

SHORT-TERM EFFECTS OF PASSIVE WARMING ON TWO INVADED PLANT
COMMUNITIES USING A NOVEL OPEN-TOP CHAMBER DESIGN

By

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ABSTRACT

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Climate change is expected to directly favor exotic plant species over native species because they tend to have wider climatic tolerances and greater phenological plasticity. Warming is also likely to indirectly favor exotic species by herbivore behaviors and/or preference and intensifying the enemy release phenomenon. To examine these direct and indirect effects, I initiated a field experiment in two heavily invaded plant communities in northern and southern Michigan, USA. Passive warming methods such as open-top chambers are often used to warm aboveground systems; however, the limited height of their design restricts their use to low-stature (~0.4 m) plant communities. I introduced a new chamber design for year-round warming in taller stature (~1.5 m) plant communities and analyzed its effects on the abiotic environment. During the second year of warming, I collected data for species cover, phenology (green-up, flowering time, timing of seed set), and cumulative leaf herbivory. The new chamber design achieved reliable levels of warming (+1.8 °C), consistent with all four Representative Concentration Pathways (RCPs) scenarios for 2046-2065 from the Intergovernmental Panel on Climate Change's 5th Assessment Report. The effects of warming were largely consistent with theoretical expectations at the northern site and favored exotic plant abundance. Warming did not favor exotic species dominance at the southern site, but rather responses indicated plants at this site experienced physiological stress, likely because ambient temperatures were already close to plant species' thermal maxima.

To Nina and Matt--for your kindness and direction throughout this adventure.

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KEY TO ABBREVIATIONS

IPCC Intergovernmental Panel on Climate Change

LTER Long Term Ecological Research

KBS Kellogg Biological Station

OTC Open-top Chamber

RCP Representative Concentration Pathways

UMBS University of Michigan Biological Station

INTRODUCTION

Exotic species that become invasive threaten both the composition and function of native ecosystems (Root et al. 2003; Walther 2010). Recent studies suggest that climate change could enhance the success of exotic species through increased survival during transport, greater establishment success, and decreased effectivity of control strategies (Theoharides and Dukes 2007; Hellmann et al. 2008). For example, warmer temperatures during transport may increase species survival and in turn, increase propagule pressure in the introduced range (Early et al. 2016). Further, exotic species that were once limited by climate constraints may experience greater establishment success under a warmer climate (Rixon et al. 2005). However, the extent to which warming will alter existing exotic species dominance remains unclear because it can depend heavily upon interactions with the biotic community of its introduced range (Van der Putten et al. 2010; Seabloom et al. 2015). Several mechanisms have been proposed to identify how warming may increase exotic dominance; however, there is little empirical evidence supporting these mechanisms once exotics are established in their introduced range (Vilà et al. 2007).

One mechanism by which exotic species may increase their local dominance compared to co-occurring native species is through unique phenological responses (Wolkovich and Cleland 2011). The vacant niche theory suggests that exotic plants are able to exploit resources in temporal niche spaces unfilled by native plants leading to greater success relative to natives over time (Elton 1958; Davis 2009). For example, longer growing seasons associated with climate change may open opportunities for exotic species to establish earlier and limit native growth through priority effects (Sale 1977; Seabloom et al. 2003).

An additional mechanism by which existing exotic species may gain abundance in their introduced systems is through greater plasticity and/or more rapid evolution than native species (Richards et al. 2006; Levine et al. 2008). With rapidly changing environments, exotic species that are able to respond to such changes may be less vulnerable to extinction (Willis et al. 2008).

Exotic species success may also be facilitated in their introduced range by herbivores that prefer native species (Keane and Crawley 2002). Climate change may moderate the magnitude and direction of herbivore impacts on exotic plant success (Fey and Cottingham 2011; Eisenhauer et al. 2012). For instance, warmer temperatures may directly increase insect survival, range, and abundance (Bale et al. 2002; Robinet & Roques 2010) as well as increase insect metabolisms leading to increased herbivore damage (Brown et al. 2004). Warming may also indirectly alter the extent of herbivore damage by altering plant nutritional quality and/or desirability. For example, if warming increases plant growth, reduced tissues C:N ratios may require herbivores to consume greater quantities in order to meet nutritional demands (Hillebrand et al. 2009; Sardans et al. 2012). If native species experience this rise in herbivory due to warming, and exotic species are released from herbivores, then we would expect exotic species to experience greater success and abundance under climate change conditions.

Studies that suggest climate change will favor exotic plant dominance in their introduced range are largely limited to predictions based on theory and experiments that incorporate biological complexity are lacking (Hellmann et al. 2008). In this thesis, I utilized passive open-top chambers to experimentally examine the individual and interactive effects of warming and species origin on short-term plant responses in highly invaded ecosystems. In Chapter 1, I introduce an updated open-top chamber design for year-round use in taller-stature plant communities that did not previously exist. In order to test the use of this new design across mid-

latitude systems, I document its abiotic effects in two common ecosystem types: a northern forest clearing and a southern early successional grassland site in Michigan, USA. In Chapter 2, I examine whether two years of continuous warming favored exotic plant success by measuring the following responses: species cover, emergence, flowering time, timing of seed set, and cumulative herbivore damage. This knowledge will allow us to better understand and improve forecasts of changes in exotic species dominance after establishment in the introduced range under a rapidly changing climate.

CHAPTER 1

OPEN-TOP CHAMBERS FOR TEMPERATURE MANIPULATION IN TALLER-STATURE
PLANT COMMUNITIES.

ABSTRACT

Open-top chambers simulate global warming by passively increasing air temperatures in field experiments. They are commonly used in low-stature alpine and arctic ecosystems, but rarely in taller-stature plant communities because of their limited height. We present a modified International Tundra Experiment (ITEX) chamber design for year-round outdoor use in warming taller-stature plant communities up to 1.5m tall. We report a full year of results for the chambers' effects on air and soil temperature, relative humidity, and soil moisture in a northern hardwood forest clearing and a southern early successional grassland site located in Michigan, USA. Detailed construction plans are also provided. The chambers elevated daytime air temperatures at 1m height by 1.8°C above ambient levels, on average over an entire year, at both the northern and southern site. The chambers did not affect relative humidity at either site. The chambers did not alter average soil temperature or moisture at the northern site and reduced soil temperatures and soil moisture at the southern site. The chambers increased variability in soil freeze/thaw cycles at both sites. The chambers achieved predicted levels of warming for mid-century (2046-2065) scenarios consistent with the majority of Representative Concentration Pathways (RCPs) in the International Panel on Climate Change 5th Assessment Report, with minimal experimental artifact. This design is a valuable tool for examining the effects of in situ warming on understudied taller-stature plant communities and creates the opportunity to expand future comparisons across a diversity of systems.

INTRODUCTION

Climate warming can have profound impacts on ecological communities (Parmesan & Yohe 2003; Root et al. 2003). Warmer temperatures affect individual growth and metabolism, shift development times, and alter survival and reproductive success (Brown et al. 2004).

Individual responses can lead to community level changes through shifts in population dynamics and species distributions (Walther 2010), and the combination of these responses can be difficult to predict. Therefore, it is critical to collect empirical observations to develop a deeper understanding of ecological community responses to warming essential to inform the sustainable management of natural systems.

Several experimental tools exist that allow researchers to manipulate air and/or soil temperature of in situ plant communities (Aronson & McNulty 2009). Active warming methods (e.g. overhead infrared lamps, heat resistance cables) are used to achieve a pre-determined level of warming (Peterjohn et al. 1994; Harte et al. 1995; Norby et al. 1997; Pelini et al. 2011). These methods have been useful for examining above and belowground ecological responses to warming; however, they often require extensive energy demands, start-up costs, and maintenance that are often not feasible for remote and budget limited research projects (Aronson & McNulty 2009).

Passive warming methods such as open-top chambers (OTCs) are often used to warm aboveground systems, especially in arctic and alpine ecosystems (Marion 1996; Walker et al. 2006). Their simple, cost effective design makes them ideal for field experiments that require replicate plots across environmental gradients or in remote areas. Passive OTCs also allow natural levels of precipitation, light, and gas exchange (Marion et al. 1997). Further, they enable winter warming, a phenomenon that is likely to impact plant community dynamics and demands further research (Kreyling 2010; Bokhorst et al. 2012). Passive OTCs provide a low-maintenance and cost effective method for researchers to examine the effects of year-round warming on plant communities (Arft et al. 1999).

Despite their utility, the limited height of passive OTCs (~0.4m) has restricted their use to low-stature plant communities, early life stages, and low productivity plant systems (Elmendorf et al. 2012). While some taller-stature OTCs exist, they are typically only used during the growing season and not in harsh winter conditions (Chiba & Terao 2014). Thus there is a gap in understanding in situ warming effects on communities such as prairies, savannahs, grasslands, and scrublands (Settele et al. 2014).

Here we provide a durable, passive, OTC design that warms taller-stature (≤ 1.5 m height) plant communities. We monitored the effects of 24 chambers on the abiotic environment over one year in two different temperate ecosystem types (forest clearing and old-agriculture field) spanning approximately 3 degrees of latitude. We report the chambers' effects on air and soil temperature, relative humidity, and soil moisture during different timeframes: year-round, in the growing season vs. the dormant season, and during daytime vs. nighttime hours. We aim to facilitate the use of passive OTCs across understudied taller-stature systems and expand knowledge of climate warming effects in a wider array of natural ecosystems.

METHODS

Study Sites

We tested 24 chambers at two sites separated by 380 km and approximately 3 degrees latitude in Michigan, USA from August 1, 2015 to July 31, 2016. The southern site, located within Kellogg Biological Station's Long Term Ecological Research site (KBS) (42° 24' 40.11"N, 85° 22' 24.46"W, 289 m a.s.l.), is a former agriculture field last cultivated roughly 40 years prior and mowed annually until 2014. The average annual air temperature (1981-2010) is 10.2°C (Menne et al. 2012). The site's vegetation is dominated by *Solidago* spp., *Poa pratensis*, and *Phleum arvense* and reaches approximately 1.5 m height (unpublished data). The northern

site, located at the University of Michigan Biological Station (UMBS) (45° 33' 40.38"N, 84° 40' 46.54"W, 239 m a.s.l.), was located within a 1.5 km² northern deciduous forest clearing created roughly 25 years prior and mowed annually until 2014. The average annual air temperature (1981-2010) is 5.5°C (Menne et al. 2012). Vegetation is dominated by *Centaurea stoebe*, *Poa compressa*, and *Pteridium* spp. and reaches approximately 0.5 m (unpublished data).

Chamber and Experimental Design

We elevated the hexagonal ITEX open-top chamber design described in Marion et al. (1997) onto 0.91 m vertical polycarbonate walls with pressure-treated wood framing (Figure 1; Welshofer et al. 2017). The resulting chamber dimensions were 1.57 m tall x 2.5 m diameter with a top opening large enough to contain a 1m² plot. We used clear, 0.32 cm Lexan polycarbonate sheets without UV protective coating to allow high solar transmittance and natural ultraviolet conditions (ePlastics, San Diego, CA, Item ID: PCCLR0.125AM48X96). We elevated the polycarbonate 10 cm above the ground surface to allow migration of ground dwelling organisms. We used cold and UV resistant cable ties to attach the frame to the polycarbonate panels through drilled holes. We screwed pressure treated plywood supports to the top 120° corners of the hexagon and attached 25.4 cm metal spikes to anchor each leg in the soil for extra support during high-wind and snowfall conditions.

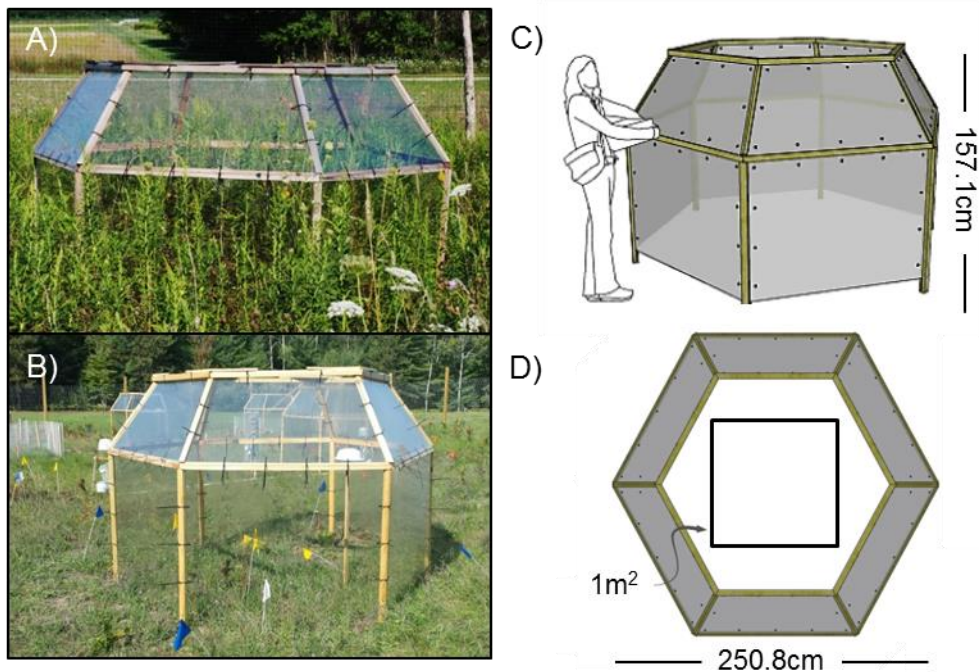


Figure 1. Chamber design and study sites. (A) Photograph of OTC in a taller-stature old agriculture field in Hickory Corners, MI, USA. (B) Photograph of OTC in an early successional northern hardwood forest clearing in Pellston, MI, USA. (C) Perspective view. (D) Aerial view.

Warmed and ambient treatments were randomly distributed across 24, 1 m² plots arranged within a 25 x 36 m deer enclosure at each site. Each OTC was centered on a warmed plot and ambient control plots were left untreated, with a 1 m buffer area on each side of each plot. As a part of a longer term fully-factorial experiment, plots additionally received insect and small mammal reduction treatments (Appendix A).

Abiotic Measurements

At the plot-level, we recorded hourly abiotic conditions from August 1, 2015 to July 31, 2016 with HOBO products (Onset Computer Corporation, Bourne, MA). Three chambered and three ambient plots at each site were instrumented with 4-channel external U12-008 data loggers that recorded air temperature at 10 cm above the soil surface and 5 cm below the soil surface, and with Microstation H21-002 data loggers that recorded hourly air temperature and relative humidity at 1m above the soil surface along with soil moisture at 5 cm below the soil surface.

We installed data loggers (Pendant UA-002-64) to record air temperature at 1m height in the remaining nine chambers at each site. We installed solar shields above each air temperature sensor (Appendix A). When a sensor malfunctioned for < 30 days, those dates were removed from all sensors in the analysis. When a sensor malfunctioned for ≥ 30 days, we removed this sensor's results from the analysis to avoid excluding dates from a substantial portion of the season (Appendix B).

Statistical Analyses

We analyzed the data on air temperature (1 m and 10 cm heights), relative humidity (1m), soil temperature (-5 cm) and soil moisture (-5 cm) for each site separately. All analyses were completed using R version 3.1.2 (R Development Core Team 2008). We used two sided, unpaired t-tests to compare the means of the hourly data ($n_{\text{chambered}} = 3$; $n_{\text{ambient}}=3$) during the following intervals: year-round (24 hour), daytime, nighttime, growing season, and non-growing season. We assessed variation in the warming treatment by calculating the standard deviation of hourly air temperature (1 m) across the remaining nine chambered plots. We compared the variability in winter and spring soil temperature of chambered vs. ambient plots with an F-test such that $H_a: \sigma^2_{\text{chambered}} > \sigma^2_{\text{ambient}}$.

We obtained daily snow depth, snowfall, and maximum five-second wind speed records at both sites during the study period of August 2015-July 2016 and from the National Centers for Environmental Information to examine the chambers' ability to withstand wind speed and heavy snow conditions (Menne et al. 2012). Data were averaged across weather stations throughout Emmet County, Michigan for the northern site and across Kalamazoo County, Michigan for the southern site.

RESULTS

Throughout the year, average air temperatures at 1m height at both sites were warmer in the chambers than in control plots (northern site chambers: increased 0.84 ± 0.25 °C SE; southern site chambers: increased 0.70 ± 0.18 °C; Figure 2A). Warming at 1 m varied according to irradiance; thus, the greatest magnitude of warming was exhibited during daytime hours ($+1.84 \pm 0.79$ °C and $+1.73 \pm 0.19$ °C at the northern and southern sites, respectively), and especially during sunny days (Figure 3), as well as during the growing season (Figure 2A, 4A and 4B). The results of all t-tests are given in Appendix C (northern site) and Appendix D (southern site).

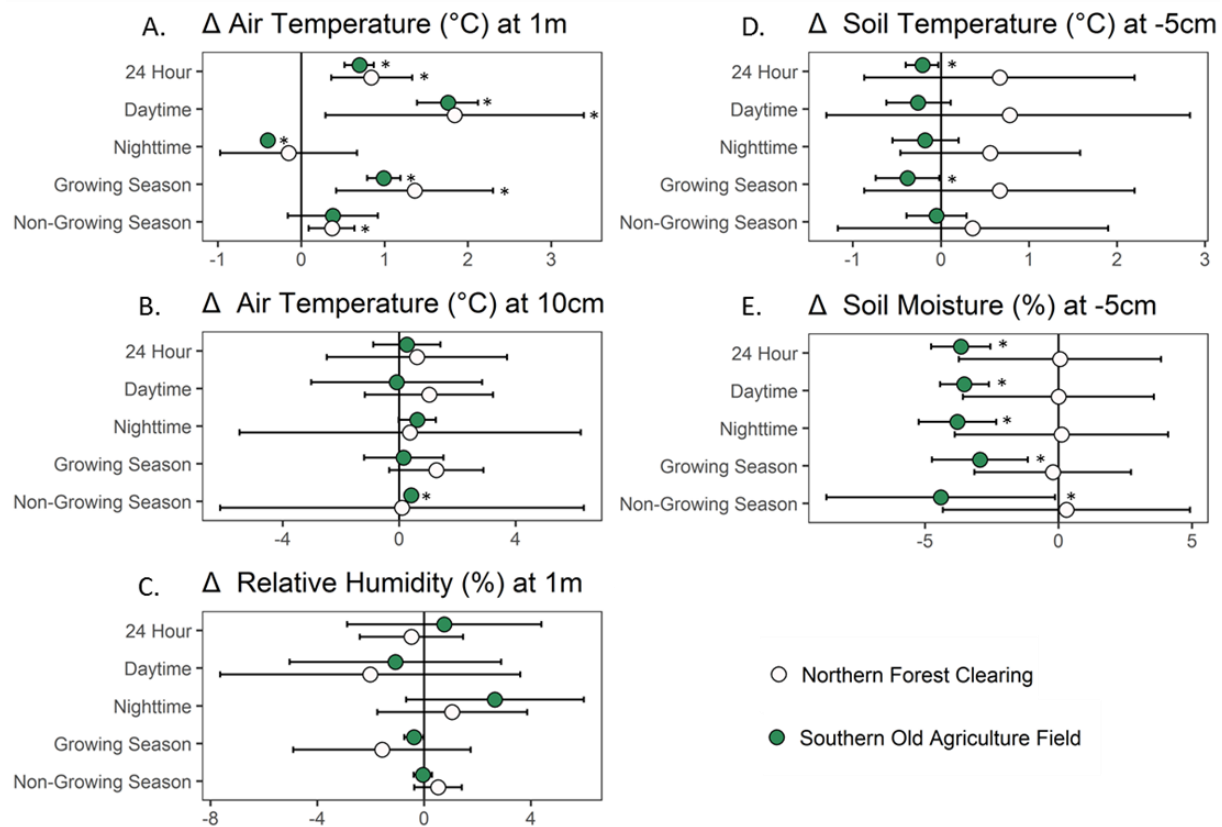


Figure 2. Mean and 95% confidence intervals for the difference between chambered and ambient plots. (A) air temperature at 1m above ground, (B) air temperature at 10cm above ground, (C) relative humidity at 1m above ground, (D) soil temperature at 5cm below the soil surface, and (E) soil moisture at 5 cm below the soil surface from August 1, 2015- July 31, 2016.

Figure 2 (cont'd). Significant differences from unpaired t-tests (n=6) denoted with (*). Some confidence intervals not visible due to small size.

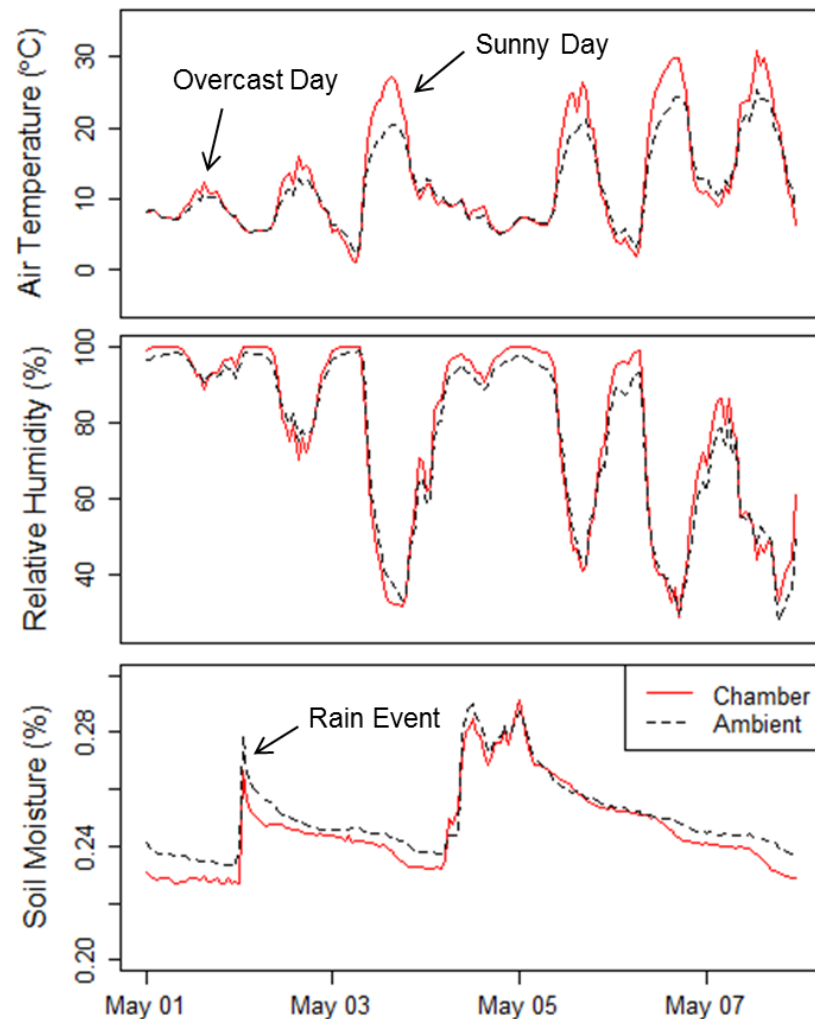


Figure 3. Time series showing variability in chamber effects. (A) air temperature at 1m height, (B) relative humidity at 1m height, and (C) soil moisture at 5cm below the soil surface due to daily weather patterns during a typical week during the growing season (May 1-7, 2016) at the southern site in Hickory Corners, MI, USA. The chambers warm air temperatures most during the day during clear sky conditions. The values shown are the average hourly values of the warmed plots (solid red) and the ambient plot (dashed black).

Air temperatures (1 m) measured in the nine remaining chambers showed that the OTC warmed consistently across plots, with slightly more variation between treatments in the southern old-agriculture field (northern site: median hourly standard deviation of 0.02 °C;

southern site: 0.23°C). The chambers did not significantly warm the air at 10 cm above the soil at either site, although nighttime air temperature at 10 cm was slightly warmer in the chambers at the southern site (Figure 2B). The chambers did not significantly alter relative humidity at 1 m at either site (Figure 2C).

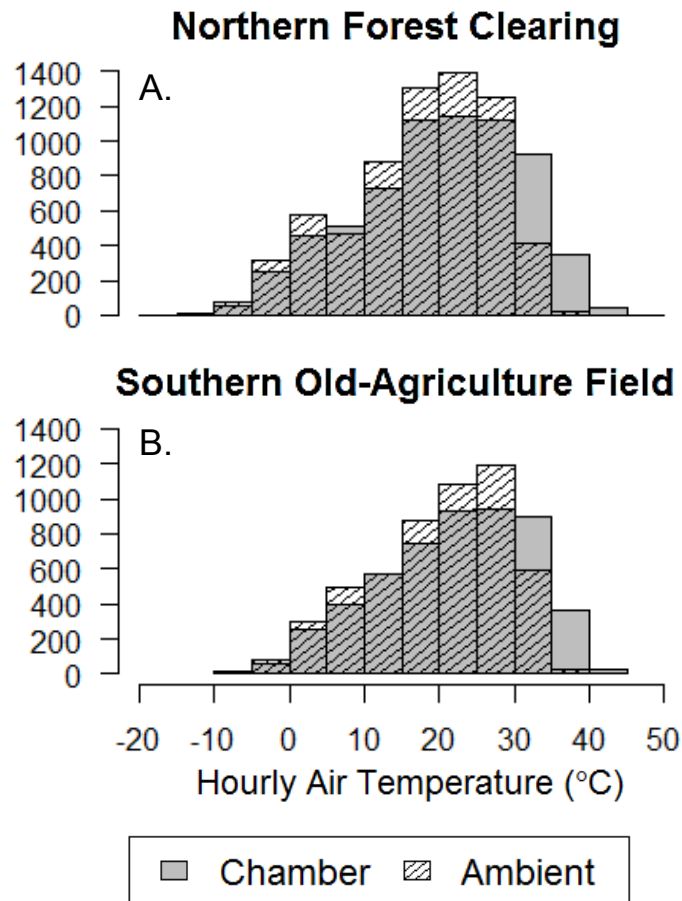


Figure 4. Frequency of hourly daytime temperatures (°C) at 1m height in chambered and ambient plots. Measurements taken during the growing season at the (A) Northern Site and (B) Southern Site. Chambered plots were warmer than ambient plots, especially on the hottest days of the year.

The chambers' effects on soil temperature and moisture varied between the two sites. The soil was cooler (-0.21 ± 0.10 °C, Figure 2D) and drier (-3.66 ± 0.57 %, Figure 2E) year-round in chambers vs. on ambient plots at the southern site. However, we found no significant difference in soil temperature and moisture between chambered and control plots at the northern site

(Figure 2D and 2E). The chambered plots exhibited greater variability in soil temperature during the non-growing season at the southern site ($F = 0.02$, $df = 2$, $p=0.05$), with 2 additional spring freeze/thaw cycles than in the ambient plots (Figure 5).

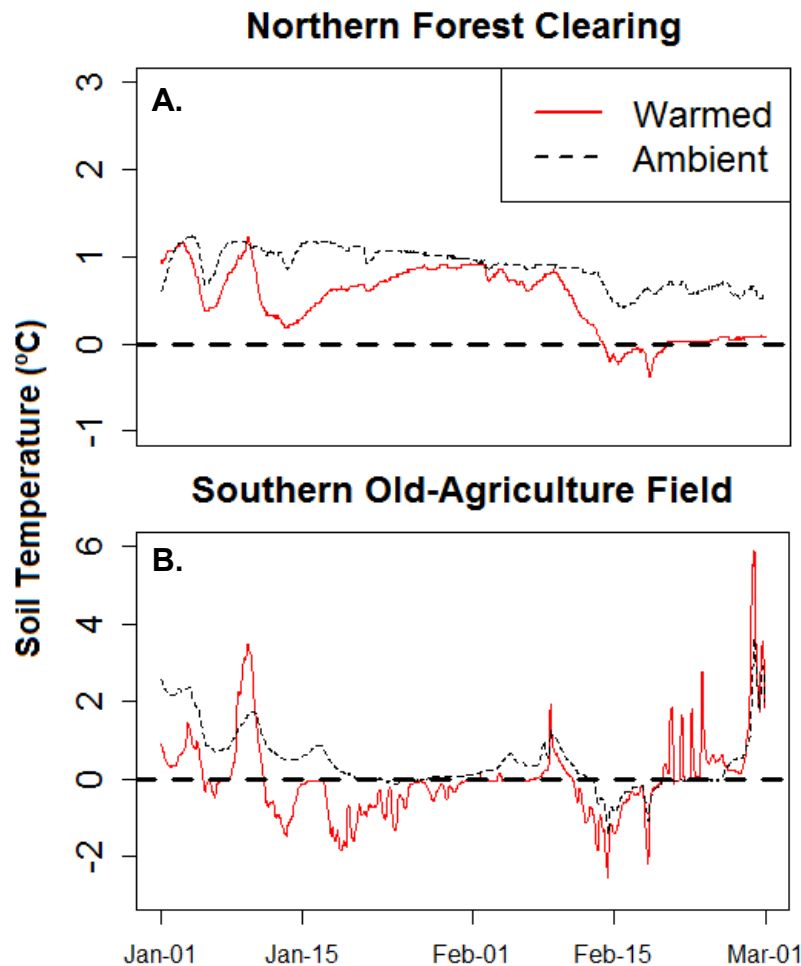


Figure 5. Hourly soil temperatures (°C) at -5cm beneath the soil surface during the winter to spring transition for a warmed and a control plot at the (A) Northern and (B) Southern sites. In winter, chambered plots exhibited greater temperature variability, cooler soil temperature, and increased freeze thaw cycles than ambient plots likely due to decreased snowpack insulation. In general, soils were colder, experienced greater variability in temperature, and experienced more freeze thaw cycles at the southern site than at the northern site during the winter.

The chambers withstood harsh weather conditions with minimal damage to the infrastructure. During the study, the northern site experienced a maximum five-second wind speed of 26.4 m/s and annual snowfall of 244 cm with a maximum snow depth of 63.5 cm. The

southern site experienced a maximum five-second wind speed of 24.6 m/s and annual snowfall of 127 cm with maximum snow depth of 22.9 cm.

DISCUSSION

Our chamber design simulated mid-century global warming scenarios in taller-stature plant communities. We observed mean daytime warming of 1.8 °C at both sites, consistent with all Representative Concentration Pathway (RCP) scenarios for 2046-2065 and three RCP scenarios for 2081-2100 predictions from the International Panel on Climate Change 5th Assessment (Stocker et al. 2014). This amount of warming is consistent with past warming experiments using passive, low-stature ITEX chambers, and is known to change the phenology, growth, survival and reproduction of low-stature plants (Arft et al. 1999).

The increased variability in soil temperature caused by the chambers led to an increase in freeze/thaw cycles also predicted to occur with climate change, likely due to reduced or intermittent snowpack providing decreased insulation (Brown & DeGaetano 2011; Henry 2008). This phenomenon was more pronounced at the southern site, where there is less snowpack that is more likely to completely melt between snowfall events than at the northern site where the greater snowpack was likely decreased but not absent. Soil freeze/thaw cycles lead to the lysis of soil microbes, resulting in changes in abundance and community structure of soil bacteria (Kumar et al. 2013). The death of these microbes may also release nitrogen and phosphorus in the soil leading to plant uptake and response (Edwards & Jefferies 2010).

The chambers led to overall cooler and drier soil in the warmed plots vs. ambient plots in the southern site, but not in the northern site. We suggest greater productivity in the southern site's chambered plots led to increased soil shading and transpiration, resulting in cooler and drier soil on the chambered plots as observed in Hollister et al. (2006). At the northern site,

moisture likely drained quickly from the sandy soil on all plots regardless of warming treatment ($\bar{x}_{\text{Northern Site}}=11.0\pm1.9\%$; $\bar{x}_{\text{Southern Site}}=20.5\pm0.5\%$). This regional variation highlights the importance of an affordable warming method to assess variability in warming responses across many sites.

The relatively simple and low-maintenance design of these taller-stature chambers encourages their use in conjunction with globally coordinated ecological experiments such as Nutrient Network and Drought-Net (Fraser et al. 2013). By combining experiments, researchers will gain the opportunity to investigate the interactive effects of numerous global change drivers in situ across taller-stature systems worldwide.

CHAPTER 2

SHORT-TERM RESPONSES TO WARMING VARY BETWEEN NATIVE VS. EXOTIC SPECIES AND WITH LATITUDE IN AN EARLY SUCCESSIONAL PLANT COMMUNITY

ABSTRACT

Climate change is expected to favor exotic plant species over native species because they tend to have wider climatic tolerances and greater phenological plasticity. Warming is also likely to intensifying the enemy release phenomenon, leading to greater exotic advantage in a changing climate. Here, we examine direct effects of warming on plant abundance and phenology, as well as indirect effects of warming propagated through herbivores, in two heavily invaded plant communities in Michigan, USA separated by approximately three degrees latitude. At the northern site, the effects of warming were largely consistent with theoretical expectations. Warming (+1.8 °C above ambient) increased exotic plant abundance by 19% but decreased native plant abundance by 31%, indicating that exotic species may be favored in a warmer world. Warming also resulted in earlier spring emergence (1.65 ± 0.77 days), earlier flowering (2.18 ± 0.92 days), and greater damage by herbivores (2-fold increase), affecting exotic and native species equally. Additionally, contrary to expectations, native and exotic plants experienced similar amounts of herbivory. Warming did not have strong ecological effects at the southern site, only resulting in a delay of flowering time by 2.42 ± 0.83 days for both native and exotic species. Consistent with the enemy release hypothesis, exotic plants experienced less herbivory than native plants at the southern site, and herbivory was lower under warming for both exotic and native species. Plants and herbivores may not have benefited from warming at the southern site because ambient temperatures were already close to the critical threshold for physiological stress, while ambient temperatures at the northern site were further from the thermal maximum.

INTRODUCTION

Understanding the mechanisms for the success of exotic plants in their introduced range is a longstanding ecological question (Tilman 1985; Davies 2011; Simberloff 2013). One proposed

mechanism for exotic success is the ability to take advantage of vacant spatial or temporal niche space (Elton 1958), especially following disturbance (Herbold & Moyle 1986). A second proposed mechanism is enemy release, in which exotic plants experience reduced herbivore, disease, and pest pressure compared to their native counterparts (Williamson 1996; Keane & Crawley 2002). However, anthropogenic climate change is likely to interact with each of these mechanisms through extended growing season length and rapidly warming temperatures (Wolkovich & Cleland 2011). These changes are also expected to shift plant-herbivore relationships (Dijkstra et al. 2012). Understanding the mechanisms that influence exotic plants' success under warmer temperatures in their introduced range is critical for understanding and forecasting plant community dynamics.

Warmer temperatures driven by climate change are known to influence the abundance of exotic species (Dukes 2010). For example, warmer temperatures could increase climatic suitability for exotic species (Dukes & Mooney 1999). Further, native species that are stressed by a rapidly changing climate may have reduced competitive ability and therefore, allow opportunities for exotic establishment or growth in the introduced range (Alpert et al. 2000; Chambers et al. 2016; Ma et al. 2017). Determining the mechanisms for exotic success and how they may be altered with a changing climate is therefore of critical importance.

Climate change may favor exotic species with phenologies that differ from their co-occurring native species in their introduced range (Wolkovich & Cleland 2011). Warmer temperatures lead to extended growing seasons and may create open niche space for exotic species that are able to establish earlier in the season or extend their life cycle past those of native species. Extended growing seasons have promoted the success of exotic species in both terrestrial and aquatic systems (Stachowicz et al. 2002; Fridley 2012). Exotic species may also be favored in their

introduced range due to high phenological plasticity (Richards et al. 2006). Accordingly, species with high phenological flexibility may have an advantage in a rapidly changing environment (Willis et al. 2008; Matesanz et al. 2010).

The success of exotic species under climate change is also likely to depend on their interactions with herbivores. Exotic plants benefit from enemy release when herbivores prefer native species and therefore indirectly enable exotic species to thrive under relatively less consumptive pressure (Bremm et al. 2016). Climate change may moderate the magnitude and direction of herbivore impacts on exotic plant success by warmer temperatures directly increasing insect metabolic rate (Bale et al. 2002; Fey & Herren 2014). The warming induced reduction of plant food quality may also require herbivores to consume greater quantities to meet nutritional demands (Hillebrand et al. 2009; Sardans et al. 2012). If native species experience increased herbivory due to warming, but this increase is lower in magnitude for exotic species (i.e. enemy release), exotic species would experience greater success under warmer climate conditions. Alternatively, herbivores may limit the growth of competitive plant species and, therefore, promote community stability (Van der Putten et al. 2010; Blois et al. 2013; Post 2013; Borer et al. 2014). Thus, forecasting community consequences of exotic plant success may depend on the influence of herbivores in a warmer world.

Climate change is expected to favor exotic species in their introduced ranges (Dukes & Mooney 1999; Hellmann et al. 2008), but further research is needed. These predictions are largely based on theory and observational studies rather than manipulative experiments (Wolkovich & Cleland 2011; Sandel & Dangremond 2012; Wolkovich et al. 2013). Experiments that test the differential effects of warming on exotic and native species often use simplified biotic communities, which may reduce the ability to make predictions under the full complexity

of realistic communities (Lu et al. 2015; Munier et al. 2010). Also, in situ field-based experimental warming of plant communities has been largely focused on high-latitude and high-elevation ecosystems with low-stature plant communities, and we lack sufficient understanding in mid-latitude and lower-elevation ecosystems (Arft et al. 1999). Finally, in order to best examine the effects of warming on exotic success we must examine ecosystems where introductions of exotics are more prevalent (Simberloff & Von Holle 1999; Turbelin et al. 2017).

We addressed these research gaps with an *in situ* field experiment that manipulated warming in highly invaded early successional, mid-latitude plant communities. We examined the effects of warming exotic v. native species for one annual cycle to test the following hypotheses:

- 1) *Warming will increase exotic species cover more than co-occurring native species cover.*
- 2) *Warming will advance exotic species phenology more than co-occurring native species phenology.*
- 3) *Warming will indirectly favor exotic species through increased leaf tissue damage by herbivores to co-occurring native species under warming.*

METHODS

Site Description

We examined two invaded, early successional plant communities in Michigan, USA separated by 354 km and approximately three degrees latitude (Figure 6A) from May 2015 through October 2016. The northern site is a forest clearing at The University of Michigan's Biological Station (UMBS) located at 45.56° N, -84.71° W and 239 meters above sea level (Figure 6B). The 1.53 km² clearing was clear-cut in 1994 and is dominated by *Danthonia spicata*, *Centaurea stoebe*, and *Poa pratensis* (Table 1). The site was maintained through mowing to prevent forest succession until the beginning of the experiment. The mean annual temperature in Emmet County where the site is located is 5.4 °C and mean annual rainfall and

snowfall are 76.7 cm and 244 cm, respectively (1981-2010 normals) (Menne et al. 2012a; Menne et al. 2012b).

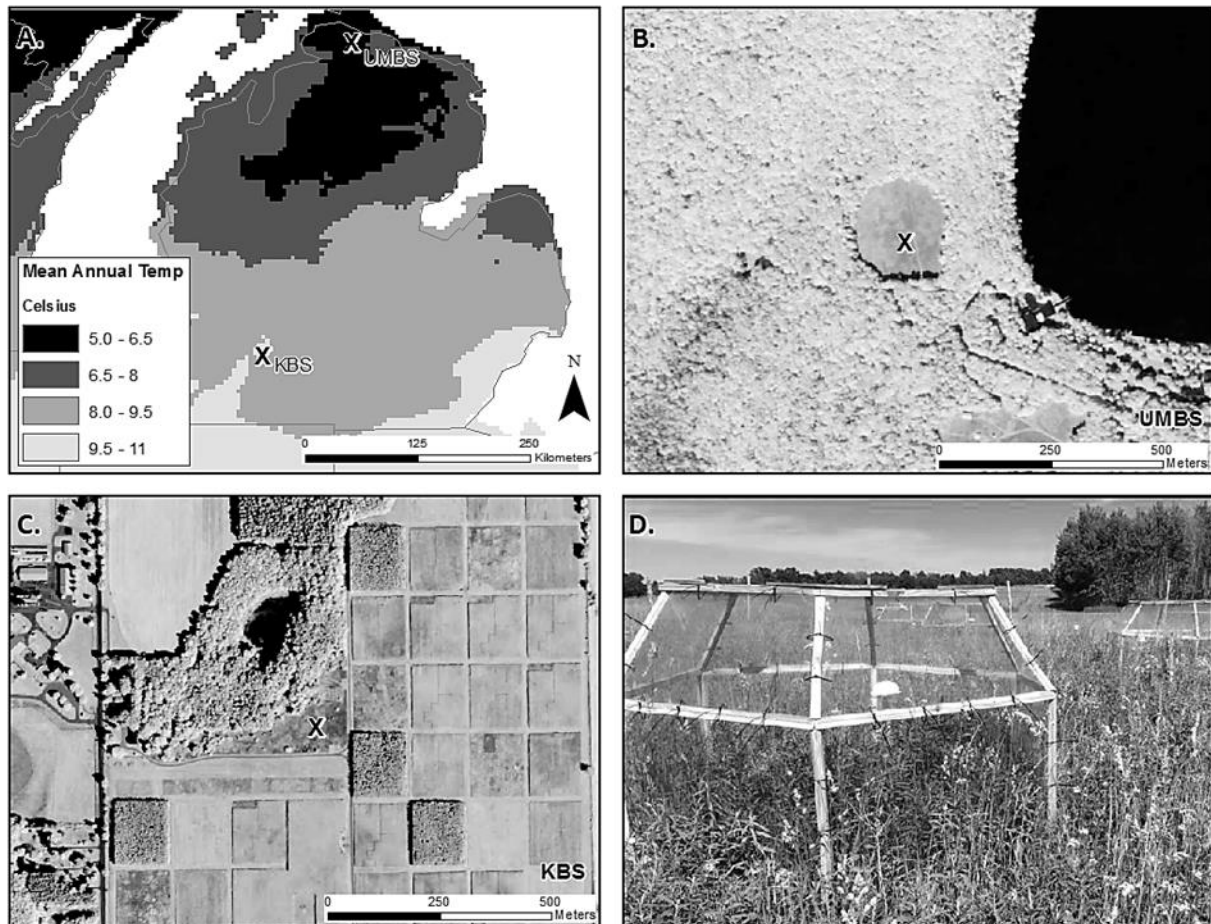


Figure 6. Site location map. A. Map of mid-western United States with study site locations and 30-year temperature normals from 1981-2010 (PRISM Climate Group 2013). B. University of Michigan Biological Station forest clearing site. C. Kellogg Biological Station successional agriculture field site. D. Open-top chamber experiment in southern old-agriculture field located at Kellogg Biological Station. In B and C, the location of the experiment is marked with an X.

The southern site is an early successional grassland (previously agriculture field) at Kellogg Biological Station's Long Term Ecological Research Site (KBS-LTER) located at 42.40° N, -85.40° W and 289 meters above sea level (Figure 6C). The site is dominated by *Solidago canadensis*, *Poa pratensis*, and *Hieracium pratense* (Table 1, Figure 6D) and was maintained through mowing to prevent succession prior to the beginning of the experiment. The

mean annual temperature in Kalamazoo County where the site is located is 10.1 °C and mean annual rainfall and snowfall are 100.4 cm and 127 cm, respectively (1981-2010 climate normals) (Menne et al. 2012a; Menne et al. 2012b).

Table 1. Species list for each site and site-level relative abundance. All origin values retrieved from USDA Plant Database at the county level. Species relative abundance based on composition estimates collected in August 2016. Relative abundance calculated for each site as the (sum of each species' cover/sum of all species)*100.

Northern Forest Clearing			Southern Old-Field		
Species	Origin	Relative Abundance (%)	Species	Origin	Relative Abundance (%)
<i>Danthonia spicata</i>	Native	38.34	<i>Solidago canadensis</i>	Native	34.27
<i>Centaurea stoebe</i>	Exotic	29.65	<i>Poa pratensis</i>	Exotic	33.74
<i>Poa pratensis</i>	Exotic	11.44	<i>Hieracium pratense</i>	Exotic	10.17
<i>Carex pensylvanica</i>	Native	6.21	<i>Phleum arvense</i>	Exotic	4.73
<i>Pteridium aquilinum</i>	Native	4.83	<i>Achillea millefolium</i>	Native	4.56
<i>Rumex acetosella</i>	Exotic	2.84	<i>Trifolium pratense</i>	Exotic	3.28
<i>Hypericum perforatum</i>	Exotic	1.11	<i>Centaurea stoebe</i>	Exotic	2.82
<i>Hieracium pilosella</i>	Exotic	<1	<i>Euthamia graminifolia</i>	Native	1.66
<i>Poa compressa</i>	Exotic	<1	<i>Rubus allegheniensis</i>	Native	1.05
<i>Quercus rubra</i>	Native	<1	<i>Potentilla recta</i>	Exotic	<1
<i>Fragaria vesca</i>	Native	<1	<i>Dactylis glomerata</i>	Exotic	<1
<i>Vaccinium angustifolium</i>	Native	<1	<i>Daucus carota</i>	Exotic	<1
<i>Solidago gigantea</i>	Native	<1	<i>Trifolium repens</i>	Exotic	<1
<i>Pilosella aurantiaca</i>	Exotic	<1	<i>Alliaria petiolata</i>	Exotic	<1
<i>Asclepias</i> sp.	Native	<1	<i>Celastrus orbiculatus</i>	Exotic	<1
<i>Betula</i> sp.	Native	<1	<i>Arrhenatherum elatius</i>	Exotic	<1
<i>Antennaria</i> sp.	Native	<1	<i>Hypericum perforatum</i>	Exotic	<1
<i>Solidago nemoralis</i>	Native	<1	<i>Elymus repens</i>	Exotic	<1
<i>Tragopogon dubius</i>	Exotic	<1	<i>Asclepias</i> sp.	Native	<1
<i>Acer rubrum</i>	Native	<1	<i>Taraxicum officinale</i>	Exotic	<1
			<i>Barbarea vulgaris</i>	Exotic	<1
			<i>Cardamine hirsuta</i>	Exotic	<1

Experimental Design

At each site, we established 24 1m² plots within a 25 meter by 36 meter area surrounded by a 3 meter tall fence to prevent deer browsing. Plots were separated by at least 4 m of buffer area to prevent edge impacts from chambers (e.g. shading) in neighboring plots and to serve as walkways for sampling. As part of a larger, long-term experiment, the plots were treated with a randomized, fully factorial design that included insect reduction and small mammal exclosure in addition to the warming treatment (Appendix A). We tested for differences between plots with the additional herbivore reduction treatments and those without herbivore treatments prior to examining each of our response variables. When the effects of herbivore reduction treatments were not significant ($p > 0.05$), we tested our hypotheses across all plots. There were no initial differences between warmed and ambient plots in average percent cover across species at either site at the beginning of the experiment (Northern Site: Warmed ($t=-0.76$, $df=126.1$, $p=0.45$) and Origin ($t=-0.01$, $df=12.89$, $p=0.99$); Southern Site: Warmed ($t=-0.84$, $df=180.21$, $p=0.40$) and Origin ($t=1.86$, $df=13.01$, $p=0.09$).

We warmed the plots year-round using a passive, open-top chamber designed to warm taller stature (≤ 1.5 m) plant communities, minimize edge effects, and allow for migration of flying and ground dwelling organisms in and out of the chambers (Molau & Mølgaard 1996; Welshofer et al. *in press*). We used clear, UV-transmitting, 1/8" Lexan Polycarbonate sheets to elevate temperatures using sunlight (ePlastics, San Diego, CA; Figure 6D). We installed the chambers during spring 2015 at both sites. The chambers warmed plots, on average, by (1.84 ± 0.79 °C and 1.73 ± 0.19 °C) in the forest clearing and old agriculture field, respectively, with no evidence for differences in relative humidity. Warming varied with irradiance and therefore exhibited the hottest temperatures (up to approximately 45 °C) during the daytime in

the growing season. The chambers reduced winter soil temperature, presumably due to reduced snowpack insulation, and resulted in greater variability in soil freeze/thaw cycles (Welshofer et al. *in press*). Here we report ecological data collected during the second growing season (2016), after nearly a full year of the warming treatment.

Data Collection

Because this study was part of a longer-term experiment, we used non-destructive sampling methods. We estimated percent cover for each species in each 1m² plot taken at the beginning of the experiment (Spring 2015) and at the end of the second growing season (August 2016). During the time of species emergence (March-May), we also visually estimated species cover in each plot every 3-4 days. KW performed all estimates to prevent bias between plots or sampling occasions. The origin of each species was classified as either 'native' or 'exotic' according to the PLANTS Database (USDA 2017).

We monitored three major plant phenological events (green-up, flowering, and seed set) at each plot every 3-4 days from March through October 2016. We defined 'emergence' as the first appearance of annual species and $\geq 50\%$ greening for perennial species for each species in each plot. We defined 'flowering' as the period between flower bud break and flower senescence. 'Seed set' was determined when an individual exhibited withering of the stigma along with swelling of the ovaries. For both flowering and seed set, we recorded the date when at least one individual for each species in each plot exhibited the phenological stage.

We visually estimated the percent of leaf tissue missing (presumably due to herbivory) at the end of the second growing season to capture cumulative damage throughout the season (Schultheis et al. 2015). We haphazardly selected four leaves vertically dispersed along the stem on three individuals of each species within each plot (n=12 leaves per species per plot). When

three individuals of that species were not present within a plot, we sampled the maximum number of individuals present. We sampled all species except for *Achillea millefolium*, because visual estimates of tissue damage on its feather-like leaves were difficult to assess. For graminoid species, many ends of the blade were removed making it difficult to determine the amount of tissue eaten. To mediate this concern, we used the average length of undamaged blades for that species as a reference for each leaf herbivory estimate. We only recorded the percent of missing plant tissue, as browning of the tissue could have been a response to abiotic stress or fungal infections (Green et al. 1990). To prevent bias, KW completed all estimates with visual aids where exact herbivory percentages were calculated using ImageJ software (Schneider et al. 2012).

Statistical Analysis

We took several steps to prepare the data for analysis. We natural log transformed each percent cover value to conform to the assumptions of general linear regression. As an index of spring green-up phenology, we computed the date at which each species reached its median cover value per plot. For time of flowering and seed set, we computed the median date that each species was observed in each phenological stage in each plot. For the leaf herbivory models, we did not consider plots with the reduced insect treatment (n=12 per site).

To evaluate the separate and interactive effects of warming and origin (native vs. exotic) on plant percent cover, emergence, flowering time, seed set, and leaf herbivory, we fit mixed-effect ANOVA models. For each response variable at each site, we used a 2-step process to compare complex and reduced models using likelihood ratio tests ($\alpha=0.05$) to select the most parsimonious model. To account for the additional treatments applied as part of the long-term experiment, even though they are not a focus of this study, we first compared the full models

including terms for insect reduction and small mammal exclusion treatments to models without those terms. Next, we compared the model including an interaction between warming and origin to a model without the interaction to test for interactive effects of warming and plant species origin on each response variable. A significant interaction term would indicate that the change in the response variable caused by warming depends on plant species origin. Plant species identity was included as a random intercept in each model to account for additional species-specific variation within all response variables. For leaf herbivory models, we used a generalized linear regression model with Poisson error, and the identity of individual plants was also included as a random intercept because multiple observations were made on each individual. 95% confidence intervals were calculated for each parameter estimate using bootstrap methods (number of simulations=999). We calculated the denominator degrees of freedom using the Satterthwaite approximation method (Bolker et al. 2009). To additionally test whether warming increased the aggregate abundance of all exotic plants at each site, we summed the total cover for all exotic species in each plot (n=24/site) and performed a non-hierarchical ANOVA with temperature treatment (warmed/ambient) as a fixed effect. We used one-way ANOVA ($\alpha=0.05$) procedures to evaluate whether initial differences in species cover between warmed and ambient plots existed prior to the start of the experiment, and completed all analyses using R version 3.1.2 (R Development Core Team 2010) and the R package lme4 (Pinheiro and Bates 2000).

RESULTS

At the northern site, the response of plant cover to warming depended on origin (Table 2, Figure 7A). Warming increased exotic plant cover by 19% and decreased native plant cover by 31% relative to the average cover in ambient plots ($((\bar{x}_{\text{warmed}} - \bar{x}_{\text{ambient}}) / \bar{x}_{\text{ambient}}) * 100$). The greatest increases in total cover were found in *Rumex acetosella*, *Poa pratensis*, and *Hypericum*

perforatum (all exotic). However, we did not find evidence that warming influenced plant cover for either native or exotic species in the southern old agriculture field (Table 2, Figure 7B). We did not find evidence for an interactive effect between warming and origin on average species cover this site (Appendix E). However, we observed the greatest increases in total cover due to warming of *Trifolium* sp. (exotic) and *Euthamia graminifolia* (native), with the greatest decreases in *Poa pratensis* and *Centaurea stoebe* (both exotic).

Table 2. Parameter estimates for the most parsimonious general linear mixed-effects model based on likelihood ratio tests (LRT) for each of five response variables explained by warming and species' origin at each site. All models included species as a random intercept. The leaf herbivory model additionally included a random intercept for individual plant identity and used Poisson error term (i.e. a generalized linear mixed-effect model). 95% confidence intervals calculated using bootstrap techniques (number of simulations=999). All parameters significantly different from zero are bolded. Positive origin effects indicate greater values for native species relative to exotic species.

Response	Northern Forest Clearing			Southern Old Agriculture Field		
	Estimate	Denom. df	95% CI	Estimate	Denom. df	95% CI
Species Cover						
Warmed	0.62	122.14	(0.16, 1.07)	-0.17	213.81	(-0.37, 0.02)
Origin	0.36	21.47	(-0.68, 1.42)	0.82	20.49	(-0.22, 1.92)
Warmed*Origin	-0.69	122.14	(-1.38, -0.07)			
Residuals		126			225	
Emergence						
Warmed	-1.65	106.34	(-3.15, -0.09)	-0.51	249.98	(-3.26, 2.23)
Origin	6.99	18.4	(0.03, 13.73)	6.38	15.29	(-1.08, 13.38)
Residuals		115			262	
Flowering Time						
Warmed	-2.18	84.19	(-4.02, -0.35)	2.42	211.24	(0.76, 3.88)
Origin	-15.17	12.88	(-42.94, 9.79)	37.14	18.94	(4.00, 70.88)
Insects	2.13	84.07	(0.41, 3.96)			
Residuals		91			225	
Seed Set Time						
Warmed	0.82	81.09	(-1.98, 3.70)	0.89	183.53	(-2.26, 3.79)
Origin	-8.62	11.09	(-31.26, 14.66)	33.77	16.75	(-1.14, 65.48)
Residuals		87			195	
Leaf Herbivory						
Warmed	0.68	102.82	(0.01, 1.29)	-0.70	187.29	(-1.30, -0.14)
Origin	1.02	8.54	(-0.72, 2.74)	1.89	8.15	(0.67, 3.22)
Residuals		466			763	

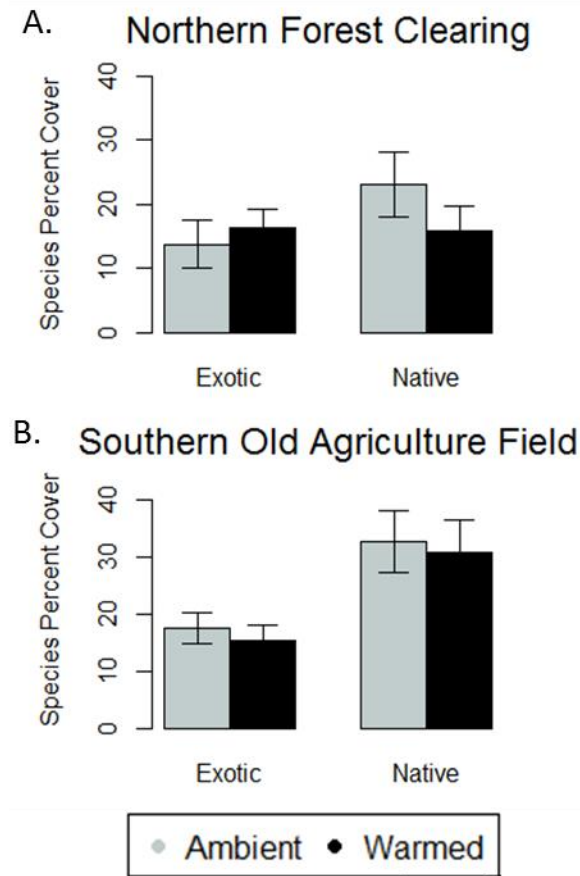


Figure 7. Species percent cover (mean $\pm$ 1SE) measured at the end of summer 2016 at the (A) northern forest clearing and (B) southern old agriculture field. Data were measured for each species in each plot at each site (n=24). An ANOVA ran on the most parsimonious model shows warming increased overall species cover at the northern site ($p<0.05$), with no other differences at the southern site or between species origin.

At the northern forest clearing, plant species emerged an average of 1.65 ± 0.77 (SE) days earlier in warmed plots than ambient plots and exotic species emerged 6.99 ± 3.44 days earlier than native plant species (Table 2, Figure 8A). Native and exotic plants shifted emergence phenology by the same amount of time, on average (i.e. the interaction of warming and origin was not present in the most parsimonious model, Appendix B). Plants flowered -2.18 ± 0.92 days earlier in the warmed plots than plants in the ambient plots at the northern site (Table 2, Figure 8C), and the magnitude of this shift was also indistinguishable between native and exotic species (Appendix B). We found that plots at the northern site without the insecticide treatment flowered

2.13±0.86 days later than plots with the insecticide treatment (Table 2). The timing of seed set did not vary according to warming treatment or origin at the northern site (Table 2, Figure 8E). At the southern old agriculture field, warming did not affect spring emergence phenology for native or exotic plants (Table 2, Figure 8B). Warming delayed plant flowering by 2.42±0.83 days for both native and exotic species (Table 2, Figure 8D). At this site, exotic plants flowered 37.14±16.57 days earlier than native plants, regardless of warming (Figure 8D). The timing of seed set also did not vary according to warming treatment or origin at the southern site (Table 2, Figure 8F). The interaction between warming and origin was not present in the most parsimonious model for any of the phenology responses at the northern or southern study site (Appendix E).

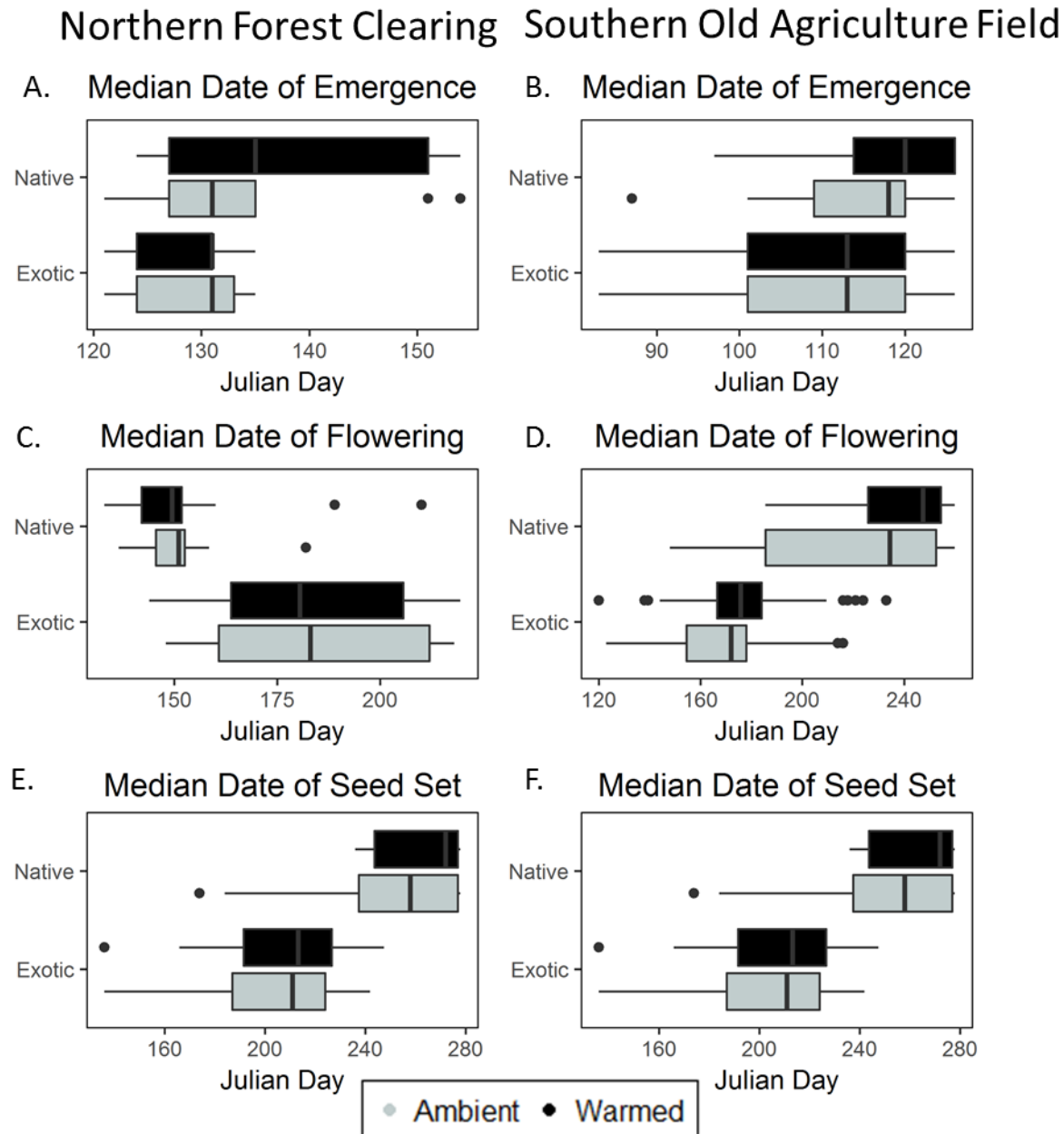


Figure 8. Phenological responses measured throughout the 2016 growing season. Data were measured for each species in each plot at each site. Boxplots display the median (central line), 25th percentile (lower bound), 75th percentile (upper bound), and smallest and largest value (ends of whiskers) no larger than 1.5x the interquartile range from the upper and lower quartiles. An ANOVA ($\alpha=0.05$) was ran on each response's most parsimonious model to determine significant differences between groups. A and B show the date where each species reached 50% of its maximum cover. B. and C. show the median date of flowering. D. and F. show the median date of seed set.

Warming increased leaf herbivory approximately two-fold at the northern site (Table 2, Figure 9A). Native and exotic species experienced similar levels of herbivory (Table 2, Figure 9A), but the way herbivory varied according to warming treatment was statistically indistinguishable for native vs. exotic species (Appendix B). Warming decreased leaf herbivory in the southern old agriculture field by approximately half, and native species experienced about 6-fold greater herbivory than exotic species (Table 2). The most parsimonious model for the southern site also did not contain a term for the interaction of warming and herbivory (Appendix B).

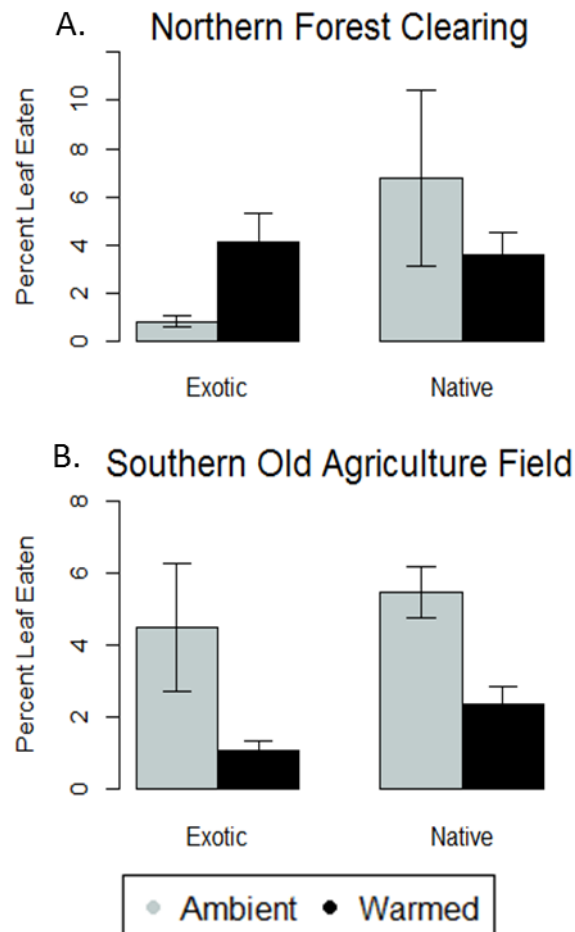


Figure 9. Percent of leaf eaten (Mean $\pm$ 1SE) at the end of summer 2016 at the (A) northern forest clearing and (B) southern old agriculture field. Data were measured for four leaves on three individuals of each species in each plot (n=12) for each site. An ANOVA ran on the most parsimonious model shows warming increased herbivory at the northern site and decreased

Figure 9 (cont'd). herbivory at the southern site. Native species also experienced more herbivory than exotic species at the southern site.

DISCUSSION

We found evidence that warming favored exotic species over native species at the northern forest clearing site, where the effects of warming were largely consistent with our predictions. However, the same levels of warming did not have strong ecological effects at the southern old agriculture field site. We suggest that plants and herbivores may not have benefited from warming at the southern site because ambient temperatures were already close to the critical threshold for physiological stress, while ambient temperatures at the northern site were cooler than the thermal maximum.

The moderate ecological effects observed at the northern forest clearing site were consistent with our expectations. Greater plant cover in warmed plots compared to ambient plots is consistent with widespread experimental studies that found warming increases plant productivity (Rustad et al. 2001) and/or increases the abundance of more productive species (Fridley et al. 2016). The observed shifts in emergence and flowering time (either earlier or later) at the northern site are consistent with the literature (Dunnell & Travers 2011; Calinger et al. 2013). Warmed plants also experienced greater herbivory than those in ambient conditions. This could be due to lower food quality and therefore increased herbivore demand (Hillebrand et al. 2009; Sardans et al. 2012). Additionally, warmer temperatures could also increase the metabolism of insects within the warmed plots, in turn increasing the amount of leaf tissue required by the herbivore (Gillooly 2001). Exotic species emerged an entire week earlier than native species, indicating their broad climate tolerance early in the growing season, but the reproductive phenology of native and exotic species responded similarly to warming.

Responses at the southern old agriculture field site indicate that plants may have experienced physiological stress (delayed flowering and reduced herbivory) when exposed to warming, highlighting the dangers of living close to the thermal maximum (Tewksbury et al. 2008). The thermal optima for individual plant species tend to cluster in a narrow range around 30° C and are surprisingly insensitive to ambient temperature (Dell et al. 2011). As a result, lower-latitude communities are more likely to be composed of organisms living at or above their critical thermal maximum (Laurance et al. 2011; Stuart-Smith et al. 2015). Given the same magnitude of warming, we would expect more local extinctions and greater declines in performance in lower-latitude communities if warming exceeds the stress threshold for a greater proportion of species (Perez et al. 2016).

Overall, we found limited evidence that exotic plant species will respond to climate change differently than native species, with only one response (cover at the northern site) including an interaction term in the most parsimonious model. The lack of differential effects of warming between native or exotic species may be due to similar ruderal traits shared by species of both origins. Because these systems are both heavily disturbed (clear-cut and agriculture), weedy species dominate their communities. Weedy species that readily establish in disturbed environments are likely to have broad climatic tolerances and be relatively insensitive to moderate warming, regardless of their continent of origin (Theoharides & Dukes 2007). For example, plant species with affinity for warmer soils and that produce wind-dispersed seeds tended to be the best colonizers of newly available habitat patches as temperatures increase in an alpine system (Matteodo et al. 2013).

This experiment suggests climate warming is not likely to differentially benefit exotic plant species as theory suggests, but rather that the magnitude and direction of community

responses may depend on the difference between environmental temperature and the thermal optima and maxima of individual species. While short-term experiments such as this increase our understanding of annual ecological variation, they also provide insight into potential mechanisms that lead to long-term ecological dynamics (Chesson & Huntly 1989; Magnuson 1990; Shriver 2016). Future research will provide insight to whether these short-term direct and indirect responses to warming translate into greater success of exotic plant species over time.

APPENDICES

APPENDIX A

Additional methods used in warming experiment.

Insect Reduction Methods- As part of the long-term experiment, we reduced insect herbivory through the application of Merit-75 WP insecticide at a concentration of 0.031 g/L with 1.2 L applied for all insect exclusion plots at each site every 13-15 days while measurements were taken during the growing season (Bayer Environmental Science, Research Triangle Park, NC). An equal amount of water (1.2 L) was applied evenly across plots where insects were not reduced within the same treatment session in order to reduce any unequal effects of added water in the insecticide to the plants. All insecticide applications were performed to dry vegetation during early morning low-wind conditions and no precipitation in the following 24 hours. Care was taken to spray all plants across sub-canopies within each plot, such that ground dwelling plants also received treatment.

Small Mammal Reduction Methods- We also reduced small mammal herbivory as part of the long-term experiment by installing 91 cm tall, 1.3 cm gauge mesh hardware cloth around 12 plots at each site at the beginning of the experiment. The cloth was buried 20-30 cm beneath the ground (Brown & Davidson 1977). The fencing was reinforced in Spring 2016 by attaching a second layer of hardware cloth along the ground to reduce plot access to burrowing mammals (Nutrient Network: A Global Research Cooperative 2008). We tested the integrity of the fences during three separate 72 hour events at each site and in each year. During each sampling event we set Sherman live traps in the fenced and unfenced plots that were baited with peanut butter and oats (H. B. Sherman Traps, Tallahassee, FL: 6.5 2.0 × 2.5 cm). The traps were checked for captures and reset every 8 hours.

Herbivore treatments do not affect air temperature- To examine whether the herbivore treatments affected the chamber's ability to warm the plots, we performed an ANOVA test using the pendants' mean hourly temperatures in plots with either type of herbivore reduction (small mammals and insects) and plots without herbivore reduction. We found no statistical differences between herbivore treatments in mean temperatures at either site (Northern Site: $F = 1.97$, $df = 2$, $p = 0.14$; Southern Site: $F=0.07$, $df =2$, $p = 0.93$).

Solar Radiation Shields- To avoid direct radiation on the sensors that would generate inaccurate readings, radiation shields were constructed using methods described by Fedler (2013).

Time-Period Methods and Statistical Analyses- We analyzed the data on air temperature (1m and 10 cm heights), relative humidity (1m), soil temperature (-5 cm) and soil moisture (-5 cm) for each site separately. We used two sided, unpaired t-tests to compare the means of the hourly data ($n_{\text{chambered}} = 3$; $n_{\text{ambient}}=3$) during the following intervals: 24-hour (entire day), daytime, nighttime, growing season, and non-growing season. We classified 'daytime' hours as those between sunrise and sunset based on nearby cities: Richland, MI and Pellston, MI (United States Naval Observatory 2016). Similarly, 'nighttime' hours were classified as the hours between sunset and sunrise. We defined 'growing season' as beginning on the spring equinox and ending the day before fall equinox and 'non-growing season' as the date beginning fall equinox and ending the day before spring equinox.

*Data Quality Control Methods-*Data were graphically and systematically screened for faulty data due to equipment issues. The sensors used in this experiment record extreme values (i.e. $\pm 999^{\circ}\text{C}$) or N/A values when physically damaged (chewed wires, loose wire connections). These values were removed from the analyses. Days that included <24 hours were also removed to standardize analyses between different timeframes. When a sensor malfunctioned for < 30 days,

those dates were removed from all sensors in the analysis. When a sensor malfunctioned for ≥ 30 days, we removed this sensor's results from the analysis to avoid excluding dates from a substantial portion of the season (Table S1). After screening, 94% and 83% of the total data across all sensor types were used for analysis at the northern and southern site, respectively.

APPENDIX B.

Dates of sensor malfunction at both sites from August 1, 2015- July 31, 2016.

Table 3. Dates of sensor malfunction due to technology damage or maintenance at the northern forest clearing and southern old-agriculture field from August 1, 2015- July 31, 2016. Each pair includes data from one chamber plot and one ambient plot using one HOBO Microstation H21-002 4-channel data logger (Air Temperature at 1m, Relative Humidity at 1m, Soil Moisture at -5cm) and one HOBO 4-channel external U12-008 data logger (Air Temperature at 10cm and Soil Temperature at -5cm). Each 4-channel data logger collected the same type of measurement from the chambered (two of the channels) and ambient (remaining two channels) plot in each pair. When a sensor malfunctioned for < 30 days, these dates were removed from all sensors in the analysis. When a sensor malfunctioned for ≥ 30 days, we removed this sensor's results from the analysis to avoid excluding dates from a substantial portion of the season.

Measurement	Pair	Chamber	Ambient	Dates Malfunctioned	Result
Northern Forest Clearing (University of Michigan Biological Station)					
Air Temp 1m, RH 1m, Soil Moisture	1	x	x	04/01/2016 12:00–04/02/2016 9:00	Dates removed from all sensors for this measurement
Air Temp 1m, RH 1m, Soil Moisture	2	x	x	05/16/2016 15:00–06/10/2016 10:00; 09/26/2015 10:00	Dates removed from all sensors for this measurement
Air Temp 10cm; Soil moisture	2	x		08/01/2015 00:00–11/24/2015 10:00	Sensor excluded from analysis
Southern Old-Agriculture Field (Kellogg Biological Station)					
Air Temp 1m	1	x		07/01/2016 4:00 – 07/31/2016 23:00	Dates removed from all sensors for this measurement
Air Temp 10cm; Soil moisture	2	x		08/01/2015 0:00 – 10/30/2015 12:00	Sensor excluded from analysis
Air Temp 1m; RH 1m	3	x		08/01/2015 0:00 – 10/30/2015 12:00	Sensor excluded from analysis
Air Temp 10cm	3	x		Variable All Year (≥ 30 days)	Sensor excluded from analysis

APPENDIX C.

Unpaired t-tests for warmed and ambient treatments at the northern forest clearing.

Table 4. Comparisons of average differences between chambered-ambient plots in the northern forest clearing at the University of Michigan Biological Station from August 1, 2015- July 31, 2016. T-tests were performed on the mean of the hourly values for each of the intervals described below. Significant differences ($p < 0.05$) are in bold text.

Measurement		t	df	n warmed, n ambient	p-value	Difference (Chamber - Ambient)	
						Mean	95% CI
Air Temperature, 1m (°C)							
	Year-round, 24 h	6.93	2.18	3,3	0.02	0.84	(0.36, 1.33)
	Daytime Only	3.87	2.91	3,3	0.032	1.84	(0.29, 3.39)
	Nighttime Only	-0.52	3.90	3,3	0.633	-0.15	(-0.97, 0.67)
	Growing Season	5.48	2.31	3,3	0.023	1.36	(0.42, 2.30)
	Non-growing Season	5.49	2.11	3,3	0.028	0.37	(0.09, 0.64)
Air Temperature, 10cm (°C)							
	Year-round, 24 h	2.21	1.05	2,2	0.26	0.61	(-2.49, 3.71)
	Daytime Only	5.00	1.08	2,2	0.11	1.03	(-1.18, 3.23)
	Nighttime Only	0.68	1.08	2,2	0.61	0.37	(-5.49, 6.24)
	Growing Season	9.99	1.00	2,2	0.06	1.28	(-0.34, 2.89)
	Non-growing Season	0.20	1.01	2,2	0.87	0.10	(-6.15, 6.35)
Relative Humidity, 1m (%)							
	Year-round, 24 h	-0.91	2.40	3,3	0.45	-0.48	(-2.41, 1.46)
	Daytime Only	-1.16	2.91	3,3	0.33	-2.02	(-7.63, 3.60)
	Nighttime Only	1.10	3.57	3,3	0.34	1.05	(-1.75, 3.85)
	Growing Season	-1.77	2.36	3,3	0.20	-1.57	(-4.90, 1.74)
	Non-growing Season	1.67	3.73	3,3	0.18	0.52	(-0.37, 1.41)
Soil Temperature, -5cm (°C)							
	Year-round, 24 h	4.73	1.07	2,2	0.12	0.67	(-0.87, 2.20)
	Daytime Only	2.27	1.48	2,2	0.19	0.78	(-1.30, 2.83)
	Nighttime Only	5.06	1.16	2,2	0.10	0.56	(-0.46, 1.58)
	Growing Season	4.73	1.07	2,2	0.12	0.67	(-0.87, 2.20)
	Non-growing Season	1.49	1.46	2,2	0.32	0.36	(-1.17, 1.90)
Soil Moisture, -5cm (%)							
	Year-round, 24 h	0.04	3.42	3,3	0.97	0.06	(-3.73, 3.84)
	Daytime Only	0.00	3.45	3,3	0.99	0.00	(-3.58, 3.57)
	Nighttime Only	0.09	3.41	3,3	0.94	0.12	(-3.88, 4.11)
	Growing Season	-0.21	3.74	3,3	0.84	-0.21	(-3.15, 2.72)
	Non-growing Season	0.20	3.28	3,3	0.86	0.30	(-4.33, 4.93)

APPENDIX D.

Unpaired t-tests for warmed and ambient treatments at the southern old-agriculture field.

Table 5. Comparisons of average differences between chambered-ambient plots in the southern old-agriculture field at Kellogg Biological Station from August 1, 2015- July 31, 2016. T-tests were performed on the mean of the hourly values for each of the intervals described below. Significant differences ($p < 0.05$) are in bold text.

						Difference (Chamber - Ambient)	
Measurement		t	df	n warmed, n ambient	p-value	Mean	95% CI
Air Temperature, 1m (°C)							
	Year-round, 24 h	13.61	2.67	2,3	0.002	0.70	(0.52, 0.87)
	Daytime Only	17.64	2.41	2,3	0.001	1.76	(1.39, 2.12)
	Nighttime Only	-22.50	2.23	2,3	0.001	-0.40	(-0.47, -0.33)
	Growing Season	21.06	2.05	2,3	0.002	0.99	(0.79, 1.19)
	Non-growing Season	5.35	1.29	2,3	0.08	0.38	(-0.16, 0.92)
Air Temperature, 10cm (°C)							
	Year-round, 24 h	2.82	1.01	2,2	0.21	0.26	(-0.89, 1.42)
	Daytime Only	-0.35	1.02	2,2	0.78	-0.09	(-3.02, 2.85)
	Nighttime Only	10.37	1.08	2,2	0.05	0.62	(-0.02, 1.26)
	Growing Season	1.21	1.15	2,2	0.46	0.15	(-1.21, 1.52)
	Non-growing Season	6.19	2.86	3,2	0.01	0.41	(0.19, 0.63)
Relative Humidity, 1m (%)							
	Year-round, 24 h	0.84	2.15	2,3	0.49	0.75	(-2.88, 4.39)
	Daytime Only	-1.15	2.04	2,3	0.37	-1.08	(-5.04, 2.88)
	Nighttime Only	3.00	2.33	2,3	0.08	2.65	(-0.68, 5.98)
	Growing Season	0.46	2.64	2,3	0.68	0.55	(-3.54, 4.64)
	Non-growing Season	1.41	2.17	2,3	0.28	0.98	(-1.81, 3.78)
Soil Temperature, -5cm (°C)							
	Year-round, 24 h	-3.75	3.02	3,3	0.03	-0.21	(-0.40, -0.03)
	Daytime Only	-1.93	3.96	3,3	0.13	-0.26	(-0.62, 0.11)
	Nighttime Only	-1.30	3.85	3,3	0.27	-0.18	(-0.55, 0.20)
	Growing Season	-3.07	3.57	3,3	0.04	-0.38	(-0.74, -0.02)
	Non-growing Season	-0.47	2.74	3,3	0.67	-0.05	(-0.39, 0.29)
Soil Moisture, -5cm (%)							
	Year-round, 24 h	-10.49	3.00	2,3	0.001	-3.66	(-4.77, -2.55)
	Daytime Only	-12.89	2.77	2,3	0.001	-3.53	(-4.44, -2.61)
	Nighttime Only	-8.48	2.88	2,3	0.004	-3.79	(-5.24, -2.33)
	Growing Season	-5.56	2.71	2,3	0.02	-2.94	(-4.74, -1.15)
	Non-growing Season	-4.47	1.98	2,3	0.05	-4.41	(-8.69, -0.13)

APPENDIX E.

Summary of likelihood ratio tests for mixed-effects model comparisons.

Table 6. Summary of likelihood ratio tests ($\alpha=0.05$) used to determine the most parsimonious mixed-effects model. Percent Cover, Emergence, Flowering Time, and Timing of Seed Set included species identification as a random effect and leaf herbivory included species identification AND individual plant identification as random effects. Significant results listed in bold.

Fixed Model Comparisons	Northern Site Summary Results	Southern Site Summary Results
ln(Percent Cover) (2015)		
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects+ Mammals vs. [M2]Cover~ Warmed+Origin+Warmed*Origin+Insects	$\chi^2=0.35$; df=1; p=0.55	$\chi^2=0.90$; df=1; p=0.34
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects vs. [M2]Cover~Warmed+Origin+Warmed*Origin	$\chi^2=0.30$; df=1; p=0.58	$\chi^2=0.84$; df=1; p=0.36
[M1]Cover~Warmed+Origin+Warmed*Origin vs. [M2]Cover~Warmed+Origin	$\chi^2=0.60$; df=1; p=0.44	$\chi^2=2.46$; df=1; p=0.12
ln(Percent Cover) (2016)		
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects+ Mammals vs. [M2]Cover~ Warmed+Origin+Warmed*Origin+Insects	$\chi^2=0.10$; df=1; p=0.75	$\chi^2=2.05$; df=1; p=0.15
[M1]Cover~Warmed+Origin+Warmed*Origin+Insects vs. [M2]Cover~Warmed+Origin+Warmed*Origin	$\chi^2=1.11$; df=1; p=0.29	$\chi^2=0.04$; df=1; p=0.85
[M1]Cover~Warmed+Origin+Warmed*Origin vs. [M2]Cover~Warmed+Origin	$\chi^2=4.23$; df=1; p=0.04	$\chi^2=0.76$; df=1; p=0.38
Emergence		
[M1]Emergence ~Warmed+Origin+Warmed*Origin+Insects+Mammals vs. [M2]Emergence~ Warmed+Origin+Warmed*Origin+Insects	$\chi^2=0.54$; df=1; p=0.46	$\chi^2=1.15$; df=1; p=0.28
[M1]Emergence~Warmed+Origin+Warmed*Origin+Inse cts vs. [M2]Cover~Warmed+Origin+Warmed*Origin	$\chi^2=0.10$; df=1; p=0.76	$\chi^2=1.92$; df=1; p=0.17
[M1]Emergence~Warmed+Origin+Warmed*Origin vs. [M2]Emergence~Warmed+Origin	$\chi^2=0.03$; df=1; p=0.86	$\chi^2=1.51$; df=1; p=0.22
Flowering Time		
[M1]Flowering Time~ Warmed+Origin+Warmed*Origin+Insects+Mammals vs. [M2] Flowering Time~ Warmed+Origin+Warmed*Origin+Insects	$\chi^2=0.32$; df=1; p=0.57	$\chi^2=0.33$; df=1; p=0.57

Table 6 (cont'd).

[M1] Flowering Time~ Warmed+Origin+Warmed*Origin+Insects vs. [M2] Flowering Time~Warmed+Origin+Warmed*Origin	$\chi^2=5.40$; df=1; p=0.02	$\chi^2=1.87$; df=1; p=0.17
[M1] Flowering Time~Warmed+Origin+Warmed*Origin vs. [M2] Flowering Time~Warmed+Origin	$\chi^2=0.65$; df=1; p=0.42	$\chi^2=0.37$; df=1; p=0.54
Timing of Seed Set		
[M1]Seed Set~ Warmed+Origin+Warmed*Origin+Insects+Mammals vs. [M2] Seed Set~ Warmed+Origin+Warmed*Origin+Insects	$\chi^2=0.08$; df=1; p=0.78	$\chi^2=0.05$; df=1; p=0.82
[M1] Seed Set~Warmed+Origin+Warmed*Origin+Insects vs. [M2] Seed Set~Warmed+Origin+Warmed*Origin	$\chi^2=0.39$; df=1; p=0.53	$\chi^2=0.32$; df=1; p=0.57
[M1] Seed Set~Warmed+Origin+Warmed*Origin vs. [M2] Seed Set ~Warmed+Origin	$\chi^2=0.00$; df=1; p=0.95	$\chi^2=0.02$; df=1; p=0.89
Leaf Herbivory		
[M1]Leaf Herbivory~Warmed+Origin+Warmed*Origin+ +Mammals vs. [M2]Leaf Herbivory~Warmed+Origin+Warmed*Origin	$\chi^2=2.43$; df=1; p=0.12	$\chi^2=1.41$; df=1; p=0.24
[M1]Leaf Herbivory~Warmed+Origin+Warmed*Origin vs. [M2]Leaf Herbivory~Warmed+Origin	$\chi^2=0.25$; df=1; p=0.62	$\chi^2=0.76$; df=1; p=0.38

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