyte	-0.1391	0.7321	-0.190	1.00
	Tree - Bryophyte	-1.5143	0.7821	-1.936	0.979
	Graminoid - Forb	-0.2709	0.2651	-1.0	1.00

Table S3.14 (cont'd)

Aboveground nitrogen	Lichen - Forb	0.3952	0.3368	1.174	1.00
	Shrub - Forb	-0.1598	0.2563	-0.624	1.00
	Total community - Forb	0.6693	0.4436	1.509	1.00
	Tree - Forb	-0.7059	0.5340	-1.322	1.00
	Lichen - Graminoid	0.6661	0.3421	1.947	0.979
	Shrub - Graminoid	0.1110	0.2284	0.486	1.00
	Total community - Graminoid	0.9402	0.4306	2.183	0.609
	Tree - Graminoid	-0.4350	0.5199	-0.837	1.00
	Shrub - Lichen	-0.5551	0.3304	-1.680	1.00
	Total community - Lichen	0.2741	0.4998	0.548	1.00
	Tree - Lichen	-1.1011	0.5745	-1.917	0.979
	Total community - Shrub	0.8291	0.4268	1.943	0.979
	Tree - Shrub	-0.5460	0.5090	-1.073	1.00
	Tree - Total community	-1.3752	0.6305	-2.181	0.609
Belowground nitrogen	Shrub - Graminoid	-0.3012	2.7089	-0.111	1.00
	Total community - Graminoid	-1.0975	2.7920	-0.393	1.00
	Tree - Graminoid	-1.0215	2.7342	-0.374	1.00
	Total community - Shrub	-0.7963	3.1517	-0.253	1.00
	Tree - Shrub	-0.7203	3.1006	-0.232	1.00
	Tree - Total community	0.0760	3.1735	0.024	1.00
Percent cover	Forb - Bryophyte	0.3538	0.1841	1.922	0.66
	Graminoid - Bryophyte	0.6851	0.1682	4.073	0.001
	Lichen - Bryophyte	0.0720	0.1988	0.362	1.00
	Pteridophyte - Bryophyte	0.9624	0.4531	2.124	0.52
	Shrub - Bryophyte	0.8567	0.1796	4.769	<0.001
	Total community - Bryophyte	0.3965	0.2310	1.716	0.95
	Graminoid - Forb	0.3313	0.1548	2.140	0.52
	Lichen - Forb	-0.2818	0.1876	-1.502	1.00
	Pteridophyte - Forb	0.6086	0.4483	1.358	1.00
	Shrub - Forb	0.5029	0.1672	3.008	0.045
	Total community - Forb	0.0427	0.2214	0.193	1.00
	Lichen - Graminoid	-0.6131	0.1721	-3.563	0.007
	Pteridophyte - Graminoid	0.2773	0.4420	0.627	1.00
	Shrub - Graminoid	0.1716	0.1495	1.148	1.00
	Total community - Graminoid	-0.2886	0.2084	-1.385	1.00
	Pteridophyte - Lichen	0.8904	0.4546	1.959	0.65
	Shrub - Lichen	0.7847	0.1833	4.282	<0.001
	Total community - Lichen	0.3245	0.2338	1.388	1.00
	Shrub - Pteridophyte	-0.1057	0.4465	-0.237	1.00
	Total community - Pteridophyte	-0.5659	0.4695	-1.205	1.00
	Total community - Shrub	-0.4602	0.2177	-2.114	0.52

Table S3.14 (cont'd)

Spring phenophases	Graminoid - Forb	-0.0494	0.1042	-0.474	1.00
	Pteridophyte - Forb	0.3710	0.4839	0.767	1.00
	Shrub - Forb	-0.1908	0.1513	-1.261	1.00
	Tree - Forb	-0.9108	0.9239	-0.986	1.00
	Pteridophyte - Graminoid	0.4204	0.4833	0.870	1.00
	Shrub - Graminoid	-0.1414	0.1576	-0.897	1.00
	Tree - Graminoid	-0.8614	0.9256	-0.931	1.00
	Shrub - Pteridophyte	-0.5618	0.5023	-1.119	1.00
	Tree - Pteridophyte	-1.2818	1.0404	-1.232	1.00
	Tree - Shrub	-0.7200	0.9286	-0.775	1.00
Fall phenophases	Graminoid - Forb	0.1488	0.1810	0.822	1.00
	Shrub - Forb	-0.2253	0.3290	-0.685	1.00
	Tree - Forb	1.901	2.2736	0.836	1.00
	Shrub - Graminoid	-0.3741	0.3370	-1.110	1.00
	Tree - Graminoid	1.7518	2.2751	0.770	1.00
	Tree - Shrub	2.1259	2.2830	0.931	1.00
Flower lifespan	Graminoid - Forb	0.08469	0.1944	0.435	0.66
	Shrub - Forb	1.6848	0.7323	2.301	0.064
	Shrub - Graminoid	1.6001	0.7368	2.172	0.064

Table S3.15. Meta-analytic multivariate model outputs testing the influence of plant native status (native or non-native) on the effect of warming for each response variable. Model structure: `rma.mv(yi, vi, mods = ~Native_Status-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Timing of warming	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass	Native (n = 76)	0.3864	0.1878	2.0572	0.0397	0.0183	0.7545
	Non-native (n = 20)	0.0657	0.2579	0.2549	0.7988	-0.439	0.5713
Belowground biomass	Native (n = 12)	1.1232	0.6978	1.6097	0.1075	-0.244	2.4909
	Non-native (n = 2)	-3.3839	1.0730	-3.154	0.0016	-5.487	-1.281
Flower number	Native (n = 68)	0.0531	0.1012	0.5244	0.6000	-0.145	0.2515
	Non-native (n = 11)	-0.0742	0.2162	-0.343	0.7314	-0.498	0.3496
Fruit number	Native (n = 28)	0.3059	0.1583	1.9319	0.0534	-0.004	0.6163
	Non-native (n = 1)	-1.0831	0.6752	-2.670	0.0076	-3.127	-0.479
Fruit weight	Native (n = 25)	0.9724	0.2402	4.0490	<0.0001	0.5017	1.4431
	Non-native (n = 2)	-1.2357	0.6615	-1.868	0.0618	-2.532	0.0609
Growth	Native (n = 106)	0.6553	0.1526	4.2936	<0.0001	0.3562	0.9544
	Non-native (n = 7)	0.7319	0.2364	3.0965	0.0020	0.2686	1.1951
Leaf growth	Native (n = 120)	0.3309	0.0867	3.8184	0.0001	0.1611	0.5007
	Non-native (n = 16)	0.3483	0.1506	2.3128	0.0207	0.0531	0.6435
Aboveground nitrogen	Native (n = 100)	-0.5568	0.1014	-5.493	<0.0001	-0.755	-0.358
	Non-native (n = 5)	-0.4495	0.3470	-1.296	0.1952	-1.129	0.2306
Belowground nitrogen	Native (n = 11)				NA		
	Non-native (n = 0)				NA		
Percent cover	Native (n = 51)	0.2280	0.0967	2.3577	0.0184	0.0385	0.4175
	Non-native (n = 9)	0.0998	0.2761	0.3613	0.7178	-0.441	0.6409
Spring phenophases	Native (n = 128)	-0.5621	0.1788	-3.143	0.0017	-0.913	-0.212
	Non-native (n = 45)	-0.5321	0.2089	-2.548	0.0108	-0.941	-0.123
Fall phenophases	Native (n = 53)	-0.7009	0.6293	-1.114	0.2654	-1.934	0.5326
	Non-native (n = 19)	-0.8636	0.6569	-1.315	0.1887	-2.151	0.4240
Flower lifespan	Native (n = 18)	-0.4361	0.4864	-0.897	0.3699	-1.389	0.5172
	Non-native (n = 17)	-0.2833	0.5308	-0.534	0.5935	-1.324	0.7570

Table S3.16. Holm-corrected comparisons for the effect of plant native status on each plant trait. Sample sizes for each comparison can be found in Table S3.15.

Variable	Native status	Estimate	SE	Z-value	P-value
Aboveground biomass	Non-native - Native	-0.3206	0.2284	-1.404	0.16
Belowground biomass	Non-native - Native	-4.507	0.9241	-4.877	<0.001
Flower number	Non-native - Native	-0.1273	0.2313	-0.55	0.58
Fruit number	Non-native - Native	-2.109	0.6935	-3.041	0.0024
Fruit weight	Non-native - Native	-2.208	0.6766	-3.264	0.0011
Growth	Non-native - Native	0.0766	0.1981	0.387	0.699
Leaf growth	Non-native - Native	0.0174	0.1531	0.114	0.909
Aboveground nitrogen	Non-native - Native	0.1073	0.3582	0.299	0.765
Belowground nitrogen	Non-native - Native				NA
Percent cover	Non-native - Native	-0.1282	0.2925	-0.438	0.661
Spring phenophases	Non-native - Native	0.0300	0.1381	0.217	0.828
Fall phenophases	Non-native - Native	-0.1626	0.2397	-0.679	0.497
Flower lifespan	Non-native - Native	0.1528	0.2478	0.616	0.538

Table S3.17. Models testing to ensure that the finer-scale variables contained within each trait grouping respond to warming similarly. Model structure: `rma.mv(yi, vi, mods = ~Var_type-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Finer scale variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Growth	Plant height (n = 90)	0.8296	0.1558	5.3259	<0.0001	0.5243	1.1350
	Shoot length (n = 45)	0.3088	0.1917	1.6105	0.1073	-0.067	0.6845
Leaf growth	Leaf area (n = 23)	0.3711	0.1197	3.1010	0.0019	0.1366	0.6057
	Leaf length (n = 45)	0.5119	0.1249	4.0972	<0.0001	0.2670	0.7567
	Leaf width (n = 27)	0.2757	0.1355	2.0354	0.0418	0.0102	0.5412
	SLA (n = 45)	0.1591	0.1095	1.4536	0.1461	-0.055	0.3737
Spring phenophases	Bud break (n = 23)	-0.4774	0.1967	-2.428	0.0152	-0.863	-0.092
	Emergence (n = 39)	-0.6007	0.1994	-3.013	0.0026	-0.992	-0.210
	Flowering (n = 89)	-0.7914	0.1834	-4.316	<0.0001	-1.151	-0.432
	Leaf appearance (n = 20)	-0.0950	0.2087	-0.455	0.6490	-0.504	0.3141
	Leaf expansion (n = 8)	-0.0114	0.2495	-0.046	0.9635	-0.550	0.4775
	Stem elongation (n = 7)	-0.5999	0.2238	-2.681	0.0073	-1.039	-0.161
Fall phenophases	Abscission (n = 23)	-0.7177	0.6221	-1.154	0.2486	-1.937	0.5016
	Seed set (n = 41)	-1.0474	0.6141	-1.706	0.0881	-2.251	0.1563
	Senescence (n = 13)	-0.2081	0.6949	-0.299	0.7645	-1.570	1.1539

Table S3.18. Models testing to ensure that the finer-scale functional groups contained within each broader functional grouping respond to warming similarly. Model structure: `rma.mv(yi, vi, mods = ~Func_group-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Finer scale variable	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Tree	Deciduous (n = 28)	0.5533	0.4256	1.2999	0.1936	-0.281	1.3875
	Evergreen (n = 40)	0.3700	0.3233	1.1443	0.2525	-0.264	1.0036
Shrub	Deciduous (n = 151)	0.0848	0.1097	0.7727	0.4397	-0.130	0.2999
	Evergreen (n = 161)	0.2030	0.1076	1.8857	0.0593	-0.008	0.4139
Forb	Leguminous forb (n = 13)	0.0584	0.0824	0.7095	0.4780	-0.103	0.2199
	Forb (n = 320)	0.0979	0.2815	0.3477	0.7280	-0.454	0.6497

Table S3.19. Meta-analytic multivariate model outputs for the effect of warming on aboveground biomass and nitrogen content between different plant tissue types. Model structure: `rma.mv(yi, vi, mods = ~Tissue_type-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Tissue type	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass	Leaf (n = 25)	0.2419	0.2486	0.9733	0.3304	-0.2453	0.7291
	Shoot (n = 12)	0.0521	0.3475	0.1500	0.8808	-0.6290	0.7332
	Stem (n = 9)	0.5000	0.2919	1.7128	0.0868	-0.0722	1.0722
	Total (n = 118)	0.5623	0.1816	3.0957	0.0020	0.2063	0.9183
	Wood (n = 5)	0.1553	0.4274	0.3633	0.7164	-0.6924	0.9930
Aboveground N content	Inflorescence (n = 1)	-3.6943	1.1117	-3.323	0.0009	-5.8731	-1.5155
	Leaf (n = 74)	-0.5501	0.1246	-4.416	<0.0001	-0.7943	-0.3060
	Reproductive tissue (n = 2)	0.1254	0.4741	0.2646	0.7913	-0.8037	1.0546
	Shoot (n = 12)	-0.2738	0.3134	-0.873	0.3824	-0.8881	0.3406
	Stem (n = 2)	-0.3031	0.8319	-0.364	0.7156	-1.9335	1.3273
	Total (n = 38)	-0.1190	0.1654	-0.720	0.4717	-0.4432	0.2051
	Vegetative tissue (n = 2)	-0.2955	0.4728	-0.625	0.5320	-1.2222	0.6312

Table S3.20. Models containing year-limited data (i.e., only the last year of data collected for each study) vs. models containing all years of data. The year-limited models and the models with all years each tested for the effects of warming on the given response variable. Model structure: `rma.mv(yi, vi, mods = ~Var_type_broad-1, random = list(~1|Pub_number/Site/Genus_Species), data = data)`.

Variable	Model type	Estimate	SE	Z-value	P-value	Lower CI	Upper CI
Aboveground biomass	Year-limited (n = 169)	0.253	0.0694	3.6412	0.0003	0.1167	0.3889
	All years (n = 234)	0.192	0.0663	2.89	0.0039	0.0617	0.3217
Belowground biomass	Year-limited (n = 44)	0.603	0.1618	3.7294	0.0002	0.2862	0.9203
	All years (n = 51)	0.562	0.1418	3.9605	<0.0001	0.2838	0.8398
Flower number	Year-limited (n = 79)	-0.076	0.0831	-0.9181	0.3586	-0.239	0.0866
	All years (n = 197)	-0.013	0.0724	-0.1858	0.8526	-0.155	0.1284
Fruit number	Year-limited (n = 34)	-0.098	0.0942	-1.0422	0.2973	-0.283	0.0865
	All years (n = 46)	-0.185	0.0867	-2.1298	0.0332	-0.354	-0.015
Fruit weight	Year-limited (n = 27)	0.578	0.1430	4.0400	<0.0001	0.2974	0.8578
	All years (n = 38)	0.447	0.1150	3.8902	0.0001	0.2220	0.6727
Growth	Year-limited (n = 135)	0.649	0.0647	10.0246	<0.0001	0.5220	0.7757
	All years (n = 291)	0.573	0.0596	9.6149	<0.0001	0.4564	0.6900
Leaf growth	Year-limited (n = 140)	0.537	0.0652	8.2374	<0.0001	0.4091	0.6646
	All years (n = 220)	0.467	0.0612	7.6260	<0.0001	0.3468	0.5867
Aboveground nitrogen	Year-limited (n = 131)	-0.409	0.0838	-4.8837	<0.0001	-0.574	-0.245
	All years (n = 191)	-0.575	0.0788	-7.2950	<0.0001	-0.729	-0.421
Belowground nitrogen	Year-limited (n = 12)	-0.108	0.2780	-0.3893	0.6971	-0.653	0.4367
	All years (n = 14)	-0.098	0.2564	-0.3836	0.7013	-0.601	0.4042

Table S3.20 (cont'd)

Percent cover	Year-limited (n = 193)	0.104	0.0740	1.4109	0.1583	-0.041	0.2495
	All years (n = 424)	0.291	0.0640	4.5452	<0.0001	0.1654	0.4162
Spring phenophases	Year-limited (n = 186)	-0.122	0.0696	-1.7582	0.0787	-0.259	0.0140
	All years (n = 209)	-0.170	0.0676	-2.5220	0.0117	-0.303	-0.038
Fall phenophases	Year-limited (n = 77)	-0.037	0.0798	-0.4676	0.6401	-0.194	0.1190
	All years (n = 96)	-0.077	0.0771	-0.9969	0.3188	-0.228	0.0743
Flower lifespan	Year-limited (n = 37)	0.136	0.0881	1.5484	0.1215	-0.036	0.3091
	All years (n = 48)	-0.005	0.0847	-0.0626	0.9501	-0.171	0.1608

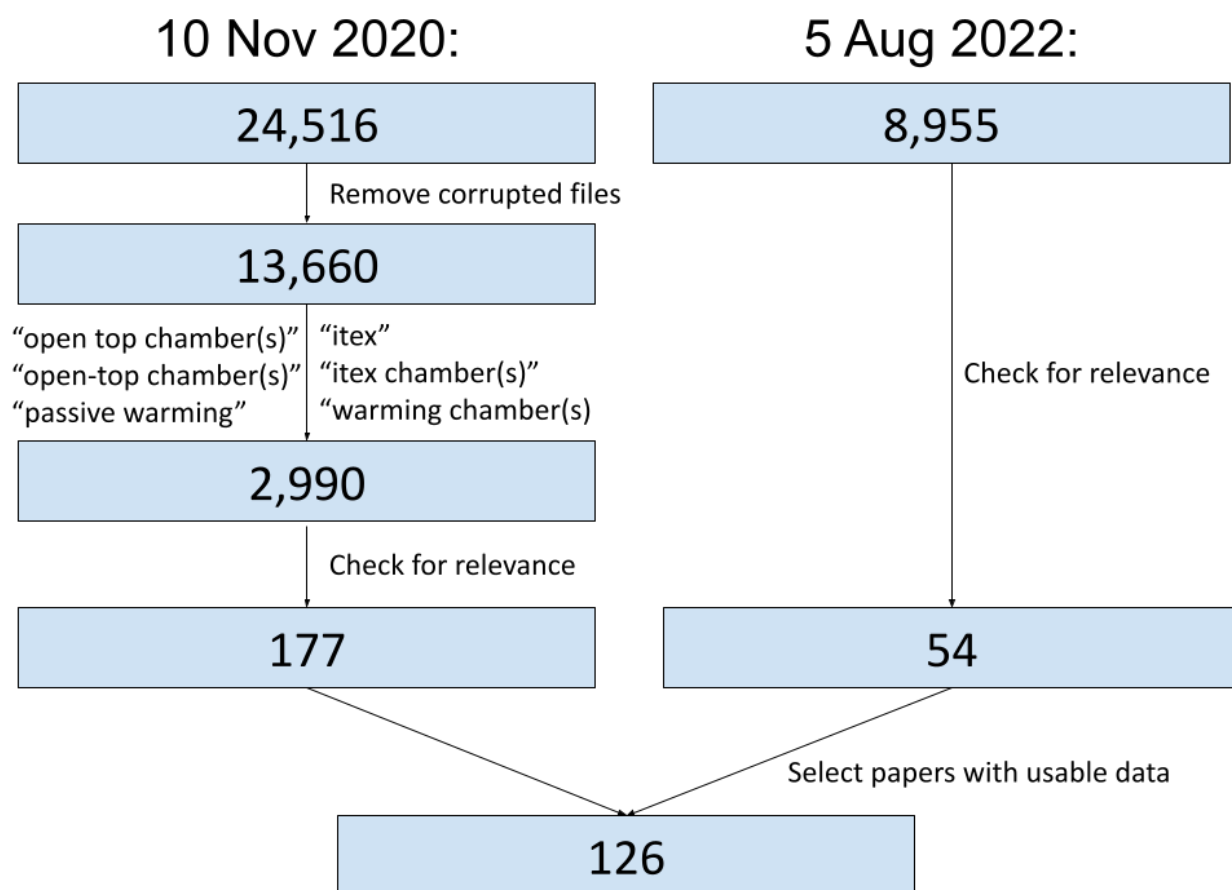


Figure S3.1. The number of papers (in the blue boxes) returned from the Scopus database search on 10 November 2020 and 5 August 2022. After removing corrupted files, conducting text mining using key phrases, checking for relevance, and selecting papers with usable data, our final number of papers used in this meta-analysis is 126.

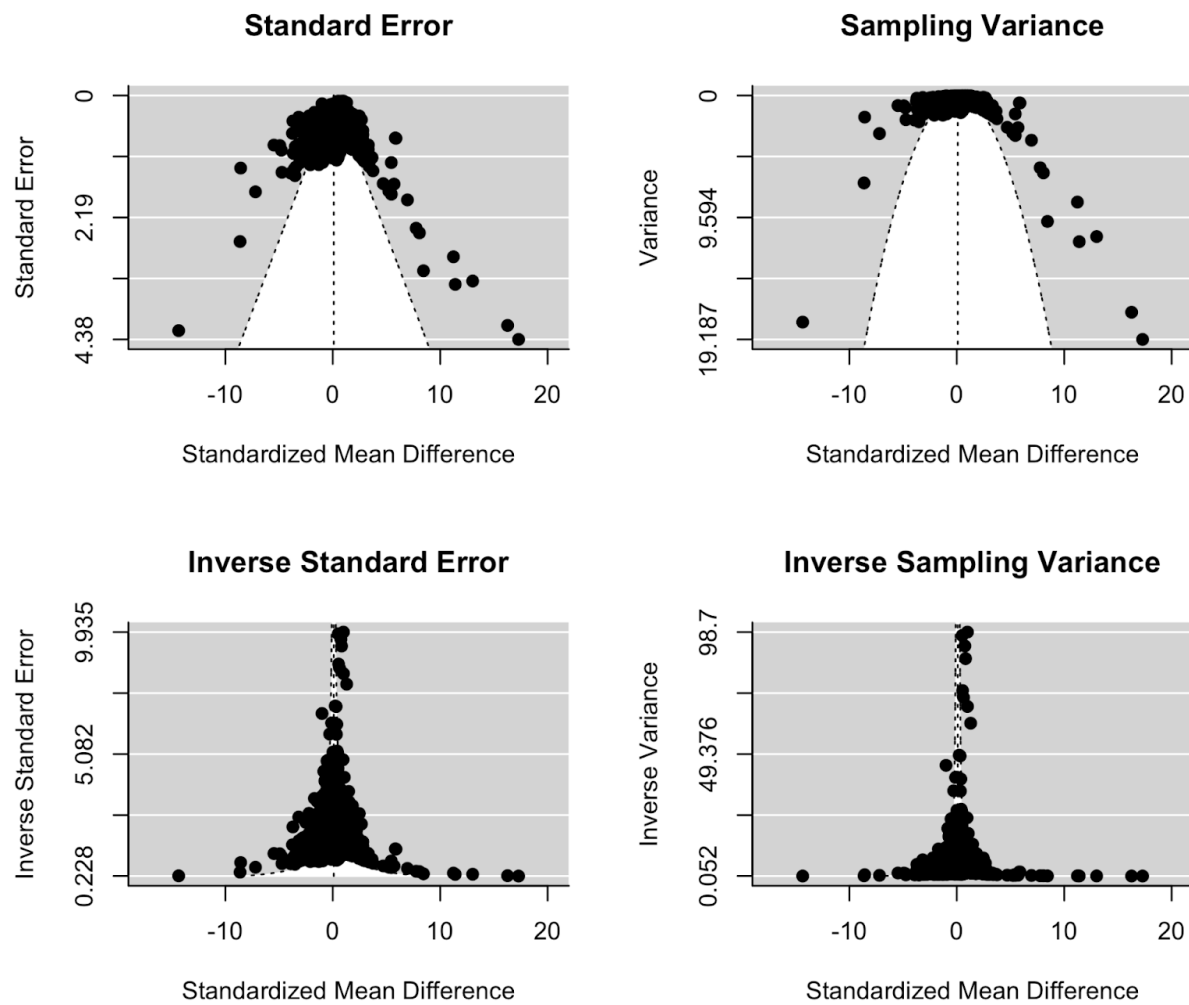


Figure S3.2. Funnel plots for the standardized mean difference (i.e., effect size) compared to standard error, sampling variance, inverse standard error, and inverse variance.

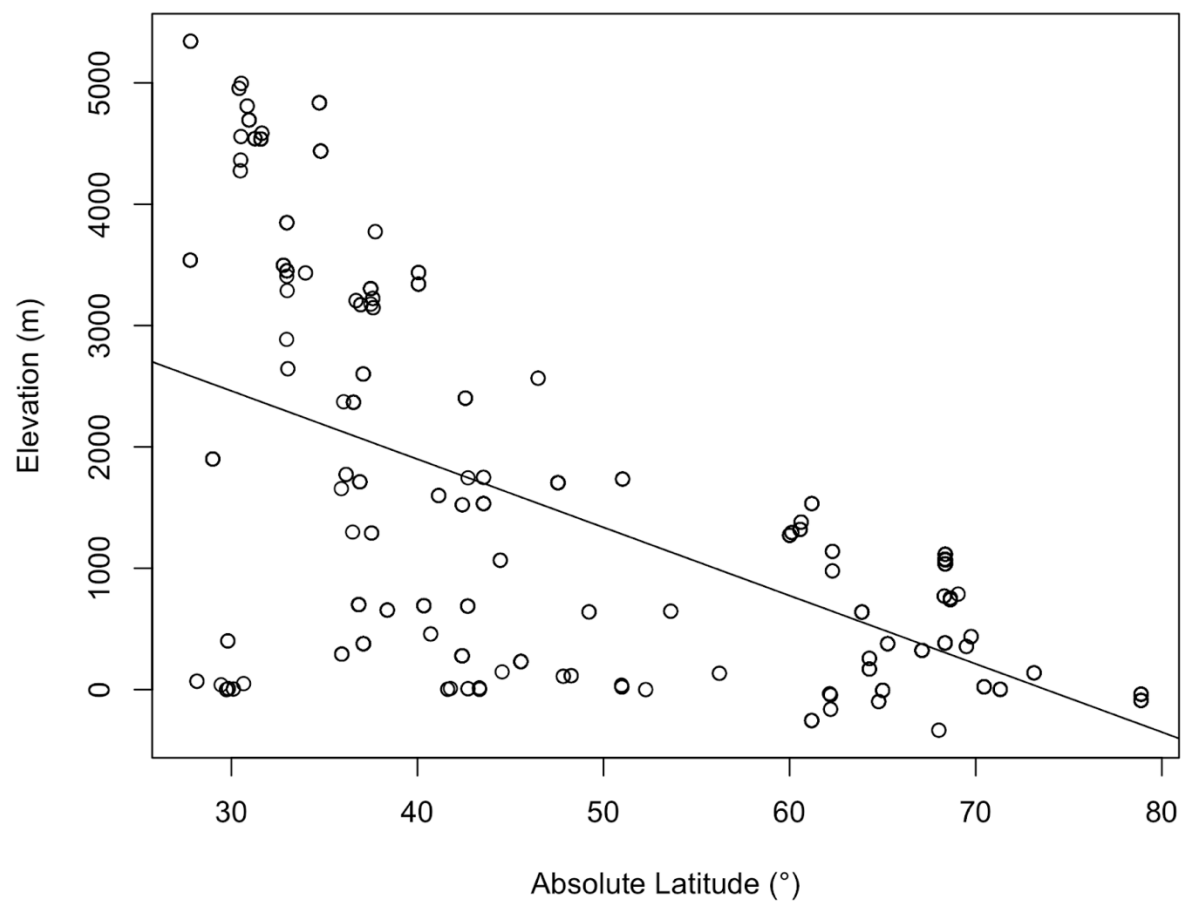


Figure S3.3. Negative correlation between elevation (m) and absolute latitude (°). Pearson's product-moment correlation: $t = -27.4$, $df = 1254$, $p < 0.001$.

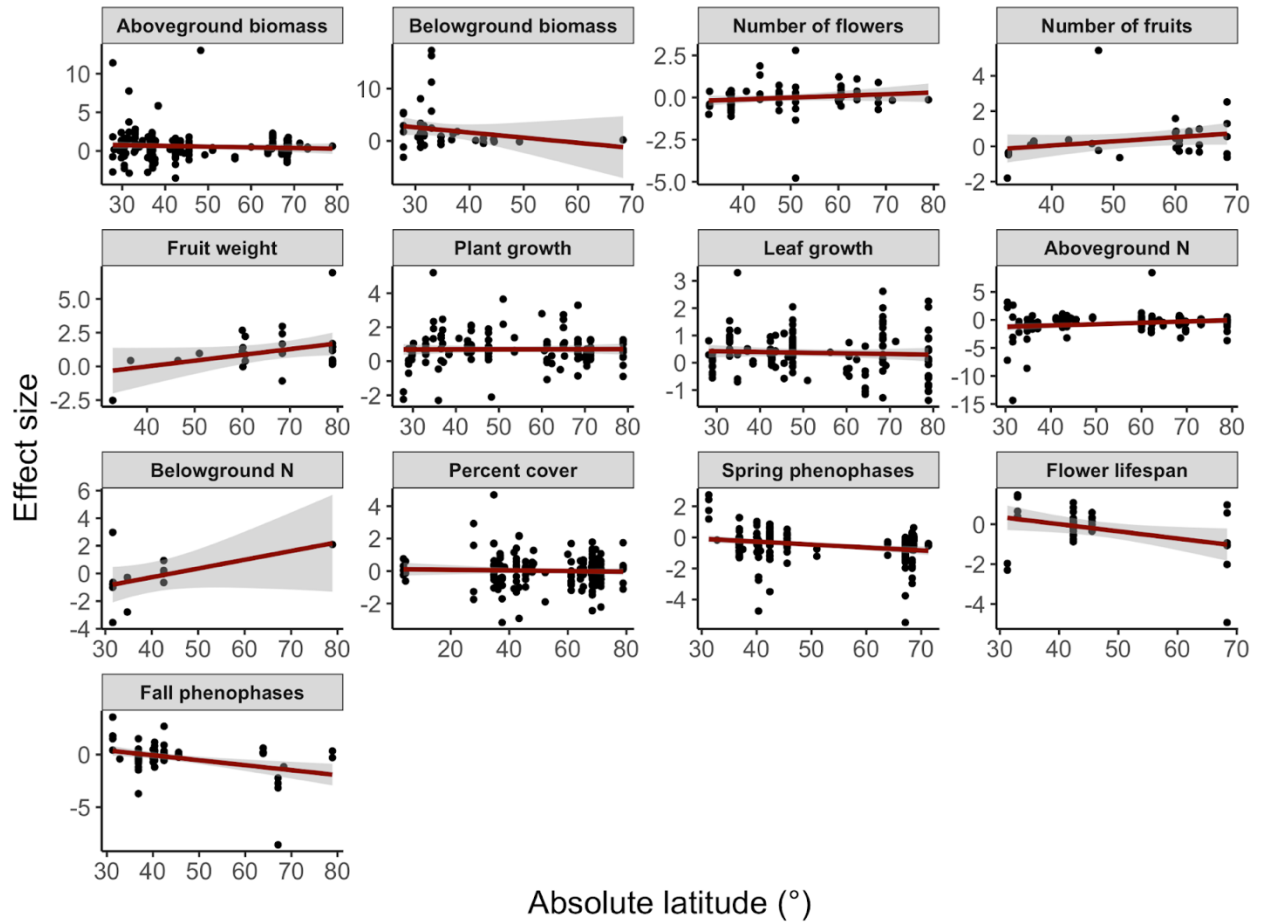


Figure S3.4. The effect of absolute latitude (°) on Hedges' g effect sizes for each trait and community property. Lines represent a linear regression with the shaded region as the 95% confidence interval.

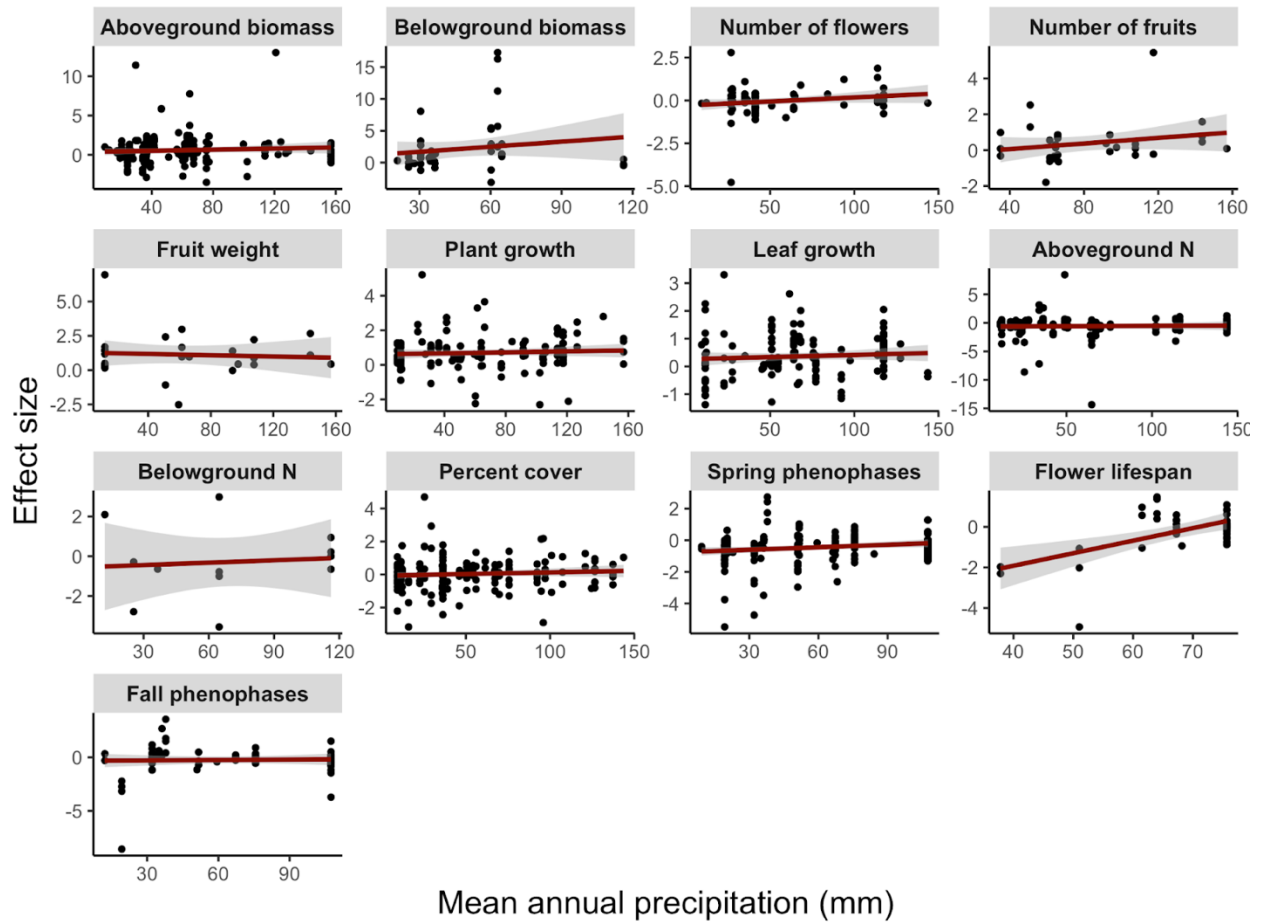


Figure S3.5. The effect of mean annual precipitation (mm) on Hedges' g effect sizes for each trait and community property. Only flower lifespan showed an effect of precipitation ($\beta = 0.069$, $z = 2.19$, $p = 0.028$). Lines represent a linear regression with the shaded region as the 95% confidence interval.

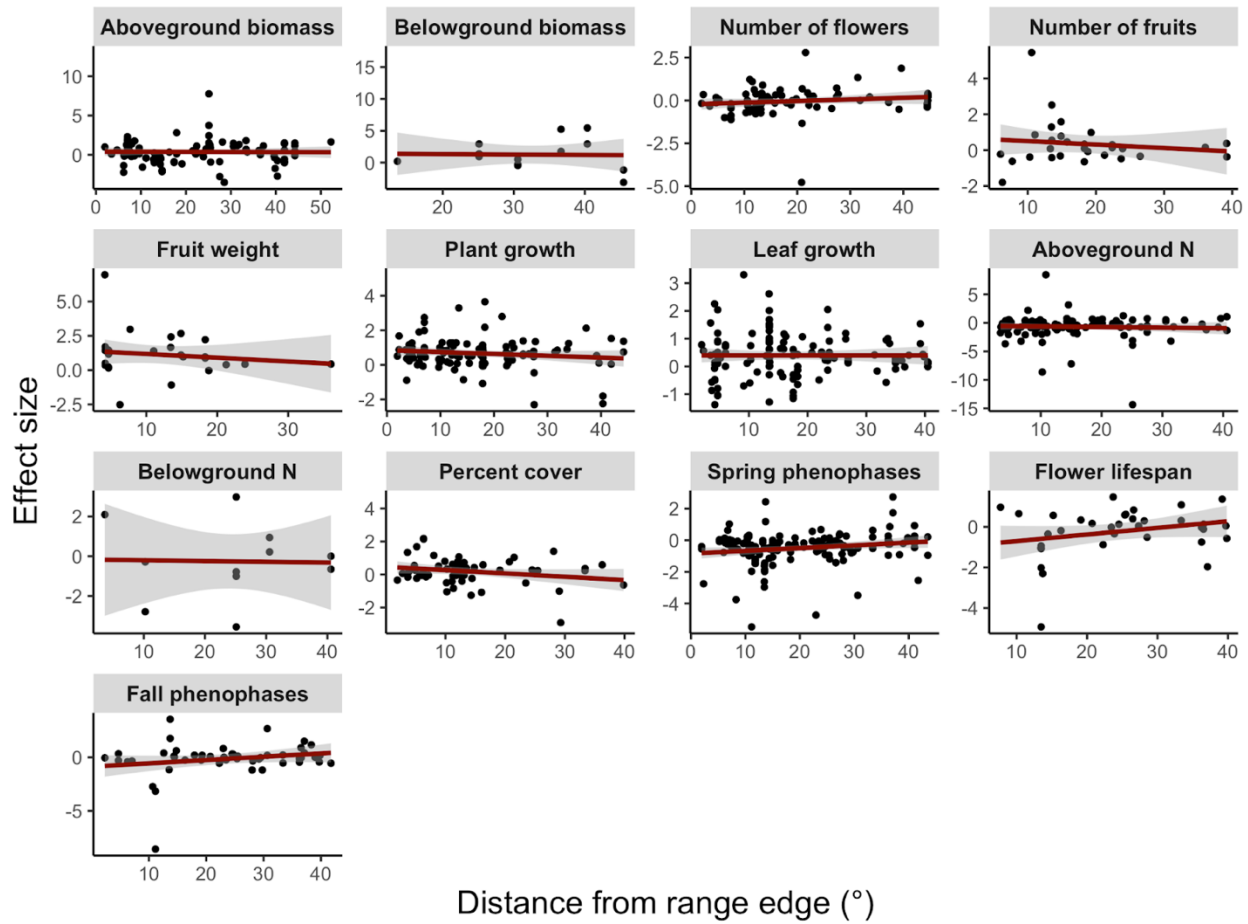


Figure S3.6. The effect of species distance from the northern range edge (°) on Hedges' g effect sizes for each trait and community property. Plant growth and percent cover demonstrated an effect of distance from range edge (Table S3.7). Lines represent a linear regression with the shaded region as the 95% confidence interval.

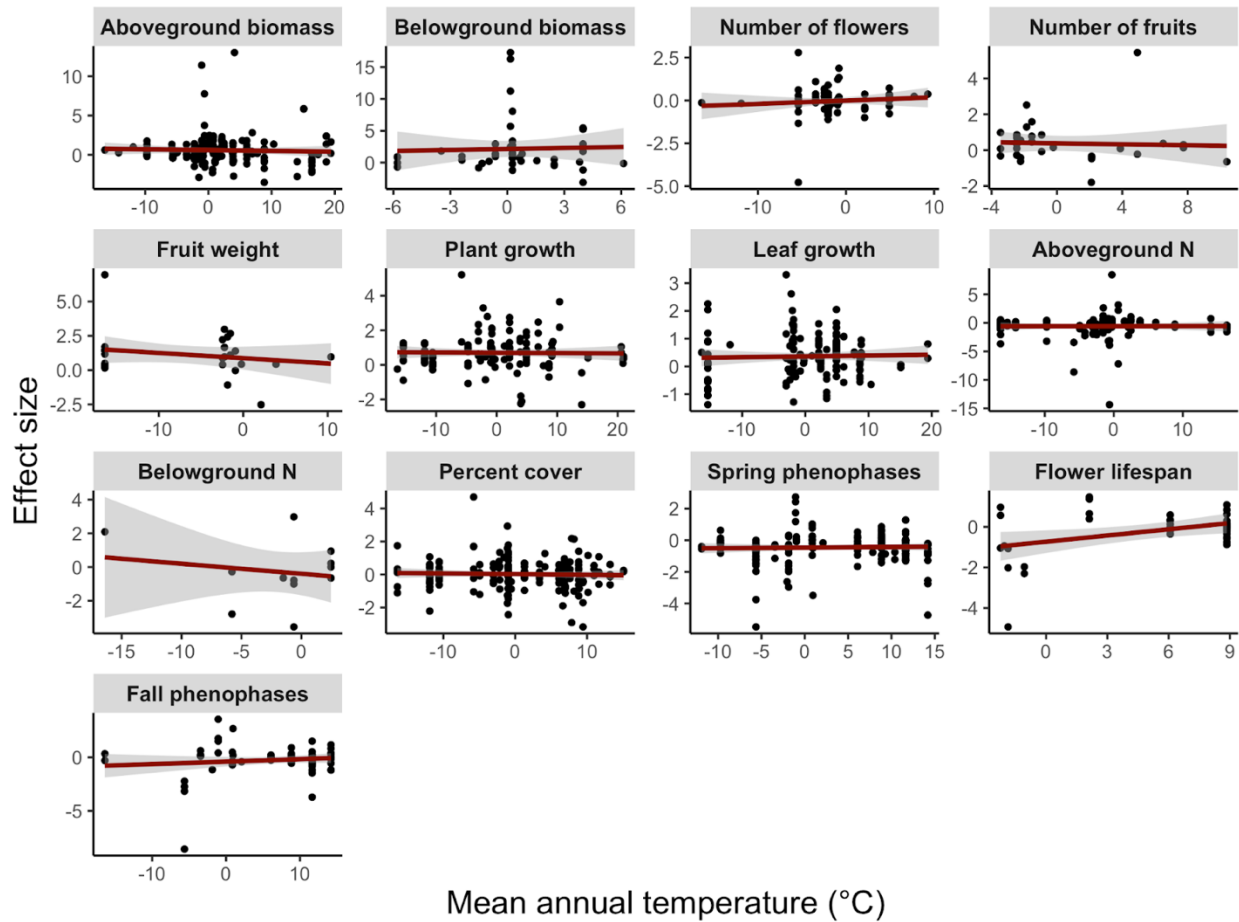


Figure S3.7. The effect of mean annual temperature (°C) on Hedges' g effect sizes for each trait and community property. No traits or properties demonstrated an effect of mean annual temperature. Lines represent a linear regression with the shaded region as the 95% confidence interval.

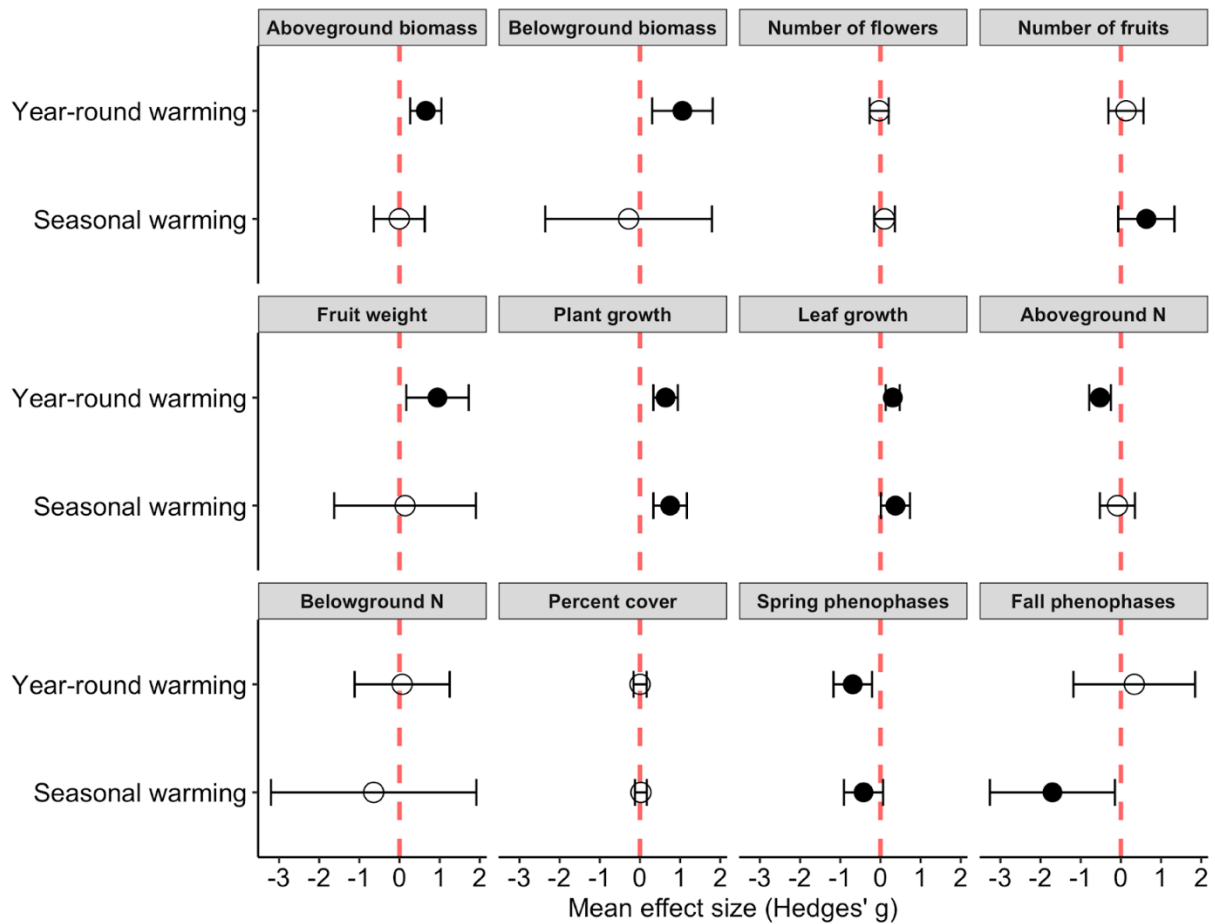


Figure S3.8. The effect of the timing of warming (year-round or seasonal) on mean Hedges' g effect size. Filled in points represent an effect size different from 0. Mean values are estimates from the mixed-effects model which accounts for species, site, and publication number. Points and error bars represent mean $\pm$ 95% confidence intervals. Flower lifespan is not included as it did not contain both year-round and seasonal warming treatments.

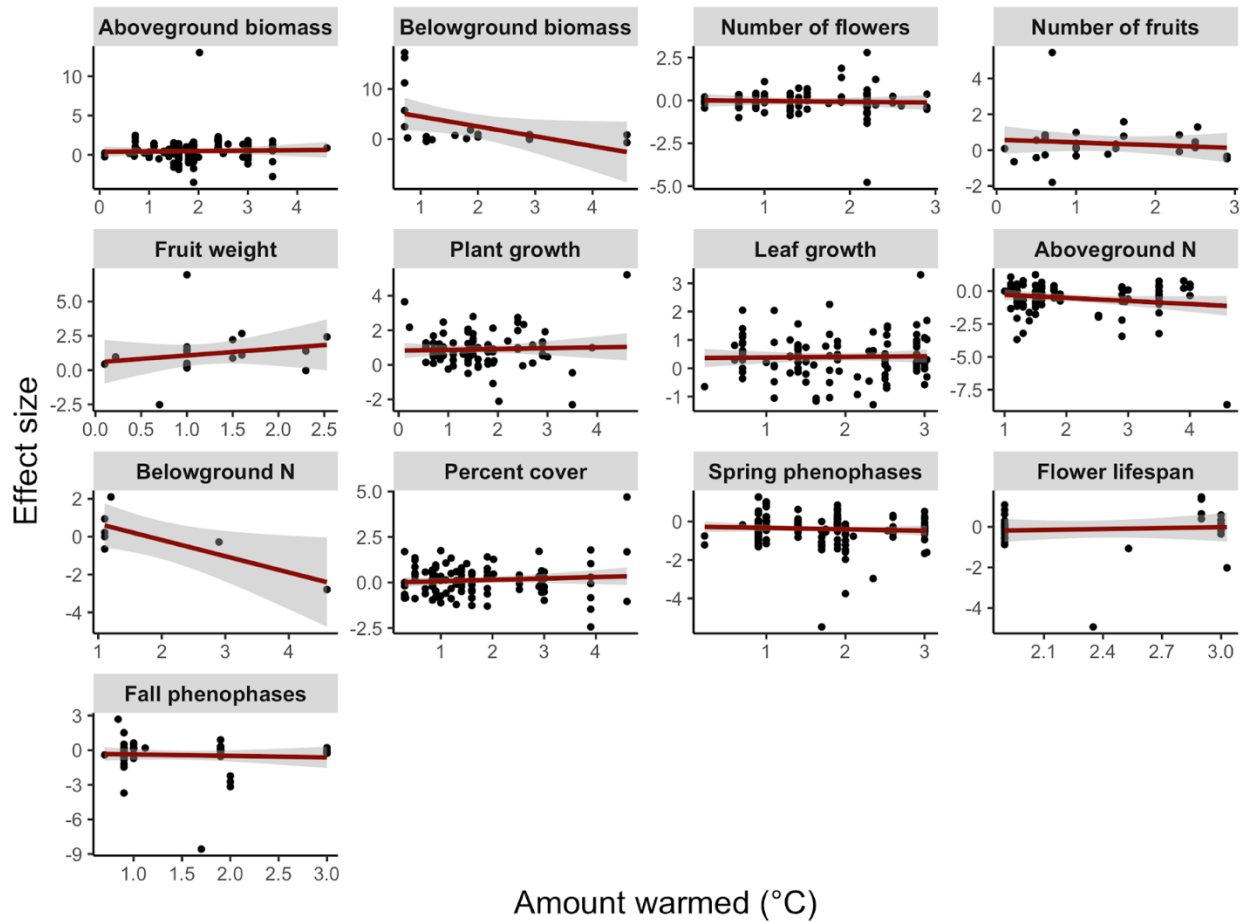


Figure S3.9. The effect of the amount warmed by the experiment (°C) on Hedges' g effect sizes for each trait and community property. Only belowground N content showed an effect of the amount warmed ($\beta = -0.98$, $z = -1.67$, $p = 0.049$). Lines represent a linear regression with the shaded region as the 95% confidence interval.

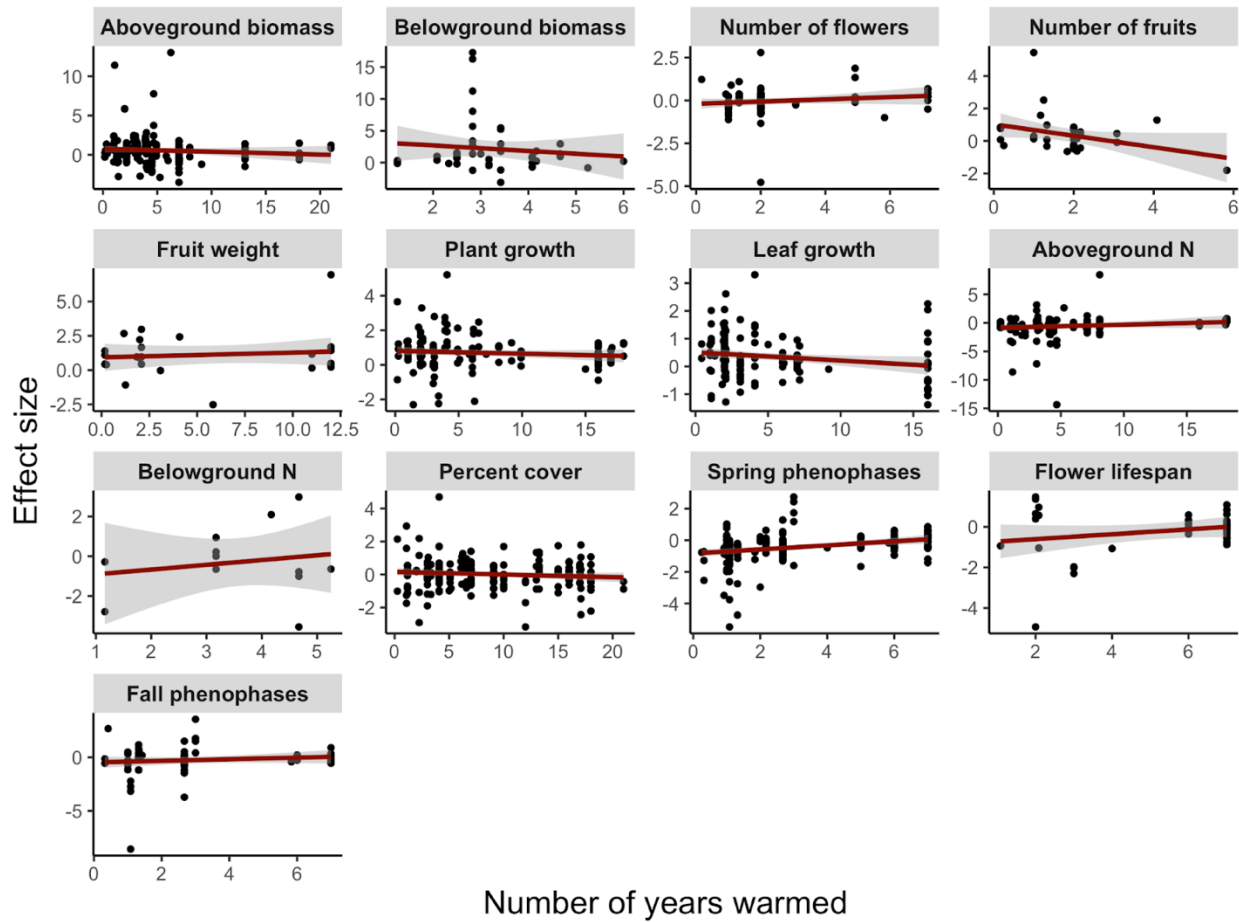


Figure S3.10. The effect of the number of years warmed by the experiment on Hedges' g effect sizes for each trait and community property. Flower lifespan, spring phenology, fruit number, and leaf growth showed an effect of the number of years warmed. Lines represent a linear regression with the shaded region as the 95% confidence interval.

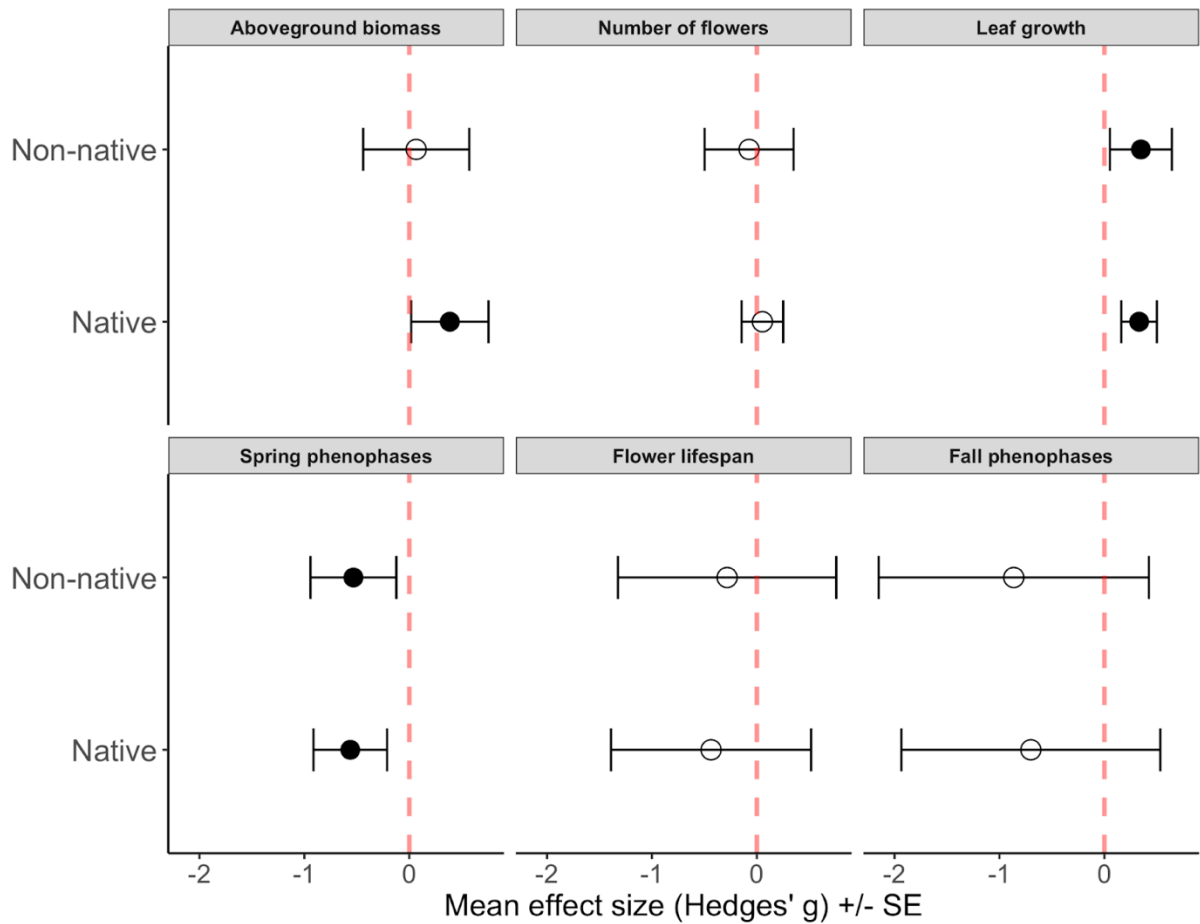


Figure S3.11. The effect plant native status (native or non-native) on mean Hedges' g effect size. Filled in points represent an effect size different from 0. Mean values are estimates from the mixed-effects model which accounts for species, site, and publication number. Points and error bars represent mean $\pm$ 95% confidence intervals. Only traits/properties with at least $n = 10$ per each plant type (native and non-native) are shown (see Table S3.15 for all traits).

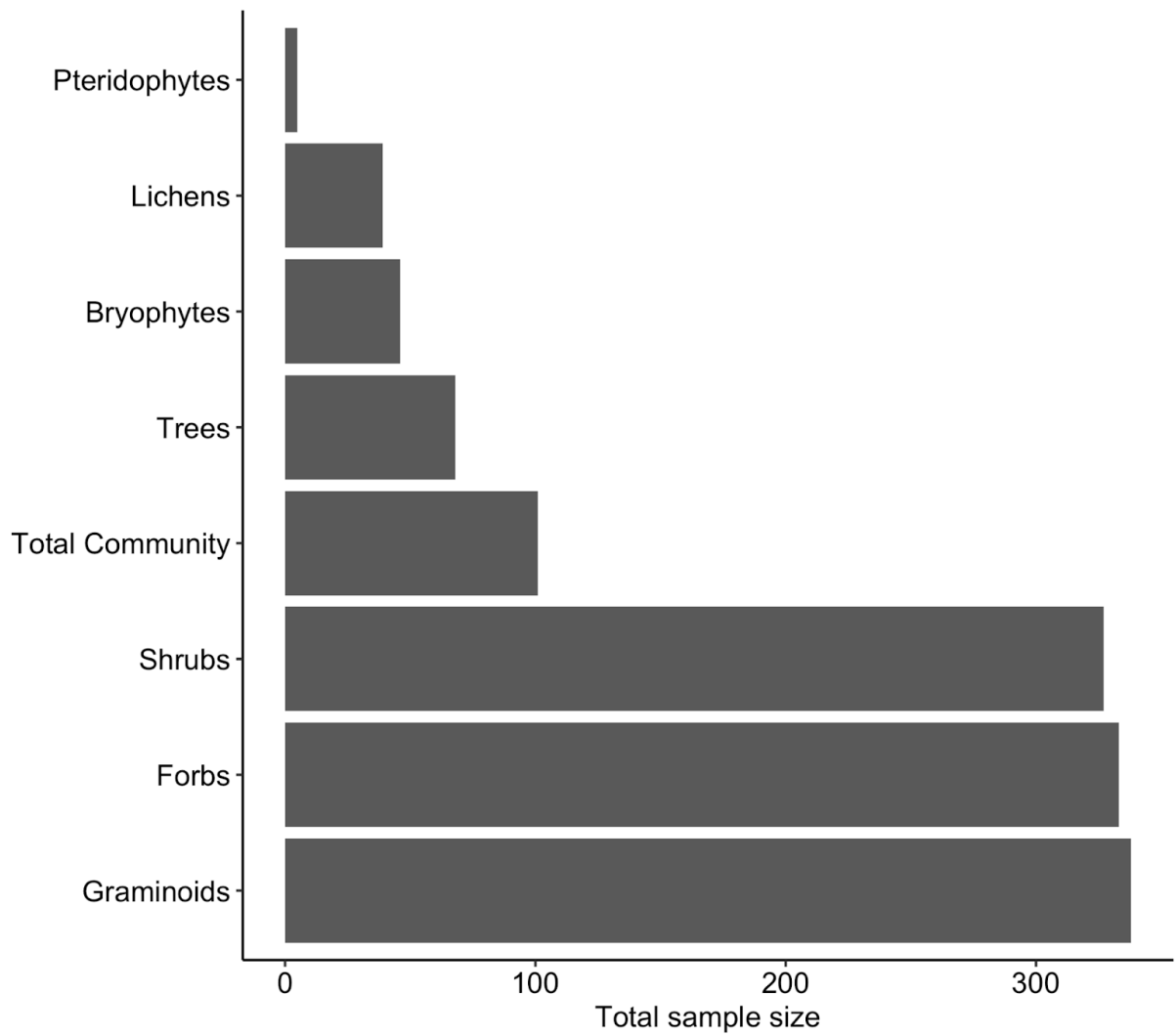


Figure S3.12. Total sample size of all plant growth forms measured by experiments in this meta-analysis.

Conclusion

Plants respond to climate change stressors in numerous, multifaceted ways. This is first highlighted in Chapter 1, in which we determined that warming and drought can alter both the composition and abundance of emitted VOCs from *Solidago altissima*. More specifically, we found that a select few compounds were especially sensitive to these climate change stressors and were significantly associated with one or more climate stressor. For example, diisopropyl adipate was associated with drought treatments (drought and warmed + drought), which could indicate that this compound may function as drought stress protection for the plant. However, this chapter highlights the need for more research on the specific functions of the emitted compounds, such as stress protection (e.g., stabilizing membranes) or communication (e.g., plant-plant or plant-insect communication). Scientists could then potentially use that knowledge to identify species that emit compounds with stress protection functions and apply that knowledge to conservation or agriculture practices under a new climate regime.

Furthermore, in Chapter 2, we determined that warming can also alter plant phenology, community composition, leaf chemistry and size, and plant productivity, and that these plant responses may be dependent upon interactions with insect herbivores. However, we find that these responses vary across both time and space. For example, warming only led to earlier flowering in a few of the years of the experiment, but not all. Furthermore, our two experimental sites (KBS and UMBS) differed greatly in terms of their community responses to warming and herbivory. This chapter highlights the need for long-term climate change experiments that span a gradient of varying environmental contexts, such as herbivory levels, plant species types, or historical temperature regimes, in order to parse apart contexts important for determining plant warming responses.

Finally, Chapter 3 determines multiple environmental, experimental, and plant-level contexts that contribute to variation in plant responses to warming. For example, latitude may play a role in determining how plant reproductive traits respond to warming. More specifically, when warmed, plants at higher latitudes may have increased input into their reproductive traits compared to plants at lower latitudes. Conservationists could use this information to better inform their decisions on species conservation strategies, as it highlights regions or species types that may respond more negatively to warming, such as how we determined that lichens and mosses tend to become less abundant when warmed.

Overall, this dissertation contributes to a growing body of knowledge on the complex responses of plants to climate change and aids our ability to answer unanswered questions, such as: Which species experience the largest fitness detriment due to warming and/or drought? Might species that experience positive effects of warming and/or drought competitively exclude others? How will these stressors affect species interactions? How can we use environmental contexts to better understand or predict plant responses to warming? With this knowledge, scientists can better plan for and predict the future structure and function of ecological communities.