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Interactions in a warmer world: effects of experimental warming, conspecific density, and herbivory on seedling dynamics

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Abstract. Many effects of a changing climate for organisms, populations, and ecosystems are already apparent. Less studied are the effects of increases in temperature on species interactions. While warming may potentially alter interactions among species, species interactions may also mediate individual species responses to ongoing climatic change. In this experiment we manipulated temperature in field-based, open-top chambers for three years to examine the relationship between biotic interactions and climatic warming on the population dynamics of seedlings of *Quercus alba*. We investigated the effect of warming on rates of insect herbivory on *Q. alba* seedlings. Additionally, we assessed the relative effects of increasing temperature, insect herbivory, and conspecific density on seedling survival. We found two unexpected results. First, we observed a negative relationship between temperature and levels of insect herbivory during each year of the experiment. Second, higher levels of herbivory were associated with higher rates of survival to the second year of the study. Although we never detected a direct effect of conspecific density on seedling survival, herbivory and conspecific seedling density did interact to influence *Q. alba* seedling survival early in the experiment. Taken together, our results indicate species responses to climatic warming may be contingent on intra- and interspecific interactions, sometimes in complicated and counter-intuitive ways.

Key words: active warming; climatic warming; insect herbivory; interspecific interaction; intraspecific interaction; *Quercus alba*; warming experiment; white oak.

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INTRODUCTION

While many studies make it abundantly clear that ongoing climatic warming has affected the phenology (Parmesan and Yohe 2003, Menzel et al. 2006, Parmesan 2006, Amano et al. 2010, Morin et al. 2010), performance (Rossi et al. 2004, Cleland et al. 2012), and distributions (Parmesan and Yohe 2003, Walther 2010, Chen et al. 2011) of species, less appreciated is the fact that climatic change might also alter both intra- and interspecific interactions (Tylianakis et al. 2008). Predictions related to the effects of ongoing climatic change largely consider the direct effects of climate on species without taking into account how interactions between species might also

affect their responses to climatic change (Davis et al. 1998, Araújo and Rahbek 2006, Buckley et al. 2010). In part, the lack of studies on the interplay between biotic interactions and climatic change arises from the general approaches taken to study the consequences of climatic change. For instance, macroecological approaches that rely on climate envelope models are generally too broad in scale to assess the role of local interactions (Araújo and Rahbek 2006). Conversely, manipulative studies in the field are often too small and too expensive to incorporate a focus on biotic interactions and instead focus on how experimental warming alters ecosystem processes or aggregate measures such as diversity or biomass (e.g., Rustad et al. 2001, Classen et al. 2010, Adair et al. 2011, Hoover et al. 2012). More experiments aimed at determining the effects of climatic warming on species interactions are needed in order to facilitate predictions about the responses of communities and ecosystems to climatic change.

Here, we use field-based, open-top, actively warmed chambers to investigate the interplay between biotic interactions and climatic warming on population dynamics of seedlings of a common eastern temperate deciduous tree, *Quercus alba*. We take advantage of a fortuitous mast event (i.e., intermittent, synchronized acorn production among many individuals within a region) to examine the combined impacts of conspecific seedling density, herbivory by insects, and experimental warming on seedling survival over three years. Factors limiting seedling establishment are a strong filter on tree recruitment (Clark et al. 1998, Hubbell et al. 1999, Brown and Wu 2005, Matthes and Larson 2006), and an understanding of these factors may provide valuable insights into predicting how future forests will respond to climatic change.

Previous studies have documented the effects of herbivory and conspecific density, both individually and together, on tree seedling survival with mixed results. For example, seedling recruitment may be negatively correlated with conspecific density because of intraspecific competition or because seedling density and the density of their natural enemies (e.g., insect herbivores) are positively correlated (Janzen 1970, Connell 1971). The effects of herbivory on plant survival are mixed, with some studies demonstrating negative effects, some positive effects, while still others show no effects on survival (Karban and Strauss 1993, Maron and Crone 2006). While conspecific density and herbivory can influence the survival of individual seedlings and in turn influence population growth rate, no studies, to our knowledge, have investigated the relative impacts of density and herbivory under experimental warming over multiple years. Doing so is critical because understanding the factors that limit establishment can elucidate the factors that govern population dynamics of forests in the future. For instance, Clark et al. (1998) found that establishment limitation at the seedling stage was one of the strongest factors limiting recruitment in southern Appalachian forests. However, few studies have examined the interplay between biotic interactions and seedling establishment of eastern deciduous trees under climatic warming.

Since January 2010, we have used actively warmed open-top chambers in an eastern temperate forest to address the following interrelated questions: (1) Does the magnitude of insect herbivory on white oak seedlings increase with warming? (2) Is the rate of population growth of *Q. alba* seedlings following a mast event affected by warming, herbivory, or conspecific seedling density? (3) Does herbivory interact with temperature and seedling density to affect seedling survival?

Materials and Methods

Study location/warming experiment

We did this study in an array of twelve actively warmed, open-top chambers (OTCs) located in an 80-year-old oak-hickory stand in Duke Forest (near Hillsborough, NC). The site receives approximately 1140 mm of precipitation year^{-1}, and the mean annual temperature is 15.5°C. The OTCs are octagonal in shape, 5 m in diameter, 1.2 m tall, and constructed around similarly-sized adult *Q. alba* (mean diameter at breast height ~20 cm). Nine of the OTCs are heated between 1.5 and 5.5°C above ambient in half-degree increments (i.e., a regression design; Cottingham et al. 2005), and three serve as ambient controls. We continuously regulate temperature in the chambers with hydronic radiators. In the nine warmed OTCs, air temperature is increased when blown

Table 1. Results determining if the estimated slope is significantly different than one for linear regressions examining the relationship between achieved temperature treatments and target temperature treatment. The upper CI and lower CI are upper and lower 95% confidence intervals for the slope estimates.

	Linear regression					Slope test
Year	Slope estimate	R^2	P	Upper CI	Lower CI	p
2010	0.98	0.94	2.61e−07	1.17	0.82	0.77
2011	0.90	0.99	4.87e−11	0.97	0.83	0.01
2012	0.90	0.94	2.08e−07	1.07	0.76	0.20

over the radiator and through two concentric rings of 15-cm diameter plastic plena that are located 1.7 and 0.8 m from the chamber walls. Hot air enters the chamber via two rows of 2-cm diameter holes located along the bottom-side of the plena. We continuously measure air temperature (°C) in all OTCs with automated dataloggers (CR1000, Campbell Scientific Inc.). The three ambient control chambers are identical in every way, except that the air is not warmed when it enters the OTC. These actively warmed chambers were turned on in early 2010 and are part of a larger, ongoing study investigating the effects of warming on community and ecosystem dynamics (see Pelini et al. 2011).

Abiotic conditions in the open-top chambers

At two locations in each chamber, we continuously measured air temperature and soil temperature in the organic and inorganic (mineral) soil (model SQ110; Apogee Instruments Inc., Logan, UT, USA). We also measured the relative humidity (HS-2000V capacitive polymer sensors; Precon, Memphis, TN, USA) and volumetric soil moisture (Model CS616 TDR probes, Campbell Scientific Inc.). We calculated vapor pressure deficit (VPD) as $(1 - (RH/100)) \times 0.61121 \times EXP((17.269 \times T)/(T + 237.3))$ where RH is the mean relative humidity and T is the mean temperature averaged over the growing season (April–September). During much of the growing season of 2012, the relative humidity sensors in two of our chambers, one of the ambient control chambers and the chamber set to +1.5°C, malfunctioned. Thus, we removed those chambers from analyses requiring relative humidity and vapor pressure deficit data. Observed temperatures in the OTCs matched target temperatures throughout the experiment (Table 1; SMA function of the SMATR package in R version 3.0.0 (Warton et al. 2013)). Unsurprisingly, some of the abiotic factors other than air temperature changed in association with the experimental temperature treatment: relative humidity significantly decreased with temperature in all years of the study; vapor pressure deficit was positively correlated with temperature treatment for all years of the study; mean soil temperature during the growing season, both at the organic and inorganic layers, was also positively correlated with air temperature. For each year of the study, soil moisture was never correlated with air temperature (Table 2).

Study species

Quercus alba (white oak), common in eastern deciduous temperate forests, is the most abundant tree species found at our field site. Its range spans from southwest Maine to northern Florida and west to eastern Texas. *Quercus alba* reproduces annually with heavier masts occurring every 3–10 years depending on weather conditions and prior reproductive history (Sork et al. 1993, Abrams 2003). Duke Forest was the site of an above-average *Q. alba* mast event during the fall of 2009 resulting in seedling densities from 41 to 135 seedlings m^{-2} within the OTCs.

Seedling surveys

In June 2010, the year following the mast event,

Table 2. Pearson's correlation coefficients between air temperature treatment and other abiotic variables. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Each independent variable is estimated as the chamber level mean during the growing season.

Variable	2010	2011	2012
Relative humidity	−0.82**	−0.78**	−0.76**
Soil moisture	−0.16	−0.24	−0.16
Vapor pressure deficit	0.67*	0.66*	0.63*
Organic soil temperature	0.90***	0.90***	0.77**
Inorganic soil temperature	0.73**	0.79**	0.46

we placed a metal tag with a unique identifier around the base of the stem of each *Q. alba* seedling within a randomly placed 1-m^2 plot located within each OTC. We surveyed each plot twice per year between 2010 and 2012 to determine seedling survival, seedling density (number of seedlings m^{-2}), and to estimate the amount of herbivory each seedling had sustained across each growing season. During the first survey each year, conducted during the early part of the growing season, we simply noted whether the seedling had survived through the winter. During the second survey, conducted at the end of the growing season, we estimated the accumulated level of foliar herbivory for each seedling. We visually estimated levels of herbivory as the percent leaf area removed by insect herbivores, including skeletonizers, leaf miners, and leaf chewers. The most common herbivores were skeletonizers, such as leaf-tying lepidoptera, and leaf chewers, such as the Asiatic Oak Weevil (*Cyrtepistomus castaneus*). We observed no new *Q. alba* seedlings in our study sites during the period in which these data were collected.

Statistical analyses

Does the magnitude of herbivory increase with warming? For each year of the study, we quantified the relationship between warming treatment and herbivory using univariate linear regression models. Herbivory is averaged across all seedlings in the permanently marked 1-m^2 plot. For all analyses using temperature treatment, we calculated the actual delta temperature as the difference between the mean air temperature in each chamber and the mean ambient air temperature measured over the growing season (April–September). To examine whether other abiotic variables might influence seedling survival, population growth rate of *Q. alba*, or herbivory, we additionally used univariate linear regression models with soil moisture, relative humidity, and vapor pressure deficit as independent variables in the models. All analyses met the assumptions of linear regression models.

Is the rate of population growth of Q. alba seedlings following a mast event affected by warming, herbivory, or conspecific seedling density? We used univariate linear regression models to determine whether the rate of population growth of *Q. alba* is associated with warming, conspecific seedling density, and herbivory during each year of the study. We did not use multiple regression owing to the low power associated with our small sample size. We calculated the rate of population growth (λ) for 2010 to 2011 and 2011 to 2012 as $\lambda = \ln(N_t/N_{t-1})$, where, N is the number of seedlings alive at year t in a plot during the spring survey, and N_{t-1} is the number of seedlings alive during the spring survey of the previous year in that same plot. For population growth calculated from 2010 to 2011, we used the mean temperature, mean plot level herbivory averaged across the seedlings in the 1-m^2 plots, and the plot level density of *Q. alba* seedlings (seedlings m^{-2}) measured during 2010. For population growth calculated from 2011 to 2012, we used these same variables measured during 2011. We additionally used univariate regression models to quantify the relationship between λ and soil moisture, relative humidity, and vapor pressure deficit.

Does herbivory interact with temperature or seedling density to affect seedling survival? Owing to our having only 12 chambers, we were limited in possible analyses to test for interactions between variables. A lack of power prevented us from examining all possible interactions among herbivory, temperature, and seedling density with typical regression analyses. However, we modified the analysis in Horton et al. (2009) to investigate possible interactions among some of these variables. In particular, we first calculated a logistic regression beta coefficient (β), where β indicates the probability that an individual seedling survived from year t to year $t + 1$ given the level of herbivory on that seedling in year t, for each chamber during each year. A positive β indicates that as levels of herbivory increase, so does the probability of surviving from one year to the next, while a negative β indicates that as levels of herbivory increase the probability of surviving decreases. To examine potential interactive effects of herbivory, temperature, and conspecific seedling density on survival, we next used multiple regression models. In the models, the dependent variable was the β calculated for each chamber, and the independent variables were mean herbivory (%) and conspecific seedling density. For all of the analyses described, the assumptions of normality were met according to the results of a Shapiro-

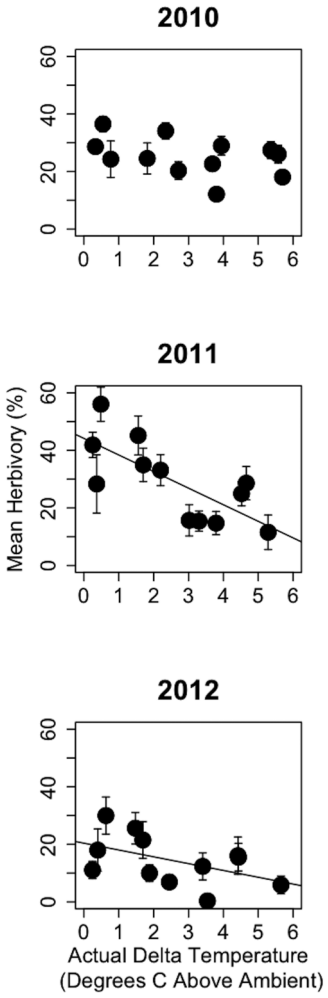


Fig. 1. Relationship between herbivory (%) and actual air temperature (degrees C above ambient air temperature) in each chamber for all three years of the study. R^2 and p values were calculated with univariate linear regression analyses. A black best-fit line is drawn for significant relationships.

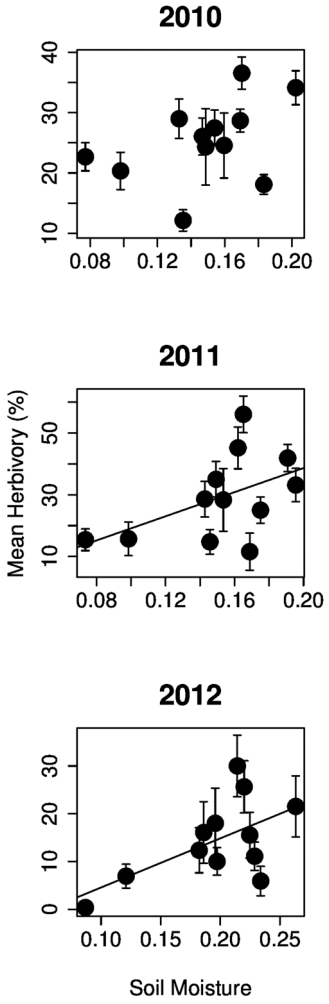


Fig. 2. Relationship between herbivory (%) and soil moisture. Herbivory is the plot-level average from each chamber. Soil moisture is an annual mean within each open-top chamber. A black best-fit line is drawn for significant relationships.

Wilk Normality Test on model residuals. We used R version 3.0.0 for all statistical analyses (R Development Core Team 2013).

Results

Does the magnitude of herbivory increase with warming? During 2010, mean herbivory (the estimated amount of leaf tissue removed) per seedling in each chamber ranged from 19% to 38%, and there was no relationship between the warming treatment and the magnitude of herbivory ($p = 0.18$; Fig. 1). In 2011, mean herbivory per seedling in each chamber ranged from about 11% to 56% and, in 2012 mean herbivory in each chamber ranged from just over 0% to about 30%. During 2011 and 2012 mean herbivory decreased significantly with increasing temperature (2011: $R^2 = 0.54$, $p = 0.006$; 2012: $R^2 = 0.24$, $p = 0.10$; Fig. 1). Herbivory decreased by an average of 6% and 3% with each degree of experimental warming for 2011 and 2012, respectively.

Herbivory was not related to relative humidity ($p > 0.15$ in all cases) or vapor pressure deficit (p

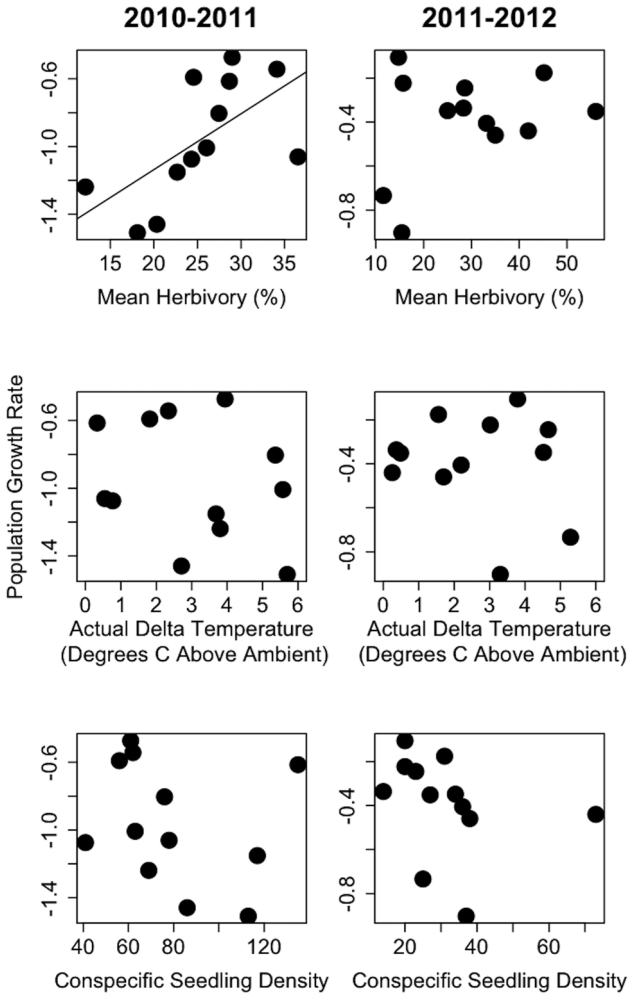


Fig. 3. Rate of population growth regressed against herbivory, temperature treatment, and conspecific seedling density for each year of the study.

> 0.30 in all cases) in any year of the study. Herbivory was not significantly associated with soil moisture in 2010 ($p = 0.16$; Fig. 2); however, there was a positive relationship between herbivory and soil moisture in 2011 ($p = 0.10$; Fig. 2) and 2012 ($p = 0.04$; Fig. 2), even though temperature and soil moisture were not correlated.

Is the rate of population growth of Q. alba seedlings following a mast event affected by warming, herbivory, or conspecific seedling density? Population growth rate of *Q. alba* seedlings (λ) was positively correlated with mean herbivory ($R^2 = 0.39$, $p = 0.03$; Fig. 3), but not seedling density ($p = 0.44$; Fig. 3) or warming ($p = 0.38$; Fig. 3) from 2010 to 2011, suggesting a potential positive association between herbivory and seedling survival. From 2011 to 2012, the rate of population growth was not correlated with mean herbivory, temperature treatment, or *Q. alba* seedling density ($p > 0.37$ in all cases; Fig. 3). Soil moisture, relative humidity, and vapor pressure deficit were not correlated with the rate of population growth of *Q. alba* seedlings in any year ($p > 0.25$ in all cases).

Does herbivory interact with temperature and seedling density to affect seedling survival? Conspecific density ($p = 0.06$), but not temperature ($p = 0.32$), predicted logistic regression beta coefficients (β) from 2010 to 2011, suggesting that the probability of seedling survival was in part due

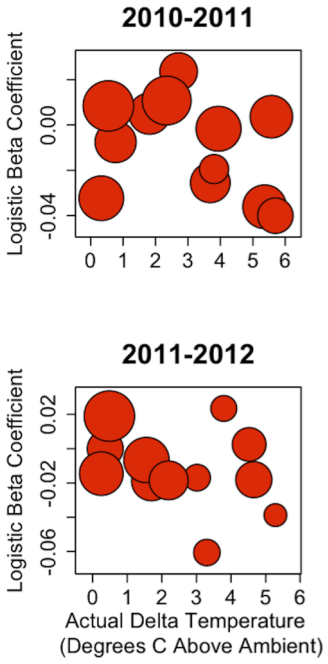


Fig. 4. Logistic regression beta versus temperature treatment (degrees C above ambient conditions) reported for years 2 and 3 of the study. Positive beta coefficients indicate a positive effect of herbivory on survival and negative beta coefficients indicate a negative effect of herbivory on survival due to herbivory. The size of each point represents the plot level mean herbivory.

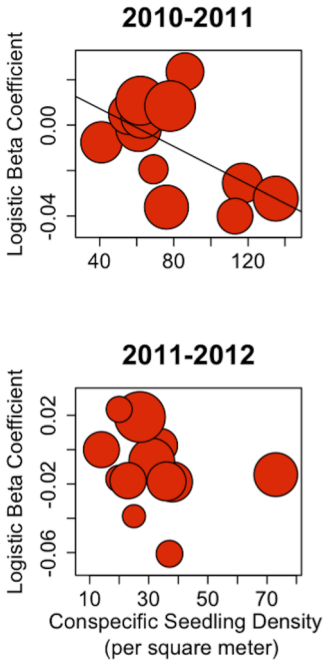


Fig. 5. Logistic regression beta versus density of seedlings (m^{-2}) in each chamber. Positive beta coefficients indicate a positive effect of herbivory on survival and negative beta coefficients indicate a negative effect of herbivory on survival due to herbivory. The size of each point represents the plot level mean herbivory.

to an interaction between herbivory and conspecific seedling density such that seedlings with herbivory which also occur in dense populations had a higher chance of mortality (Figs. 4 and 5; Table 3). We did not detect a relationship between the logistic regression beta coefficients and temperature ($p = 0.21$) or conspecific seedling density ($p = 0.25$; Figs. 4 and 5; Table 3) from 2011 to 2012.

Discussion

Ongoing climatic change can affect the performance and fitness of individuals, the dynamics of populations, the structure of communities and the distribution of species (Parmesan and Yohe 2003, Rossi et al. 2004, Menzel et al. 2006, Parmesan 2006, Amano et al. 2010, Morin et al. 2010, Walther 2010, Chen et al. 2011, Cleland et al. 2012). The effects of climatic change may be mediated by interactions among species, or climatic change may alter the outcomes of interactions among species, though this has been less extensively documented in the literature (e.g., Dury et al. 1998, Stiling et al. 2002, Hamilton et al. 2004, Rossi et al. 2004, Villalpando et al. 2009).

Two somewhat surprising results emerged from this three-year experimental study. First, rates of herbivory on *Q. alba* seedlings decreased as experimental temperatures increased up to 5.5°C above ambient. Second, higher levels of herbivory were associated with lower rates of seedling mortality going into the second year of the study; that is, across all temperature treatments, seedlings that were attacked more by herbivores had a higher probability of surviving to the next year. Although there was never a direct effect of density on seedling survival in any year of the experiment, herbivory and conspecific seedling density did interact to influence *Q. alba* seedling survival early in the

Table 3. Results of multiple regression models used to determine possible interactive effects between herbivory, conspecific seedling density, and temperature treatment (Whole Model: 2010–2011: $R^2 = 0.42$, $p = 0.09$; 2011–2012: $R^2 = 0.22$, $p = 0.33$). The dependent variable in the multiple regression models was the β value extracted from logistic regression models of herbivory against survival into the next growing season; a positive β value indicates that as levels of herbivory increase, so does the probability of surviving from one year to the next, while a negative β value indicates that as levels of herbivory increase the probability of surviving decreases.

Independent variable	F	Partial r^2	p
2010–2011			
Conspecific seedling density	4.74	0.35	**0.06**
Temperature treatment	1.59	0.15	0.24
2011–2012			
Conspecific seedling density	1.45	0.14	0.26
Temperature treatment	1.86	0.17	0.21

experiment. However, this effect was only observed during the first year of the experiment when seedling densities were highest. Taken together, our results indicate species responses to climatic warming may be contingent on intra- and interspecific interactions, sometimes in complicated and counter-intuitive ways.

Herbivory can influence plant population dynamics (Crawley 1983, Mulder 1999), and ongoing climatic change is likely to mediate the effects of herbivory on plant populations (Bale et al. 2002). During each year of our study we observed lower amounts of herbivory, or at least a trend toward lower amounts of herbivory, on *Q. alba* seedlings at higher temperatures (Fig. 1). These results diverge with theory (Hillebrand et al. 2009) and previous empirical studies (Coley and Aide 1991, Adams and Zhang 2009, Schemske et al. 2009, Currano et al. 2010, de Sassi and Tylianakis 2012) which have suggested that herbivory and temperature should be positively correlated.

So why should herbivory decrease under experimental warming? A recent study by O'Connor et al. (2011) used consumer prey models to predict the effects of temperature on insect herbivore abundance and found that the abundance of insect herbivores was negatively correlated with temperature. If such a scenario were applicable to our system, then increased temperatures would be associated with a decreasing abundance of herbivores such that the decrease in herbivory observed in our study may arise simply because of a reduction in the abundance of insect herbivores. We did not attempt to sample herbivore populations throughout the experiment because we did not want to alter their potential effects on the seedlings. However, previous work in this system demonstrates that the responses of other insect taxa to warming are often idiosyncratic, with the abundance and activity of some insect taxa responding positively to warming while others respond negatively to warming (Diamond et al. 2012, Stuble et al. 2013). Another possibility is that generalist herbivores switch from feeding on *Q. alba* to other species as temperatures increase. This would lead to apparent decreases in herbivory on *Q. alba* though overall levels of herbivory in the entire plant community might increase or not change at all with temperature. A common insect herbivore found at our study site, *Cyrtepistomus castaneus*, has been found to be associated with many species of host plants (Frederick and Gering 2006). Furthermore, our open-top chamber design may act differentially on the adult and juvenile stages of the lepidopteran skeletonizers observed in our study system. It is possible that adult lepidopteran skeletonizers in our system choose oviposition locations based on environmental cues such as temperature resulting in the observed decreases in herbivory in warmer chambers.

While the negative relationship between herbivory and temperature observed in our study may indicate direct effects of warming on insect herbivores, increased temperature may also indirectly affect herbivores through changes in the phenology or quality of their host plant or by affecting the natural enemies of herbivores. Previous studies suggest differences in the mechanisms underlying the phenology of plants and insects may lead to asynchronies in insect herbivores and their host plants (Visser and Both 2005). In our study system, this could alter the timing of herbivory, which could have important effects on the carbon balance maintained in *Q. alba* seedlings. In another active warming experiment at the same site in Duke Forest, plants in warmed treatments exhibited earlier budburst

than those at ambient temperatures (Salk 2011). This suggests *Q. alba* seedlings exposed to warming may have less herbivory because of advanced budburst and thus advanced leaf age. In a study on another oak species, Mopper and Simberloff (1995) found that the oaks that produced leaves earlier in the spring had lower rates of herbivory than those that produced leaves later in the growing season. In addition to host plant phenology, the decline in herbivory with increasing temperature may also be explained by variation in host plant quality under warming. In a study by Dury et al. (1998) on another species of oak, leaf nitrogen concentration decreased and condensed tannins content increased as a result of experimental warming.

Finally, the negative relationship between herbivory and temperature may arise because of the varying responses of different trophic levels to the warming treatments (Tylianakis et al. 2008). For example, in grassland systems Barton and Schmitz (2009) demonstrated that top-down predator effects interact with warming to decrease grasshopper abundance. Additionally, a study on the relative effects of mosquito larvae in a pitcher plant community shows a similar positive relationship between temperature and top-down processes (Hoekman 2010). While this was not quantified in our study, it is possible that warming led to an increase in the top-down predator effects on insect herbivores resulting in lower rates of herbivory in the warmest chambers. Future work in this system could distinguish among this suite of potential mechanisms. Nevertheless, direct interactions between plants and the herbivores are not necessarily straightforward.

Quercus alba recruitment is marked by a high rate of mortality in the transition from the seedling to the sapling stage (Crow 1988, Nowacki et al. 1990, Abrams 2003). While previous work suggests insect herbivory is associated with decreases in oak seedling growth and survival (McPherson 1993, Marquis and Whelan 1994), going into 2011, our study plots with more herbivory had lower rates of seedling mortality. This fact suggests a potential positive association between herbivory on *Q. alba* and *Q. alba* seedling dynamics. Together with the negative relationship between herbivory and temperature also observed in our study, these results suggest a potential weakening of an important stage of *Q. alba* seedling recruitment. Higher levels of herbivory on seedlings recruiting under a canopy may be beneficial in that it may reduce respiration rates lowering the amount of carbon released by the seedling. Future greenhouse studies or studies completed in gaps may shed more light on this. On the other hand, this positive association between herbivory and survival may actually be a symptom of water stress. We are potentially observing less herbivory on plants that are water-stressed and, at the same time, plants that are water-stressed die more frequently. Previous studies have shown that water dynamics are an important factor limiting tree seedling survival (McQuilken 1940, Williams and Hobbs 1989, De Steven 1991, Bragg et al. 1993, Inouye et al. 1994). However, in our study it is unclear if *Q. alba* seedlings are actually water-stressed along the experimental temperature gradient. Although we never detected an effect of soil moisture, relative humidity or vapor pressure deficit on seedling survival, there was a positive relationship between soil moisture and herbivory.

Although we did not observe a direct effect of conspecific seedling density on survival, there was an interaction between herbivory and conspecific seedling density such that herbivory at higher seedling densities was correlated with a lower probability of survival to the second year. Janzen-Connell effects (i.e., patterns of negative density dependence related to natural enemies; Janzen 1970, Connell 1971) are one likely explanation in this and other systems (e.g., Hille Ris Lambers et al. 2002, Comita et al. 2010, Martin and Canham 2010, Metz et al. 2010). Negative-density effects may contribute to the maintenance of species diversity by leading to higher mortality rates in conspecific seedlings.

As tree species respond to climatic change, it will be especially important to understand the various factors contributing to seedling survival during recruitment. While other anthropogenic pressures, such as logging and fire suppression, are already contributing to problems with *Q. alba* regeneration (Abrams 2003), our results suggest that it will also be important to consider interspecific and intraspecific species interactions at the seedling stage when predicting survival dynamics in the context of climatic warming.

Furthermore, as indicated in our study, the response of a species to climate change may be more complicated than can be predicted from just one factor. In our study we found that the responses of white oak seedlings to our warming manipulation were complex and depended on the impact of warming on herbivory, soil water dynamics, and density dependent effects. Future studies examining the dynamics of species under ongoing climate change should also consider contingencies such as these prior to making broad sweeping generalizations.

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