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Abundance of spring- and winter-active arthropods declines with warming

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Abstract. Because ectotherm activity and metabolism are sensitive to temperature, terrestrial arthropods may be especially responsive to ongoing climatic warming. Here, we quantified responses of arthropod abundance to two years of warming in an outdoor temperature manipulation experiment at Duke Forest, North Carolina, USA. Nine open-top chambers were individually heated year-round from 1.5° to 5.5°C above ambient temperature. From two years of monthly pitfall trapping, we collected and identified 4,468 arthropods representing 24 orders. We initially predicted that arthropods would experience the greatest negative effects of experimental warming during the summer months, when temperatures reach their yearly maximum and arthropods may be close to their maximum thermal tolerance limits. Instead, we found that the strongest negative effects on arthropod abundance occurred during the winter and spring, when ambient temperatures are relatively cooler, whereas the effects of experimental warming on abundance were not significant during the summer or fall. During the spring of 2012, the warmest spring on record for the southeastern USA, total arthropod abundance declined 20% per °C of experimental warming. Abundance declines were driven largely by flies (Diptera), which were the most abundant insect order, representing approximately a third of all arthropods collected. The most abundant arthropod family, Mycetophilidae (fungus gnats), declined 64% per °C of warming during the spring of 2012. Although previous research on climatic warming has focused on the impact of maximum yearly temperatures on organismal performance, our results are more consistent with the cool-season sensitivity hypothesis, which posits that arthropods adapted for cooler conditions are likely to face the strongest negative effects of warming during the cooler seasons.

Key words: abundance declines; arthropods; climate change; global warming; insects; seasonality.

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Introduction

The effects of climatic warming are expected to vary over space and time. Numerous studies have found that the effects of climate change vary geographically as a function of latitude (Addo-Bediako et al. 2000, Deutsch et al. 2008, Diamond et al. 2012*b*, Pinsky et al. 2019), elevation (Sunday et al. 2014, Freeman et al. 2018), and microhabitat (Scheffers et al. 2013, Baudier et al. 2015, Bennett et al. 2015, Pincebourde and Woods 2020). Far fewer studies have investigated temporal variability in the effects of climate warming (but see Badeck et al. 2004, Gallinat et al. 2015, Williams et al. 2015). Temperate ecosystems exhibit strong seasonal variability in climate, and organisms that are active during a single season may only experience a small window of this variability in a given year. The effects of climatic warming may therefore affect organisms differently depending on what time of year they are active.

Seasonal effects of climatic warming may be particularly important for arthropods, which compose over half the world's animal diversity (Mora et al. 2011). Recent large-scale insect declines have been documented worldwide, driven primarily by anthropogenic forces (Hallmann et al. 2017, Lister and Garcia 2018, Wepprich et al. 2019, van Klink et al. 2020, Wagner 2020). Some estimates conclude that over 40% of all insect species are currently at risk of extinction (Dirzo et al. 2014). These losses are driven in part by changes in climate (Conrad et al. 2006, Vanbergen and the Insect Pollinators Initiative 2013), and any loss in biodiversity is precipitated by abundance declines. However, the effects of climate change on arthropods are expected to vary among species (Robinet and Roques 2010, Boggs 2016). As small-bodied ectotherms, arthropods tend to be thermophilic and reach peak activity during warm periods of the year (Tauber and Tauber 1976, Wolda 1988). However, arthropods also exhibit a wide degree of seasonal specialization even within a single habitat. Species that serve as pollinators, for example, are often most active during spring when flowering peaks in temperate regions (Memmott et al. 2007). Other arthropods are active only during winter, including winter-active ground beetles (Carabidae; Jaskuła and Soszyńska-Maj 2011) and extremophiles like snow fleas (Collembola; Bissoyi et al. 2019) and ice crawlers (Grylloblattidae; Schoville et al. 2015).

The wide range of thermal specialization in arthropods may make them especially sensitive to seasonal variation in the effects of climatic warming. In arthropods, climate-driven shifts in phenology have been well documented in recent decades, with a general trend toward earlier seasonal activity (Walther et al. 2002, Parmesan 2006, Ovaskainen et al. 2013). However, if arthropod phenologies do not shift fast enough to match the current pace of warming, then their responses will depend both on the magnitude of warming they experience and their thermal sensitivity. Summer-active arthropods experience the highest overall temperatures and may be under higher thermal stress as a result of warming than arthropods active in cooler seasons (the warm-season sensitivity hypothesis). However, organisms that are regularly exposed to high temperatures are also predicted to be the most tolerant of extreme hot temperatures (Angilletta 2009). Geographic trends have supported this prediction, with organisms occurring in temperate regions expressing broader thermal tolerances than organisms in tropical climates (Addo-Bediako et al. 2000, Deutsch et al. 2008, Sunday et al. 2011, Diamond et al. 2012*b*). Likewise, organisms that live in microhabitats that are more exposed to solar heating tend to have higher thermal limits (Baudier et al. 2015, Kaspari et al. 2015), as do organisms active at midday (Kay and Whitford 1978). Critical thermal limits can predict sub-lethal performance (Penick et al. 2017), such that species with lower thermal limits can experience negative effects of warming even if air temperatures do not approach their thermal maxima. Therefore, organisms active in cooler seasons may be less tolerant of warming and experience the largest negative effects (the cool-season sensitivity hypothesis). Some phenological studies have supported this prediction, with organisms' phenologies responding more (or only) to spring warming (Diamond et al. 2011, Parmesan and Hanley 2015). Additionally, there may be taxon-specific sensitivity to warming, depending on whether taxa are already limited by warm-season or cool-season activity.

Here, we studied temporal variation in the response of arthropod abundance to warming as

part of a long-term, field-based temperature manipulation experiment (Pelini et al. 2011). We asked (1) Does experimental warming affect arthropod abundance? (2) Does the effect of experimental warming vary by season? And (3) does the effect of experimental warming vary among taxa? If the strongest effects of experimental warming occur when temperatures reach their yearly maximum, then we predicted that arthropod abundance would decrease in the warmest chambers during summer, consistent with the warm-season sensitivity hypothesis. If arthropods active during cooler seasons are less tolerant of high temperatures than arthropods adapted to summer conditions, we predicted that arthropod abundance would decrease in heated chambers during winter, spring, and/or fall, consistent with the cool-season sensitivity hypothesis.

Methods

Study site and warming experiment

We studied the effects of climate warming on arthropod abundance within the context of a field-based, experimental warming array at Duke Forest, North Carolina, USA (35.8667, −79.9958, 130 m asl). Duke Forest is an 80-year-old oak-hickory stand representative of lowland forests in eastern North America (mean annual temperature = 15.5°C, mean annual precipitation = 1140 mm; Christensen 1977). The warming array consisted of 12 open-top chambers that were 5 m in diameter and centered around a single white oak, *Quercus alba* (Fig. 1). The walls of the chambers were 1.2 m high and raised 2–3 cm from the forest floor to allow unrestricted movement of arthropods. Beginning in 2010, chambers were heated year-round using thermostat-controlled forced air passed over hydronic heaters. Nine chambers were assigned a target temperature in 0.5°C increments from 1.5 to 5.5°C (i.e., 1.5°, 2.0°, 2.5°, …, 5.5°C), and three chambers received unheated air to serve as ambient controls (Fig. 2; see Pelini et al. 2011). The range of temperatures spanned by the warming treatments encompassed climate projections of increased mean annual temperature from 1° to 5°C over the next century (Intergovernmental Panel on Climate Change 2014). Raw temperature data were recorded at hourly intervals via a ground-based sensor network of thermistors inside each chamber. We calculated realized warming (delta or ΔT) in each chamber by comparing average chamber air temperature to the averaged mean air temperature of the three control chambers for each sampling month.

Arthropod sampling and identification

Arthropods were sampled monthly from warming chambers using pitfall traps (5 cm in diameter) between January 2011 and December 2012. Four pitfall traps were placed inside each chamber 1 m from the outer wall. Traps were filled with 60–80 mL ethylene glycol and left uncovered for 48 h during days without precipitation. Arthropods collected in pitfall traps were preserved in 95% EtOH until identification. We combined counts from the four pitfalls traps in each chamber. We identified arthropods to taxonomic order for all collections and later identified arthropods to family for spring 2012 (March–May), which was a season of record heat for the southeastern USA and the season for which we saw the greatest effects of warming. From these family-level data, we excluded data from one control chamber (chamber #11) in April, due to inconsistency in arthropod identification. Additionally, changes in laboratory personnel over the study period resulted in inconsistent sorting of micro-arthropods from the order Collembola (springtails) and the subclass Acari (mites and ticks). While these arthropods are highly abundant in the leaf litter, we chose to exclude them from the analysis.

Previous studies from this site have focused on the effects of warming on ants, which live in perennial colonies that are active over many seasons (e.g., Diamond et al. 2012*a*, Stuble et al. 2013, Pelini et al. 2014, Resasco et al. 2014, Diamond et al. 2016). Here, we excluded ants from our analysis to focus on all other arthropods, the majority of which are active for only a short period of the year and are highly temperature-dependent (Pearse 1946), potentially making them more sensitive to variation in seasonal responses to warming than organisms active year-round. Additionally, ant abundance counts in pitfall traps are prone to overinflation and require a separate analysis framework (Gotelli et al. 2011).

This study was replicated and conducted concurrently at Harvard Forest, Massachusetts, USA

Fig. 1. Warming chamber at Duke Forest, North Carolina, USA. The chambers were 5 m in diameter and warmed by heated air blown through vents surrounding a central white oak (*Quercus alba*) (photo: James Waters).

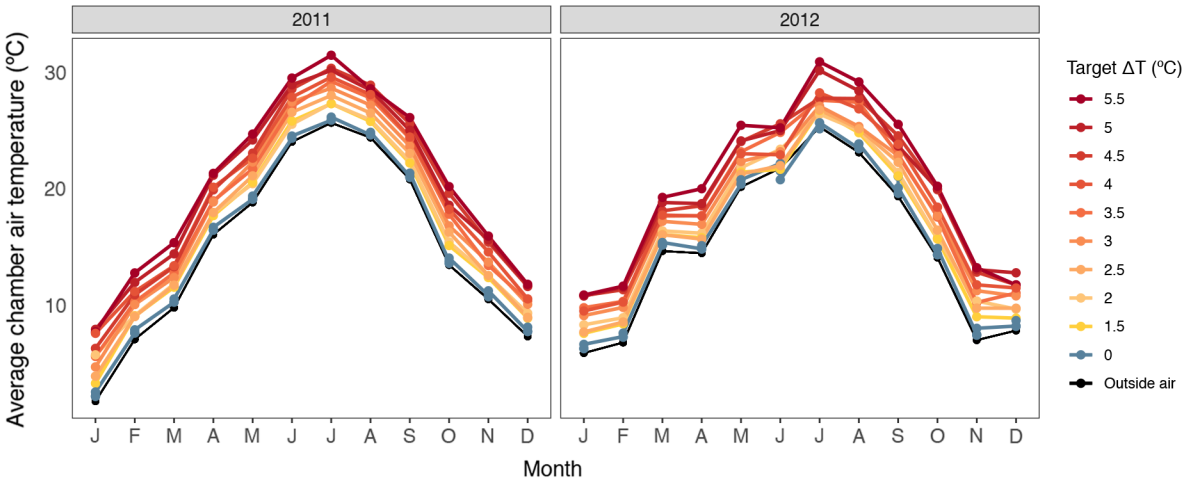

Fig. 2. Mean chamber air temperature (°C) for the two years of this study (2011–2012). Nine chambers were heated via warmed air and three chambers received unheated ambient air as a control. Heated chambers were assigned a single target temperature (ΔT) above ambient in 0.5°C increments from 1.5° to 5.5°C.

(42.53, −72.19, 300 m asl). Arthropod abundances were too low at Harvard Forest for a comparative analysis, particularly in colder seasons.

Data analysis.—All statistical analyses were conducted in R v. 3.6.1 (R Core Team 2019), using the package MASS v7.3-53 (Ripley et al. 2013) to build our statistical models.

Does experimental warming affect arthropod abundance?.—To test the overall effects of experimental warming on arthropod abundance, we

first summed abundance counts across all orders into a single value for each chamber/month/year combination. We then fit a generalized linear model (GLM) to test how arthropod abundance was influenced by realized chamber warming (ΔT), using a negative binomial error distribution to account for overdispersion of abundance. We used Akaike's Information Criterion (AIC) to compare the goodness of fit of models with year as an interactive effect, an additive effect, and with year excluded from the model.

Does the effect of experimental warming on arthropod abundance vary by season?.—To describe how arthropod abundance changed throughout the season with experimental warming, we fit a generalized linear model on the interaction between realized chamber warming (ΔT) and each unique season-year combination (i.e., winter 2011, winter 2012), with a negative binomial error distribution. We used AIC to compare the goodness of fit of models with year as an interactive effect, an additive effect, excluded from the model, and as a combined factor with season. We assigned each month to a season following the National Oceanic and Atmospheric Administration standard: winter, December–February; spring, March–May; summer, June–August; and fall, September–November.

While our assignments of months to season reflect climatic divisions in North Carolina (Arguez et al. 2010), we additionally tested every possible continuous three-month block across both years. The results are qualitatively similar (Appendix S1: Table S1, Fig. S1).

Does the effect of warming vary among taxa?.—To test whether the effect of warming varied among taxa, we selected abundance count data and removed the 6 orders with fewer than 20 total observations across the two-year sampling period (1.4% of total arthropods collected). We then used a generalized linear model to evaluate the interaction of realized chamber warming (ΔT) and order with year as an additive effect, using a negative binomial error distribution to account for overdispersion of abundance. We used AIC to compare the goodness of fit of models with year as an interactive effect, an additive effect, and with year excluded from the model. For the spring of 2012, for which we have family-level identification, we used an analogous modeling approach to evaluate the interaction of realized chamber warming and family.

Results

In total, we collected 4468 arthropods, 2089 in 2011 and 2379 in 2012, from 24 orders (Fig. 3a). Over half of all arthropods were in three orders: Diptera, Coleoptera, and Araneae, representing 32.1%, 14.8%, and 12.4% of all arthropods collected, respectively. For the spring of 2012, we identified 416 arthropods to 44 families (Fig. 3b, Appendix S1: Fig. S2). The most abundant families were Mycetophilidae (fungus gnats) and Cecidomyiidae (gall midges), which made up 34.6% and 15.1% of all specimens, respectively.

Does experimental warming affect arthropod abundance?

Overall, arthropod abundance marginally declined with warming (GLM, $P = 0.06$; Table 1).

Does the effect of experimental warming on arthropod abundance vary by season?

The effect of arthropod abundance varied by season (GLM, $P = 0.02$; Fig. 4, Tables 2, 3). The strongest effects occurred in the winter and spring with no significant effects during the summer and fall. In 2011, arthropod abundance declined 16.32% per degree of warming in the winter (GLM, $P = 0.02$), marginally declined in the spring ($P = 0.06$), and was unchanged in the summer ($P = 0.86$) and fall ($P = 0.40$). In 2012, arthropod abundance marginally declined in the winter (GLM, $P = 0.06$), declined 20.53% per degree of warming in the spring ($P < 0.01$), and was unchanged in the summer ($P = 0.42$) and fall ($P = 0.15$).

Does the effect of warming vary by taxa?

The effect of warming varied among orders (Fig. 5, Table 4). The three most abundant orders, Diptera (flies), Coleoptera (beetles), and Araneae (spiders), representing nearly 60% of all arthropods collected, showed mixed responses to warming. Diptera declined in abundance by 14.04% per degree of warming (GLM, $P = 0.03$, $N = 1433$), while the abundance of Coleoptera and Araneae was unchanged (Table 5). Two

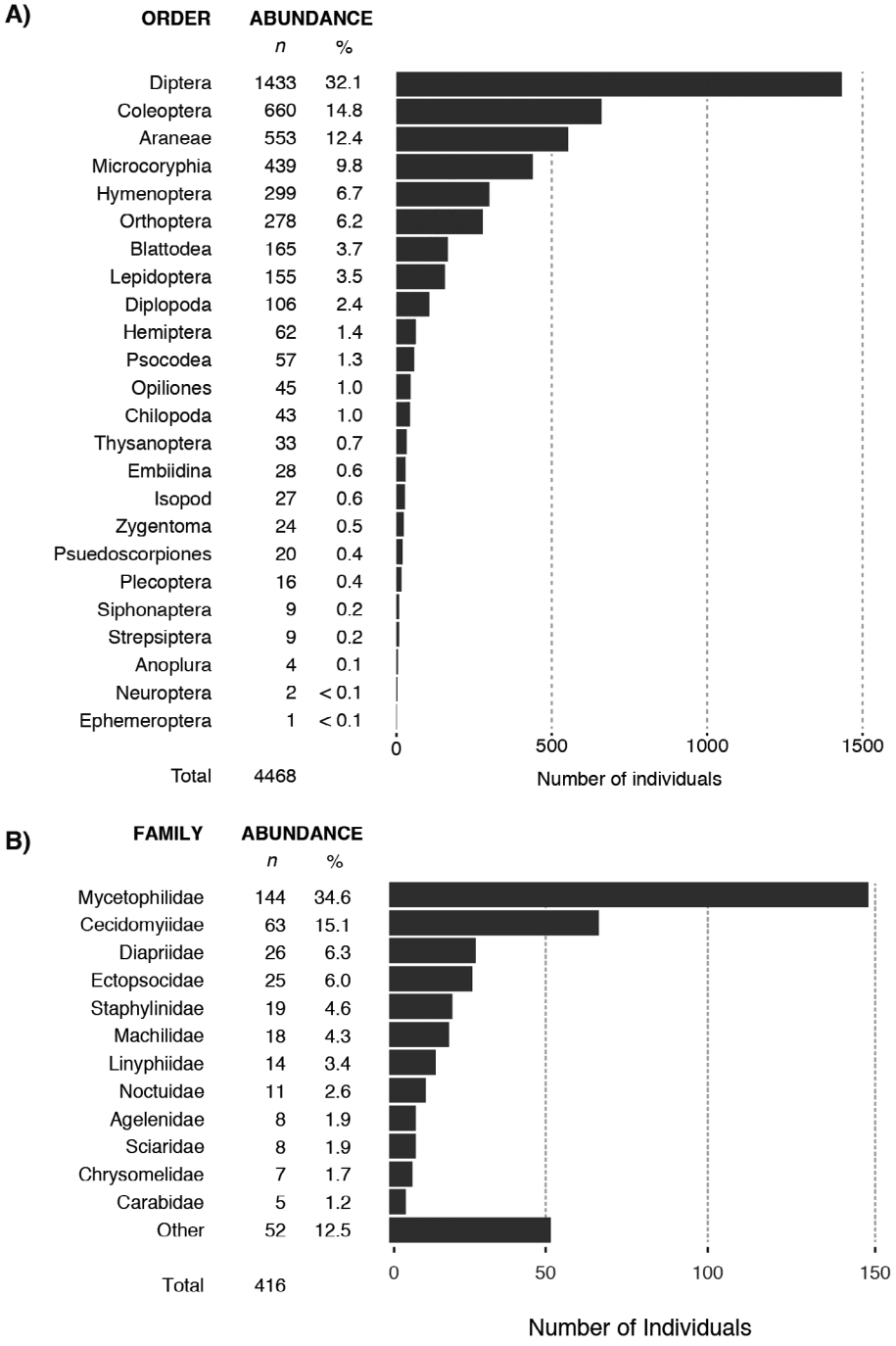

Fig. 3. Arthropod abundance by taxa. (A) Relative abundance of arthropods by order across the study period. (B) Relative abundance of arthropods by family for the spring (March–May) of 2012.

additional orders responded to warming: Lepidoptera (butterflies and moths) abundance declined 18.80% per degree of warming (GLM, $P = 0.01$, $N = 155$), and Psocodea (book lice and bark lice) abundance declined 22.89% per degree of warming ($P = 0.02$, $N = 57$).

For the spring of 2012, the effect of warming varied by family (Fig. 6, Table 5, Appendix S1:

Table S2). While most arthropod families did not respond to warming, the most abundant family, Mycetophilidae (fungus gnats, Diptera), representing 34.62% of all insects collected that season, declined in abundance by 64.37% per degree of warming (GLM, $P < 0.01$, $N = 144$).

Discussion

We initially predicted that warming would show the strongest effects on arthropod abundance during the summer, when temperatures reach their yearly maximum, but we did not find evidence of this. Instead, warming had the strongest effect on arthropod abundance during the relatively cooler seasons. Abundance declined in the spring and winter and was unchanged in the summer and fall. These results support the cool-season sensitivity hypothesis,

Table 1. Generalized linear model describing the relationship between chamber warming (ΔT) and arthropod abundance.

Term	Estimate	SE	z Value	P value
Intercept	3.97	0.09	43.21	<0.01
ΔT	−0.06	0.03	−1.91	0.06

Table 2. Type III ANOVA of a generalized linear model describing the relationship between chamber warming (ΔT) and season-year on arthropod abundance.

Term	χ^2	df	P value
ΔT	0.76	1	0.38
Season-year	79.47	7	<0.01
ΔT:season-year	16.56	7	0.02

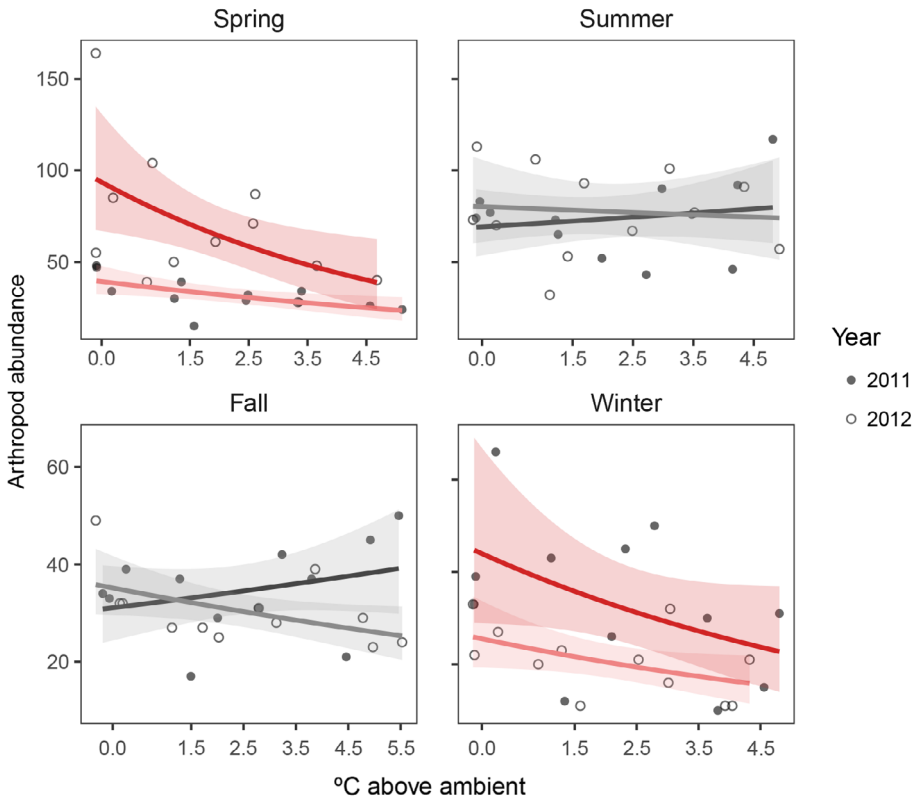

Fig. 4. Arthropod abundance response to experimental warming varies by season and year. Abundance declined in the spring and winter and was unchanged in the summer and fall. Points are total arthropod abundance in each chamber. Red indicates $P \leq 0.05$, pink indicates $P \leq 0.10$, and shading represents 95% confidence intervals.

which posits that arthropods adapted to the cooler conditions of winter, spring, and fall will be more sensitive to climate warming than arthropods that are adapted to the warmer conditions of summer. In general, these findings suggest that arthropods active in summer may be relatively tolerant of warming, while arthropods active in during cooler periods of the year are likely more susceptible to the negative effects of warming despite facing cooler maximum temperatures.

Table 3. Generalized linear model describing the relationship between chamber warming (ΔT) and season-year on arthropod abundance.

Term	Estimate	SE	t	P value
(Intercept)	3.44	0.15	22.38	<0.01
ΔT	0.04	0.05	0.85	0.40
Fall 2012	0.12	0.22	0.55	0.58
Spring 2011	0.23	0.21	1.07	0.28
Spring 2012	1.10	0.20	5.44	<0.01
Summer 2011	0.80	0.21	3.81	<0.01
Summer 2012	0.95	0.20	4.68	<0.01
Winter 2011	0.34	0.21	1.61	0.11
Winter 2012	−0.20	0.22	−0.89	0.37
Fall 2012:ΔT	−0.10	0.07	−1.44	0.15
Spring 2011:ΔT	−0.14	0.07	−1.87	0.06
Spring 2012:ΔT	−0.23	0.08	−3.03	<0.01
Summer 2011:ΔT	−0.01	0.07	−0.17	0.86
Summer 2012:ΔT	−0.06	0.07	−0.81	0.42
Winter 2011:ΔT	−0.18	0.07	−2.39	0.02
Winter 2012:ΔT	−0.15	0.08	−1.86	0.06

Note: Fall 2011 is the baseline to which other seasons are compared.

Our sampling period included the spring of 2012, which was the warmest spring on record for much of the USA, including North Carolina (Johnson et al. 2013). In North Carolina, the season was 2.5°C above average (Climate at a Glance, National Oceanic and Atmospheric Administration, https://www.ncdc.noaa.gov/cag/). We observed a decline in total arthropod abundance of 20.5% per degree of experimental warming during this time period (Fig. 4), which included a 64.4% abundance decline per degree of warming of the most abundant arthropod family (Fig. 6). Given that arthropods active in spring and winter were more sensitive to warming, we may predict that they have narrower thermal tolerances than arthropods active in summer or those active year-round (Bujan et al.

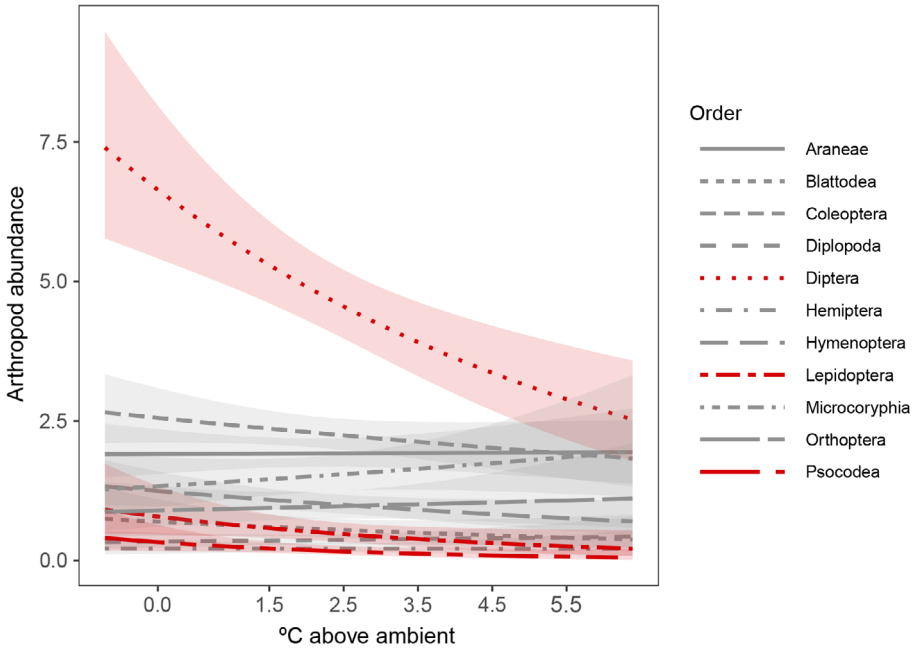

Fig. 5. Arthropod abundance response to the warming treatment for the eleven most common arthropod orders. The most abundant order, Diptera, declined with warming. Red indicates $P \leq 0.05$, and shading represents 95% confidence intervals.

Table 4. Generalized linear model describing the relationship between chamber warming (ΔT) and abundance between orders, with year as an additive effect.

Term	Estimate	SE	t	P value
Intercept	0.57	0.14	3.99	<0.01
ΔT	0.01	0.05	0.16	0.87
Blattodea	−1.01	0.22	−4.63	<0.01
Chilopoda	−2.77	0.32	−8.68	<0.01
Coleoptera	0.30	0.19	1.55	0.12
Diplopoda	−1.72	0.24	−7.09	<0.01
Diptera	1.24	0.19	6.57	<0.01
Embiidina	−3.14	0.37	−8.58	<0.01
Hemiptera	−2.17	0.27	−7.96	<0.01
Hymenoptera	−0.44	0.20	−2.15	0.03
Isopod	−3.40	0.39	−8.64	<0.01
Lepidoptera	−0.90	0.22	−4.16	<0.01
Microcoryphia	−0.37	0.20	−1.84	0.07
Opiliones	−2.20	0.28	−7.76	<0.01
Orthoptera	−0.77	0.21	−3.70	<0.01
Psocodea	−1.82	0.26	−7.00	<0.01
Thysanoptera	−2.50	0.31	−8.06	<0.01
Zygentoma	−2.93	0.35	−8.26	<0.01
Year 2012	0.15	0.06	2.57	0.01
ΔT:Blattodea	−0.10	0.08	−1.19	0.23
ΔT:Chilopoda	0.09	0.11	0.86	0.39
ΔT:Coleoptera	−0.06	0.07	−0.86	0.39
ΔT:Diplopoda	0.03	0.09	0.33	0.74
ΔT:Diptera	−0.15	0.07	−2.23	0.03
ΔT:Embiidina	0.07	0.12	0.55	0.58
ΔT:Hemiptera	−0.01	0.10	−0.10	0.92
ΔT:Hymenoptera	−0.09	0.07	−1.26	0.21
ΔT:Isopod	0.15	0.13	1.20	0.23
ΔT:Lepidoptera	−0.21	0.08	−2.50	0.01
ΔT:Microcoryphia	0.05	0.07	0.76	0.44
ΔT:Opiliones	−0.17	0.11	−1.52	0.13
ΔT:Orthoptera	0.03	0.07	0.46	0.64
ΔT:Psocodea	−0.26	0.11	−2.39	0.02
ΔT:Thysanoptera	−0.17	0.13	−1.35	0.18
ΔT:Zygentoma	−0.10	0.14	−0.76	0.45

Note: Araneae is the baseline to which other orders are compared.

Table 5. Generalized linear model describing the relationship between chamber warming (ΔT) and abundance for the ten most abundant arthropod families for the spring months (March–May) of 2012.

Term	Estimate	SE	t	P value
(Intercept)	−1.24	0.73	−1.70	0.09
ΔT	0.11	0.29	0.39	0.70
Cecidomyiidae	2.37	0.84	2.83	<0.01
Diapriidae	1.65	0.87	1.90	0.06
Ectopsocidae	2.21	0.86	2.57	0.01
Lycosidae	−1.24	1.33	−0.93	0.35
Machilidae	1.08	0.90	1.20	0.23
Mycetophilidae	4.15	0.83	5.00	<0.01
Noctuidae	0.48	0.96	0.50	0.62
Sciaridae	−0.57	1.11	−0.51	0.61
Staphylinidae	0.61	0.93	0.65	0.51
ΔT:Cecidomyiidae	−0.16	0.34	−0.47	0.64
ΔT:Diapriidae	−0.25	0.36	−0.71	0.48
ΔT:Ectopsocidae	−0.71	0.38	−1.86	0.06
ΔT:Lycosidae	0.23	0.48	0.48	0.63
ΔT:Machilidae	−0.14	0.37	−0.38	0.71
ΔT:Mycetophilidae	−1.03	0.35	−2.91	<0.01
ΔT:Noctuidae	−0.08	0.39	−0.20	0.84
ΔT:Sciaridae	0.23	0.41	0.56	0.58
ΔT:Staphylinidae	0.12	0.36	0.32	0.75

Notes: See supplement for all families (Appendix S1: Table S2). Agelenidae is the baseline to which other families are compared.

2020). In this sense, arthropods active in the spring and winter share qualities with tropical organisms, which also have relatively low upper thermal limits and may be living closer to their thermal maximum (Tewksbury et al. 2008, Huey et al. 2009). Compared with the tropics, however, temperate regions are expected to experience greater warming (Intergovernmental Panel on Climate Change 2014). There is evidence that Northern Hemisphere mid-latitude winters are experiencing warming at a rate twice the global average (Masson-Delmotte 2018). Additionally, arthropods active during the transition from winter to spring may be challenged by disjointed shifts in phenology with other organisms on which they depend (Stenseth and Mysterud 2002, Both et al. 2009, Hegland et al. 2009).

Over a third of all individual arthropods active during the spring of 2012 were from the fly family Mycetophilidae (fungus gnats), which showed strong declines in abundance with warming (Fig. 6). Fungus gnat larvae are major decomposers, feeding on fungal fruiting bodies, spores, and hyphae (Rindal et al. 2007). Adults are relatively small, though they may serve as important pollinators or prey sources for other organisms (Mesler et al. 1980). We predict that losing fungus gnats where they are abundant would affect decomposition dynamics and other aspects of forest health. Previous research on fungus gnats in boreal forests found that relatively undisturbed, old growth stands are required to maintain diversity, and adults are generally intolerant of hot, dry conditions (Økland 1996). Our results support these findings and indicate that

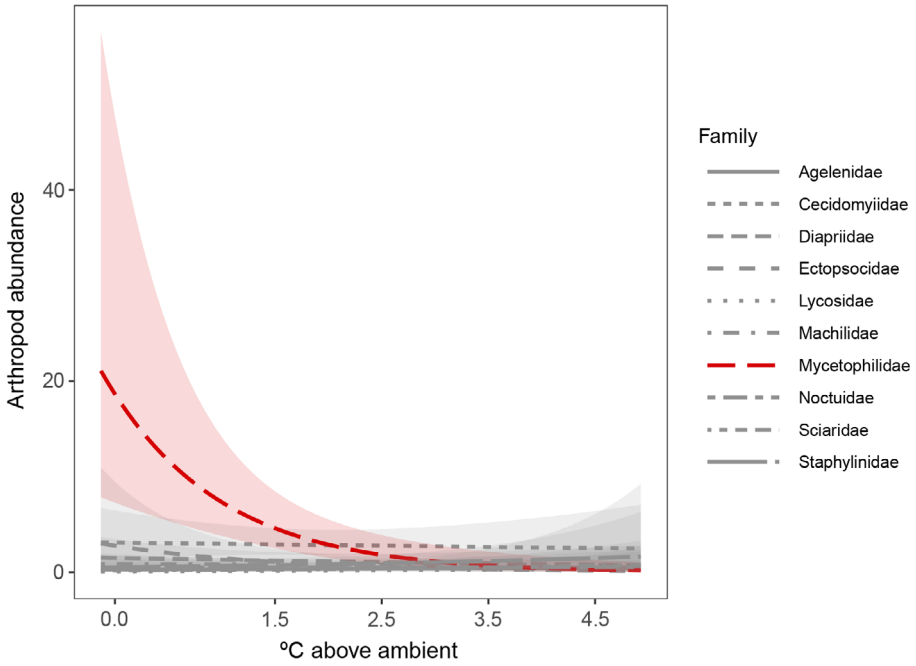

Fig. 6. Arthropod abundance response to warming treatment during the spring of 2012 for the ten most common arthropod families. The most abundant family, Mycetophilidae, declined with warming. Red indicates $P \leq 0.05$, and shading represents 95% confidence intervals.

the family may be particularly vulnerable to climate change. The effect of warming on fungus gnats may be mediated through trophic interactions, rather than physiological limits. Warming may alter fungal communities by drying soils (Treseder et al. 2016, Solly et al. 2017), which may then limit insects that rely on fungal food sources.

Our taxonomic identification of arthropods was relatively coarse (order, a subset to family). We observed declines in Diptera (flies), the most abundant order, and in Lepidoptera (butterflies and moths) and Psocodea (book lice and bark lice). The abundance of other arthropod groups was unchanged by warming, possibly suggesting broad resilience to climatic warming. However, our coarse taxonomic resolution was unlikely to capture changes in community composition at lower taxonomic levels. Differential responses to climatic warming frequently occur at the species level (Le Roux and McGeoch 2008, Forrest 2016, Lehmann et al. 2020) and would not have been detectable in this study. Additionally, community reorganization in response to warming may occur without abundance declines at broader taxonomic scales (Kardol et al. 2011).

Changes in arthropod phenology have been well documented in response to recent warming (Ovaskainen et al. 2013, Ge et al. 2015), but we did not test for phenological advance in the context of our experimental warming arrays. We sampled arthropods monthly, which likely would not have captured changes in phenology that can occur on the order of days (Maurer et al. 2018, Renner and Zohner 2018). Whether arthropods alter their phenology or not, our results indicate that warming may cause declines in abundance across broad time scales. This large window of vulnerability suggests that changes in phenology may be insufficient to completely buffer organisms from negative effects of climatic warming.

The warming treatments were applied in a regression design (See Cottingham et al. 2005), and consequently, there was no replication of the warming treatments and we were unable to

account for plot-level effects. Additionally, our experimental array allowed arthropod movement between chambers. Chambers were slightly raised off the forest floor to accommodate crawling arthropods and were 1.2 m tall, sufficiently short as to not restrict insect flight (Freeman 1945). If a chamber was inhospitable for an arthropod, they either moved out of the chamber or died. In our experiment, arthropods may have abandoned the warmest chambers, but under climatic warming, unless arthropods are able to migrate sufficiently far to track preferred temperatures, they will be unable to escape inhospitable temperatures. Taken together, our results suggest that arthropods active during spring and winter may be particularly vulnerable to the negative effects of warming.

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