

Temperature cues phenological synchrony in ant-mediated seed dispersal

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Abstract

Species-specific climate responses within ecological communities may disrupt the synchrony of co-evolved mutualisms that are based on the shared timing of seasonal events, such as seed dispersal by ants (myrmecochory). The spring phenology of plants and ants coincides with marked changes in temperature, light and moisture. We investigate how these environmental drivers influence both seed release by early and late spring woodland herb species, and initiation of spring foraging by seed-dispersing ants. We pair experimental herbaceous transplants with artificial ant bait stations across north- and south-facing slopes at two contrasting geographic locations. This use of space enables robust identification of plant fruiting and ant foraging cues, and the use of transplants permits us to assess plasticity in plant phenology. We find that warming temperatures act as the primary phenological cue for plant fruiting and ant foraging. Moreover, the plasticity in plant response across locations, despite transplants being from the same source, suggests a high degree of portability in the seed-dispersing mutualism. However, we also find evidence for potential climate-driven facilitative failure that may lead to phenological asynchrony. Specifically, at the location where the early flowering species (*Hepatica nobilis*) is decreasing in abundance and distribution, we find far fewer seed-dispersing ants foraging during its fruit set than during that of the later flowering *Hexastylis arifolia*. Notably, the key seed disperser, *Aphaenogaster rudis*, fails to emerge during early fruit set at this location. At the second location, *A. picea* forages equally during early and late seed release. These results indicate that climate-driven changes might shift species-specific interactions in a plant–ant mutualism resulting in winners and losers within the myrmecochorous plant guild.

Keywords: *Aphaenogaster picea*, *Aphaenogaster rudis*, climate change, *Hepatica nobilis*, *Hexastylis arifolia*, myrmecochory, woodland herbs

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Introduction

Climate change prompts spatial and temporal shifts in the distribution and seasonal phenology of many species, but the nature and magnitude of these shifts are species-specific (Walther *et al.*, 2002; Parmesan & Yohe, 2003). Such species-specific climate responses can disrupt the composition of current ecological communities, and it suggests that future communities will assemble with novel members (Root *et al.*, 2003; Williams & Jackson, 2007). As ecological communities exist as a collection of species that are influenced and structured by interactions among individuals (Connell, 1975; Keddy, 2001; Gross, 2008), the assembly of ‘no analog’ communities (compositions unlike those currently observed, Williams & Jackson, 2007) likely will change the

nature and strength of current biotic interactions. Such interactions are often climate dependent (Leathwick & Austin, 2001; Cavender-Bares, 2009; Warren *et al.*, 2010) so that the individual climate responses of interacting species may disrupt the efficacy of coevolved mutualisms that are based on the shared timing of seasonal events, such as flowering and pollinator emergence (Parmesan, 2007; Brook, 2009).

Many spring-flowering plant propagules are dispersed by ants in temperate forests (Beattie & Hughes, 2002; Rico-Gray & Oliveira, 2007). The early flowering phenology in ant-dispersed plants (myrmecochores) may be an adaptation to increase seed dispersal rates if fruiting is concomitant with peak seasonal ant foraging (Oberrath & Boehning-Gease, 2002; Guitian & Garrido, 2006; Boulay *et al.*, 2007). Ant dispersal minimizes negative plant-density effects and alleviates maladaptive seed predation by insects and rodents (Fedriani *et al.*, 2004; Boulay *et al.*, 2007, 2009; Ness & Morin, 2008). Lipid-rich seed appendages benefit the ants by providing nutrition for larvae, leading to

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improved colony fitness (Marshall *et al.*, 1979; Morales & Heithaus, 1998; Bono & Heithaus, 2002; Gammans *et al.*, 2005).

Plant phenology is strongly influenced by microclimate (Dahlgren *et al.*, 2007), and differences in temperature, photoperiod and moisture are integral drivers of variation in flowering and fruiting (Rathcke & Lacey, 1985). Additional influences include soil nutrients and biotic interactions, as well as ecotype (Marquis, 1988; Debussche *et al.*, 2004), but it is temperature and photoperiod that drive the coarse-scale timing of plant flowering and fruiting, and precipitation exerts great influence (Rathcke & Lacey, 1985; Sherry *et al.*, 2007). The timing of ant seasonal foraging is species specific (Fellers, 1989) and appears driven by temperature (Fellers, 1989; Zelikova *et al.*, 2008 and references therein), although Warren *et al.* (2010) showed that soil moisture also may play an important role. Ants from the genus *Aphaenogaster* predominately disperse seeds in the deciduous forests of the eastern US (Ness *et al.*, 2009). However, this genera are not the earliest spring foragers (Fellers, 1989) and may not be key dispersers for all myrmecochorous plants (Servigne & Detrain, 2008), particularly the earliest flowering plants such as *Hepatica* spp. (e.g., Supporting Information, Appendix S1; Ness *et al.*, 2009). The overlap between the phenology intervals for myrmecochore fruiting and ant foraging has been investigated in the context of habitat (e.g.; Oberrath & Boehning-Gease, 2002; Zelikova *et al.*, 2008), but the assessment and prediction of how these interactions may shift in a rapidly changing climate requires direct linkage between ant and plant phenology and their abiotic drivers.

The overall goal of this project was to determine factors driving potential synchrony in the spring fruiting phenology of two myrmecochorous plants, *Hexastylis arifolia* and *Hepatica nobilis*, and the foraging phenology of contiguous seed-dispersing ant assemblages. The question driving this goal was how this synchrony may persist in the context of rapid climate change. We used experimental transplants on north- and south-facing slopes in the Georgia Piedmont (US) and southern Appalachian Mountains (US), paired with ant bait stations, to investigate phenological synchrony between plant fruiting and ant foraging. We used the temporal and spatial variation in the experimental set up to discern the influence of temperature, light and soil moisture upon the transplants, opportunistic ants and the plant–ant interactions. We hypothesized that spring temperature ascension drives the progression of *H. nobilis* and *H. arifolia* fruiting phenology. Given that additional abiotic drivers influence plant phenology (Rathcke & Lacey, 1985; Sherry *et al.*, 2007), we also tested the influence of light, soil moisture and relative

humidity. Similarly, ant foraging patterns are associated with temperature changes (Fellers, 1989; Zelikova *et al.*, 2008), and we hypothesized that the spring emergence and foraging of seed-dispersing ants is primarily governed by temperature. We also explored the influence of light, soil moisture and relative humidity on ant phenology, all of which are known to influence ant foraging and nest location selection (Smallwood, 1982; Warren *et al.*, 2010).

In addition, we investigate whether the highly localized dispersal of myrmecochore propagules by ants ($\sim 1 \text{ m yr}^{-1}$, Cain *et al.*, 1998; Gomez & Espadaler, 1998) leads to local adaptation and spatially segregated ecotypes (see Galen *et al.*, 1991 and references contained therein). The coordination of critical life history stages with ambient climate conditions, such as flowering and fruiting, is a crucial adaptive trait in plants (Larcher, 1983 and references contained therein). For example, when transplanted, cold-habitat species often maintain phenological response to seasonal cues consistent with a shorter growing season (i.e., bloom later, senesce earlier, Dickerson & Sweet, 1971; Larcher, 1983; Galen *et al.*, 1991). Conserved phenology has not been investigated in myrmecochorous plants, including *H. nobilis* and *H. arifolia*, but these two species gave little indication of local adaptation in survival and performance when transplanted within 5 and 100 km of their origin (Warren, 2010), which comprise the two locations where phenology is examined here. We test whether fruiting phenology is highly conserved by examining seed timing between local and regional translocations and across slope aspects. A conserved phenology might spell the demise of these woodland herb species, which comprise an important component of forest diversity in the eastern US (Beattie & Hughes, 2002; Ness *et al.*, 2009), whereas a plastic phenology might enable their mutualism with ants to persist in the face of climate change.

Materials and methods

Study species and sites

H. arifolia Michx. is a small understory evergreen with a distribution limited to the Southeastern United States: northern Florida to Virginia, North Carolina to the Mississippi River. *H. nobilis* P. Miller is a small evergreen that occurs from northern Florida to Nova Scotia, west to Alabama and Missouri and Montana. It is also widespread in Asia and Europe. Both species are small, long-lived (30+ years) woodland herbs most common in the moist, cool and shady conditions of mature mesic deciduous forests (Inghe & Tamm, 1988; Giladi, 2004; Warren, 2008, 2010). Both species bloom in early spring, produce ant-dispersed propagules and lack clonal reproduction (Motten, 1982; Giladi, 2004).

In February 2006, *H. nobilis* and *H. arifolia* were collected as adults at Whitehall Forest (WHF) in Athens, GA (US). The plants were transplanted to north- and south-facing slopes at WHF and Coweeta Hydrological Laboratory (CWT), which is 100 km north of WHF. The topographical relief and precipitation are far greater at CWT than WHF (CWT: 750–1025 m elevation, 1826 mm annual precipitation; WHF: 150–240 m elevation, 1219 mm annual precipitation). This study design captures abiotic gradients in temperature and soil moisture that approach the extremes found in the study habitats (Warren, 2010; Warren & Bradford, 2010). Geographic and slope aspect gradients have been linked with variations in phenology (Dahlgren *et al.*, 2007; De Frenne *et al.*, 2009), and we use the spatial variance in the experimental design to decouple the individual influences of the abiotic drivers. For this experiment, we used eight 30 m² study grids – four at WHF and CWT, equally split across north- and south-facing slopes – which contained 82 *H. nobilis* and 68 *H. arifolia* transplants, that had been growing at the sites for >4 years (Warren, 2007, 2010; Warren & Bradford, 2010).

Plant phenology was scored weekly by monitoring each individual between February 24 and June 1, 2010. June 1 coincided with completion of fruiting by all plant individuals and hence was the end point for the study. A scoring index similar to Sherry *et al.* (2007) was used to monitor fruiting phenology: 1 = unopened flower bud; 2 = opened flower; 3 = old flower (postanthesis); 4 = initiated fruit; 5 = dehisced fruit. A second index was used to monitor leaf phenology: 1 = leaf bud open; 2 = unfurling leaf; 3 = fully expanded leaf. *H. arifolia* reproduces far less consistently than *H. nobilis* (Giladi, 2004; Warren, 2007, 2010), as observed here ($n = 12$ *H. arifolia* flowers; 51 *H. nobilis* flowers). Because leaf size is tightly linked with reproduction in both plants (Harris, 2000; Giladi, 2004; Warren, 2007), the relationship between transplant leaf and fruit phenology in reproductive transplants (*H. nobilis*: $\text{coeff} = 1.12 + 1.86x$, $\text{SE} = 0.79$, $P < 0.0001$, $R^2 = 0.83$; *H. arifolia*: $\text{coeff} = 0.46 + 1.74x$, $\text{SE} = 0.77$, $P < 0.0001$, $R^2 = 0.82$) was used to estimate fruiting phenology in nonreproductive transplants.

Ant foraging was measured by placing four bait stations loaded with tuna at the corners of each 5 × 6 m grid ($n = 32$ total). Ants are attracted to lipid-rich appendages on myrmecochorous seeds called elaiosomes, which act as a dead insect analogue for scavenging, nongranivorous ant species (Hughes *et al.*, 1994; Boulay *et al.*, 2007). Tuna contains many of the same diglycerides as elaiosomes and is a standard bait technique used to sample seed-collecting ant communities (Bestelmeyer *et al.*, 2000). The bait stations were monitored for 90 min, sufficient time to determine the relative abundance of foragers and species frequency (Bestelmeyer *et al.*, 2000). When using tuna as a seed proxy, it is important to consider both the abundance of ant visitors and the frequency of stations visited as some species may recruit large numbers of workers, but are poor dispersers or locate few stations (Lynch *et al.*, 1980; Fellers, 1987; Ness *et al.*, 2009).

Given that we found *A. picea* workers foraging and visiting bait stations at considerably cooler temperatures than *A. rudis*, we also set up pitfall traps at WHF and conducted timed searches to confirm the presence of *A. rudis* at the study sites

during week 11. We placed a pitfall trap 100 m (to avoid interfering with the main experiment) from each WHF grid ($n = 4$ traps) and monitored each for 7 days (May 10–17). The traps consisted of a plastic sample cup buried so the lip was flush with ground level for easy access to foraging ants. The traps were filled with propylene glycol and protected from rainfall with a 20 × 20 cm square plywood cover attached to a ground stake. This permitted us to detect ant foragers even if they avoided the tuna bait stations. The absence of *A. rudis* foragers made us question whether colonies near our study grids had been compromised, such as by invasive exotic ants, so we also conducted timed searches beneath logs and stones in habitat near the study grids to observe *A. rudis* colonies.

Abiotic monitoring

Ambient temperature and relative humidity were monitored continuously February 24 to June 1, 2010 by placing a HOBO U23 Pro v2 Temperature/Relative Humidity data logger (Onset, Cape Cod, MA, USA), in the center of each grid. The dataloggers were positioned 15 cm above the ground beneath a wood radiation shield. Soil temperature, diffuse light and soil moisture measurements were taken weekly ($n = 14$ weeks) at the corners and center of each 30 m² grid ($n = 5$ measurement points per grid, with measures averaged by grid). Soil temperature was measured with a T-shaped digital thermometer inserted 8 cm into the soil. Percent photosynthetically active radiation (PPFD, diffuse light) was calculated as the difference between plot-level PAR readings and a fully exposed PAR reference site. The understory measurements were taken with an LI-191 line quantum sensor and the open reference measurements were taken with an LI-200 spherical PAR sensor and logged with a LI-1400 datalogger (LiCor Inc., Lincoln, NE, USA). Measurements were taken during early morning (08:00–09:00 hours) to minimize relative error in diffuse light. Volumetric soil moisture (%) was measured with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific Inc., Logan, UT, USA).

Data analysis

The mean values of plant and ant foraging indices and abiotic measures were averaged by grid for temporal and spatial analyses. Several modes of temperature measurement were taken, and each was tested for the best predictive ability on plant and ant phenology. Temperature data were collected continuously using a single datalogger per grid and weekly using a soil probe at the corners of each grid. Moreover, mean, minimum and maximum daily temperatures were calculated from these data. Expectedly, all temperature data parameters displayed a high degree of collinearity (variance inflation factor >26), and could not be evaluated in the same model. Akaike Information Criterion (AIC) was used to select between temperature parameters (in separate models). Minimum daily temperature derived from the continuous dataloggers best predicted temporal variance in plant and ant phenology and was used in all time series models except *H. nobilis* phenology, which was best predicted by mean daily

temperature. Mean temperature derived from the soil probe best predicted spatial variance in plant and ant phenology and was used in all logistic regression models. The inclusion of the additional environmental variables (diffuse light, soil moisture and relative humidity) did not cause unreasonable collinearity (variance inflation <4). Error in count-type data typically does not follow a normal distribution, and for that reason models were examined using Gaussian, Poisson and binomial error distributions. The Gaussian error distribution best fit plant fruiting phenology whereas the Poisson distribution provided the best fit for ant-foraging phenology (based on AIC). The main ant species observed in this study were *A. picea* (CWT), *A. rudis* (WHF) and *Prenolepis imparis* (CWT, WHF). Preliminary analysis indicated no statistical difference in the abiotic responses of *Aphaenogaster* spp. and *P. imparis* between sites (but see discussion for comment on the differences in magnitude of response between sites for the *Aphaenogaster* spp.) so the results were pooled by genera.

Temporal analysis. Time series of plant (fruit formation and maturing) and ant (foraging at bait stations) phenology were analyzed to determine their abiotic drivers (diffuse light, soil moisture, temperature and relative humidity). Spring phenology coincides with a multitude of temporal environmental changes that may or may not drive biological changes. To account for this temporal autocorrelation, time series analysis with autoregressive error was used to analyze the changes in plant and ant phenology as a function of abiotic changes. The data were modeled using Box-Jenkins autoregressive moving average models (ARMA) (Box *et al.*, 1994) using the R software package (R Development Team, 2005) to account for the autocorrelation between observations inherent in time series analysis. The autoregressive portion resembles a linear regression of the current time series value against one or more previous values; the moving average is essentially a filtering function that compares the current value against random error in previous values (Shumway & Stoffer, 2006). Generalized Least Squares (GLS) regressions with maximum likelihood were used to analyze the models. The GLS model accommodates correlated errors that may be unequal. The model order (degree of autocorrelation) was selected based on the autocorrelation (ACF) and partial autocorrelation (PACF) functions (Shumway & Stoffer, 2006).

The similarity in phenological plant fruiting progression in individual grids, within and across sites, was also analyzed using GLS models. The 14-week phenology was compared among grids within the same sites and then among grids across sites to determine whether the fruiting progression was more similar among proximal or distal grids. Because of the high degree of collinearity, each model was analyzed separately and mean AIC values were used to evaluate model fits for within- and across-group comparisons.

Spatial analysis. The two locations containing study grids were located 100 km apart, and the grids themselves were at a distance of 1–2 km from one another. To account for spatial autocorrelation within grids, we used linear mixed models (LMMs) assuming a Gaussian distribution (identity link

function) with location as a random effect to evaluate variation in *H. nobilis* and *H. arifolia* fruiting phenology as functions of diffuse light (%), soil moisture (%), temperature (°C) and relative humidity. Similarly, we used generalized linear mixed models (GLMMs) assuming a Poisson distribution (log link function) with location as a random effect to evaluate variation in ant foraging phenology as functions of diffuse light (%), soil moisture (%), temperature (°C) and relative humidity. The mixed models were fit using the Laplace approximation in the 'lme4' package (Bates & Maechler, 2009) for the R statistical programming environment (R Development Core Team, 2005). The inclusion or exclusion of the fixed effects and their interactions in the 'best fit' models was based on AIC values. Average AIC weights were used for models with similar fit ($\Delta AIC < 5$). The significance of retained parameters is reported.

Results

Plant and ant phenology progressed similarly through the spring, so while *H. nobilis* and *H. arifolia* fruit matured, foraging increased for the ant species. These phenomena appeared related to warming temperature (Fig. 1). Indeed, considerable environmental variation was recorded across space (grids) and time (February–June) in minimum temperature (−6.2 to 12.9 °C). There was also marked variation in diffuse light (0.6–83%), soil moisture (8.2–33.5%) and relative humidity (41–95%). Across locations, during the months February–June WHF average temperatures were about 2.75 °C higher, and average soil moisture about 8% lower, than at CWT (see Appendix S1 for weeks 1, 7 and 14). Diffuse light was about 50% higher at CWT than WHF early in the season, but the establishment of the tree canopy reduced it to about 3% at both sites (Appendix S1). Whereas there was a great deal of weekly fluctuation in relative humidity, the mean for the season only differed by about 2.5% between sites (Appendix S1).

Temporal phenological progression

The greatest advances in plant and ant phenology occurred during weeks 5–9 (Figs 1 and 2). At the midpoint (week 7), plant fruiting phenology was advanced significantly more ($t = 1.76$, $df = 14$, $P = 0.05$) at WHF than CWT (Fig. 2a and b, Appendix S1). *H. nobilis* fruiting phenology at CWT lagged behind WHF by 1–2 weeks through most of the study period (Fig. 2a) whereas *H. arifolia* phenology only differed between sites during the weeks 5–10 (Fig. 2b). The decrease in *H. arifolia* phenology in week 10 coincided with a substantial drop in minimum daily temperatures (Fig. 1). *H. nobilis* dropped 80–99% of its fruits during weeks 7–10 at WHF and weeks 8–11 at CWT; *H. arifolia* dropped 80–99% of its fruits during weeks 11–14 at

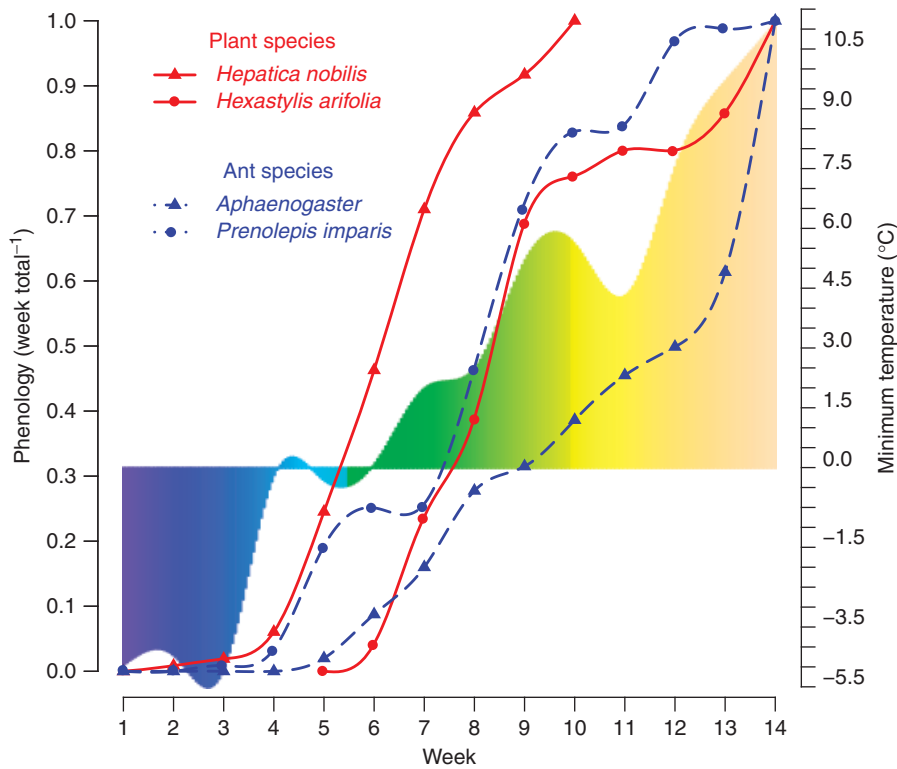


Fig. 1 Plant and ant spring phenology and minimum daily temperature pooled across sites (Whitehall Forest and Coweeta LTER). The phenological progression of *Hepatica nobilis* and *Hexastylis arifolia* is a cumulative index; the phenological progression of *Aphaenogaster rudis* and *A. picea* is the cumulative number of individuals observed at bait stations each week as a proportion of the total found (left axis). Minimum daily temperature (gray shading) is given on the right axis.

both sites. At WHF, *A. rudis* was observed significantly less ($t = -1.74$, $df = 15$, $P = 0.05$) during *H. nobilis* fruiting (15% of *A. rudis*) than during *H. arifolia* fruiting (76% of *A. rudis*) (Fig. 2c). At CWT, *A. picea* foraging was the same ($t = -0.58$, $df = 15$, $P = 0.57$) during seed release for both plant species (30–36%) (Fig. 2c). *P. imparis* foraging at CWT declined between the *H. nobilis* (41%) and *H. arifolia* (23%) fruiting periods, but the decrease was not significant ($t = 0.75$, $df = 15$, $P = 0.46$) (Fig. 2d). Similarly, the *P. imparis* foraging decline at WHF (34–21%) was not significant ($t = 0.85$, $df = 15$, $P = 0.41$) (Fig. 2d).

Across WHF and CWT, a total of 2513 individuals of 11 ant species were observed at the bait stations (*A. picea*, *A. rudis*, *Camponotus chromaiodes*, *Camponotus pennsylvanicus*, *Cremogaster ashmeadi*, *Formica biophilica*, *Formica subsericea*, *Lasius alienus*, *Pheidole dentate*, *P. imparis* and an unknown sp.). *P. imparis* was the most common ant species (1570 observed, 62.5%), followed by *Aphaenogaster* spp. (215 observed, 8.6%). Nonetheless, the frequency of bait station visits was similar between *P. imparis* (4.1%) and *Aphaenogaster* spp. (4.3%). Overall, the cumulative number of foraging ants

was similar between sites ($t = 0.04$, $df = 14$, $P = 0.48$) (Appendix S1, Fig. 2d). Yet until week 14, *A. picea* foraged in significantly greater numbers at CWT than *A. rudis* did at WHF (Fig. 2c). Notably, other than weeks 6 and 8, *A. rudis* rarely foraged until week 13. No *A. rudis* individuals were observed foraging at WHF until the minimum daily temperature stayed above 0°C whereas *A. picea* began foraging when the minimum daily temperature rose above -3°C. In addition, *A. picea* frequency never dropped below 0 when minimum daily temperatures were greater than 4°C whereas *A. rudis* only foraged consistently when minimum daily temperatures were greater than 10°C. *P. imparis* began foraging by week 3 and peaked in week 9; its weekly foraging patterns at WHF and CWT were remarkably similar (Fig. 2d).

Statistically significant responses in plant fruiting and ant foraging phenology followed changes in environmental conditions. Whereas *A. picea* and *A. rudis* responded to different temperature thresholds, and thus phenological timing of foraging, the abiotic responses were the same and pooled for statistical analysis by *Aphaenogaster* spp. Both *H. nobilis* and *H. arifolia* fruiting

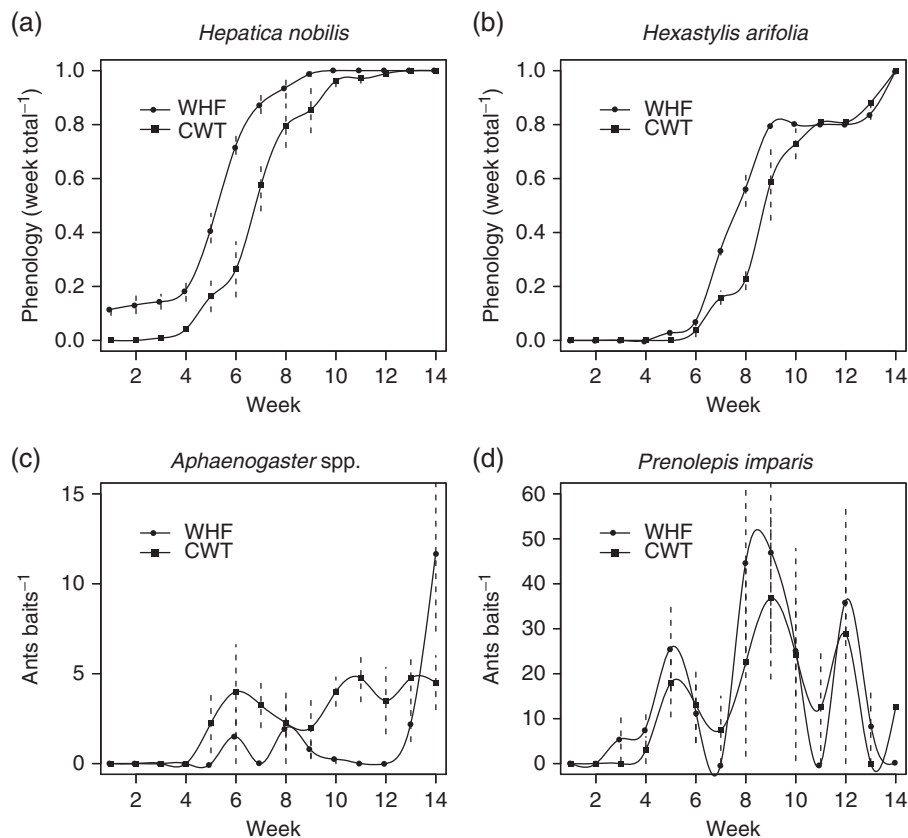


Fig. 2 Plant (a, b) and ant (c, d) spring phenology at WHF (Whitehall Forest) and CWT (Coweeta LTER). Mean values are given \pm SE for each week. Note the difference in y -axis scales between ant species (c, d).

phenology progressed significantly ($P < 0.05$) with temperature through the spring season (Table 1). *H. nobilis* also fruited earlier with increased soil moisture and later with increased diffuse light and relative humidity; *H. arifolia* fruiting decreased with light. Ant foraging increased significantly ($P < 0.05$) with temperature only, with both *Aphaenogaster* spp. and *P. imparis* visiting bait stations in greater numbers as temperatures increased through spring (Table 1).

Pitfall traps located near the WHF study grids revealed no *A. rudis* foragers during week 11 when they also were not detected at tuna bait stations. We also conducted timed searches during the same week, and we were able to locate two *A. rudis* colonies within 10 min (six colonies in rotting logs, two under stones) near each study grid ($n = 4$).

Spatial phenological progression

As ant and plant phenology varied with environmental variables across time, it also varied significantly with environmental variables across space. Both *H. nobilis* and *H. arifolia* fruiting phenology increased signifi-

cantly ($P < 0.001$) where temperature was higher, and *H. arifolia* fruited later where light was higher (Table 2). Ant foraging increased significantly with several environmental variables, but *Aphaenogaster* spp. and *P. imparis* responded differently across study grids. *Aphaenogaster* spp. foraged significantly earlier where light and temperature were highest whereas *P. imparis* foraged significantly later where soil moisture and relative humidity were higher (Table 2).

All of the transplants were collected from WHF and transplanted to WHF and CWT; however, variation in fruiting phenology was greater across (mean AIC = 25.5, *H. nobilis*; 25.9, *H. arifolia*) than within sites (mean AIC = 14.9, *H. nobilis*; 14.3, *H. arifolia*) for both plants. The greatest difference between phenology models across sites occurred between north-facing (and hence cooler) slopes at CWT and south-facing (and hence warmer) slopes at WHF for *H. nobilis* (mean AIC = 33.5) and *H. arifolia* (mean AIC = 34.1). In contrast, the phenology similarities between south-facing slopes at CWT, and north-facing slopes at WHF for *H. nobilis* (mean AIC = 15.9) and *H. arifolia* (mean AIC = 13.9), were similar to the within site differences.

Table 1 Temporal predictors of plant and ant phenology using autoregressive moving average models (ARMA)

Model	Fixed effects	Estimate	SE	t-value
<i>(a) Plant fruiting phenology</i>				
<i>Hepatica nobilis</i> (Lag: 2 weeks)	Light	-5.36	1.13	-4.74**
	Soil moisture	0.18	0.08	2.13*
	Temperature	0.27	0.03	8.41***
	Relative humidity	-1.97	1.06	-1.85*
<i>Hexastylis arifolia</i> (Lag: 2 weeks)	Light	-3.35	1.76	-1.91*
	Soil moisture	0.12	0.09	1.23 ^{ns}
	Temperature	0.29	0.09	3.09*
	Relative humidity	-1.31	2.29	-0.57 ^{ns}
<i>(b) Ant foraging phenology</i>				
<i>Aphaenogaster</i> spp. (Lag: 1 week)	Light	-4.76	10.68	-0.45 ^{ns}
	Soil moisture	0.49	0.55	0.89 ^{ns}
	Temperature	1.53	0.54	2.81*
	Relative humidity	-3.46	13.29	-0.26 ^{ns}
<i>Prenolepsis imparis</i> (Lag: 1 week)	Light	-95.65	75.86	-1.26 ^{ns}
	Soil moisture	3.42	3.94	0.87 ^{ns}
	Temperature	11.92	3.69	3.23**
	Relative humidity	-10.41	91.26	-0.12 ^{ns}

All time series models include diffuse light (%), soil moisture (%), minimum daily temperature (°C) and relative humidity (%) and were fit using generalized least squares. The autoregressive (ACF) and partial autoregressive (PACF) functions were selected using AIC. The significance of the slope values for retained coefficients are given.

**** $P < 0.001$.

*** $P < 0.01$.

** $P < 0.05$.

* $P < 0.1$.

AIC, Akaike Information Criterion; ns, not significant.

Table 2 Spatial predictors of plant and ant phenology using linear mixed models

Model	Fixed effects	Estimate	SE	t,z-value
<i>(a) Plant fruiting phenology (Gaussian distribution, t)</i>				
<i>Hepatica nobilis</i>	Light	-0.56	0.46	-1.21 ^{ns}
	Soil moisture	0.01	0.01	1.01 ^{ns}
	Temperature	0.10	0.03	3.49***
	Relative humidity	-3.46	2.34	-1.48 ^{ns}
<i>Hexastylis arifolia</i>	Light	-1.63	0.42	-3.89***
	Soil moisture	-0.01	0.01	-0.05 ^{ns}
	Temperature	0.19	0.03	6.06***
	Relative humidity	-3.96	2.13	-1.86 ^{ns}
<i>(b) Ant foraging phenology (Poisson distribution, z)</i>				
<i>Aphaenogaster</i> spp.	Light	5.11	2.69	1.91****
	Temperature	0.38	0.18	2.11*
<i>Prenolepsis imparis</i>	Soil moisture	-3.24	0.61	-5.36***
	Relative humidity	-14.55	1.88	-7.76***

All models included diffuse light (%), soil moisture (%), temperature (°C), and relative humidity (%) along with their interaction terms as fixed effects and site as a random effect. Coefficients were selected using average AIC weights from best-fit models, and the significance of slope values for retained coefficients are given.

**** $P < 0.001$.

*** $P < 0.01$.

* $P < 0.1$.

AIC, Akaike Information Criterion; ns, not significant.

Discussion

Warming temperatures are the dominant phenological cue for both plant seed set and ant foraging. Although other factors influence plant fruiting phenology (Table 1), the primacy of temperature as the phenological driver facilitates synchrony in ant-mediated seed dispersal. Notably, there is no indication that fruiting phenology is genetically conserved as temperature drives localized phenology regardless of transplant origin. The plasticity in plant response suggests a high degree of portability in the seed-dispersing mutualism, which might help maintain it through considerable climate shifts. The ants, however, do not invoke similarly optimistic projections. By examining species-specific patterning between just two plants and two ants across two sites, we find evidence for potential climate-driven asynchrony in facilitation phenology. Fewer seed-dispersing ants forage during the early seed set of *H. nobilis* than the relatively later seed set of *H. arifolia*. More importantly, the key seed disperser, *A. rudis*, fails to emerge during *H. nobilis* fruit set at WHF whereas *A. picea* forages equally during *H. nobilis* and *H. arifolia* fruit set at CWT. Together, our results indicate that climate-driven changes might shift species-specific interactions in ant-facilitated seed dispersal so there are in winners and losers within the myrmecochorous plant guild.

Plant phenology

H. nobilis has the wider distribution of the two plant species, and its range includes alpine and boreal habitats (USDA, 2008). As such, it appears less sensitive to cold temperature extremes – and notably its phenology corresponds best with mean daily temperature whereas *H. arifolia* phenology corresponds best with minimum daily temperature (Fig. 1, Table 1). The response by both plant species to warming temperatures is consistent with most early blooming species for which warming temperatures are the most important phenological cue (Fitter & Fitter, 2002; Sherry *et al.*, 2007; Kudo *et al.*, 2008; De Frenne *et al.*, 2009). However, the demonstrated plasticity in the phenological response at local and regional scales contrasts with findings in other studies (Dickerson & Sweet, 1971; Larcher, 1983; Galen *et al.*, 1991) where ecotypes display more conserved phenological responses. At least for our study species, this phenological plasticity might enable their mutualism with seed-dispersing ants to persist despite climate change.

The phenological progression of both plant species also corresponds with light, though the negative correlation appears, at least initially, counterintuitive. We noted during our work that plants on south-facing slopes appeared more light stressed than those on north-facing slopes, consistent

with previous findings for these species (Warren, 2010). Given that leaf reddening due to increased anthocyanins is an excellent indication of photostress (Gould *et al.*, 2010; Nikiforou & Manetas, 2010), we quantified leaf reddening by area and intensity. Leaf reddening was significantly higher in plants on south- than north-facing slopes ($t = 3.93$, $df = 95$, $P = 0.0002$), where light exposure was significantly higher ($t = 2.12$, $df = 100$, $P = 0.04$) due to the lower solar zenith angle during spring (Cantlon, 1953). It appears, then, that light stress on south-facing slopes slowed phenological advance. This finding highlights that, although warming temperatures might be the dominant phenological cue, other plant resource requirements need to be measured in phenological studies if we are to gain a full understanding of how phenology might respond to changing environmental conditions. Along these same lines, we found *H. nobilis* phenology also increased somewhat with higher soil moisture and lower relative humidity. Given the expected trade-off for understory plants between shade and drought tolerance (Smith & Huston, 1989), this observation seems best explained by increases in moisture availability, but further work is required to test moisture's role in fruiting phenology.

After accounting for temporal autocorrelation, it remains possible that plant fruiting phenology and spring warming simply coincide because both progress during seasonal change. For this reason, we also examined phenology spatially across sites and slope aspect. The climate differences across north- and south-facing slopes located 100 m apart often vary more than that between sites located 100 km apart (Warren, 2010). As with temporal change, temperature was clearly the phenological driver for both plants across the landscape, and the negative association with increased light remained significant for *H. arifolia* (Fig. 1, Table 2). The fruiting phenology at CWT lags approximately two weeks behind WHF, particularly for *H. nobilis* (Fig. 1a and b). As we used transplants from WHF, the lag at CWT suggests considerable plasticity in the phenological response – indicating they responded to local temperature cues. WHF is approx. 100 km closer to the equator, 700 m lower in elevation and consequently approx. 2.75 °C warmer than CWT. Moreover, the fruiting phenology of plants in the warmer grids at CWT (i.e., south-facing) was similar to that in the north-facing grids at WHF. So, although we collected our data across one spring, the use of space (locations and slope aspects) permits us to identify temperature as a robust driver of fruiting phenology for our two understory herbs.

Ant phenology

The progression in spring ant foraging only corresponds with minimum daily temperatures (Fig. 1, Table

1). Our findings are consistent with previous work showing that temperature drives ant behavior (Brian, 1956; Bernstein, 1979; Lynch *et al.*, 1980; Cerda *et al.*, 1997; Retana & Cerda, 2000; Dunn *et al.*, 2007). *Aphaenogaster* spp. forage earlier and more often where light and temperatures are higher – likely due to maximizing temperatures for brood development in their shallow nests (Smallwood, 1982). In contrast, we found *P. imparis* more active in drier, less humid habitats (Table 2). *P. imparis* commonly mobilizes aggressive workers from large colonies to dominate food sources (Lynch *et al.*, 1980; Dunn *et al.*, 2007). Here, we observe more than seven *P. imparis* individuals for every one *Aphaenogaster* spp., yet the frequency of bait station visits for each is remarkably similar. These patterns indicate that each species equally utilize bait stations, but *P. imparis* recruits far more colony members to the feast. Whereas *P. imparis* far outnumbers *Aphaenogaster* spp., the ecological importance of *Aphaenogaster* spp. outweighs that of *P. imparis* (Giladi, 2006; Ness *et al.*, 2009).

The *Aphaenogaster* genera may be the central and most effective myrmecochore dispersers in North American forests (Ness *et al.*, 2009). *P. imparis* often monopolizes food resources (Lynch *et al.*, 1980), but it typically ignores myrmecochorous seeds or consumes elaiosomes without providing any dispersal services (Giladi, 2004; Ness *et al.*, 2009). The additional ant species observed here exhibit a wide range of foraging activities, including arboreal searching (*Camponotus* spp and *C. ashmeadi*), and often dominate *Aphaenogaster* spp. in direct encounters (particularly the *Formica* and *Lasius* spp.), but they only occasionally collect and transport myrmecochore seeds (Giladi, 2004; Ness *et al.*, 2009).

Aphaenogaster spp. are subordinate to most seed-dispersing ants, but they demonstrate quick and clever foraging strategies to circumvent dominant species and are essentially ubiquitous in North American forest habitats (Lynch *et al.*, 1980; Mitchell *et al.*, 2002; Ness *et al.*, 2009). Moreover, their placement and frequent abandonment of nests, and adroit treatment of dispersed seeds, makes them integral for successful myrmecochore dispersal (see Giladi, 2006; Ness *et al.*, 2009 and references therein). Yet we find *P. imparis* foraging synchronous with *H. nobilis* seed release at both study sites, and *A. rudis* foraging generally is absent during *H. nobilis* seed release at WHF. Seasonal partitioning in ant foraging has been observed frequently across species (Lynch *et al.*, 1980; Fellers, 1989; Cerda *et al.*, 1997; Albrecht & Gotelli, 2001), but there is little work exploring ecological differences among *Aphaenogaster* spp. (e.g., Talbot, 1934) across their putative geographic distributions (Creighton, 1950; Umphrey, 1996). For this reason, the pronounced delay in *A. rudis* foraging at WHF, especially in comparison with *A. picea* at the much cooler CWT site, is unexpected.

Given that we have robust soil and air temperature measurements, our observations suggest pronounced *Aphaenogaster* species-specific temperature thresholds for foraging: *A. rudis* appears to require much warmer temperatures (>10 °C) than *A. picea* (>4 °C). This may not be surprising considering that *A. picea* is associated with high elevations and more northerly habitats (Creighton, 1950; Umphrey, 1996), but our observations demonstrate that *Aphaenogaster* spp. do not necessarily begin foraging earlier at warmer sites. Our pitfall traps and timed searches confirm that *A. rudis* workers remain dormant inside logs and below stones at the same cooler temperatures we find *A. picea* workers foraging and visiting bait stations. We believe that our findings may be the first to demonstrate that geographic variation in *Aphaenogaster* spp. distributions might translate to pronounced ecological effects – in our case on the efficacy of ant–plant mutualisms through the temperature response of ants' foraging phenology. Whereas several researchers have investigated geographic variation in ant–plant mutualisms (Garrido *et al.*, 2002; Boulay *et al.*, 2006; Rey & Manzaneda, 2007), there is little information on geographic and environmental variation within a single ant genera, which is particularly relevant for *Aphaenogaster* considering its critical role in North American myrmecochory (Ness *et al.*, 2009). Notably then, most researchers investigating North American myrmecochory only identify *Aphaenogaster* spp. by genera (see Ness *et al.*, 2009), which may limit our ability to predict how ant–plant mutualisms will be affected by environmental change.

Ant–plant synchrony

The initiation of the *A. picea* foraging in weeks 5–6 meant that it coincided with fruit set in both the early fruiting *H. nobilis* and later fruiting *H. arifolia*. In contrast, *A. rudis* began substantive foraging in weeks 13–14 so that it only coincided with *H. arifolia* fruiting. Thus, we find temperature-cued synchrony between plant and ant phenology, but its success depends on specific ant species so we also find asynchrony between an early fruiting plant and late foraging ant. Whereas long-term study may strengthen the results and provide further insights, our use of broad (location) and fine (grids) spatial scales, experimental transplants and bait stations, and a broad range of abiotic conditions, gives us confidence that our inferences are robust. Using this design, we show that climate-based asynchrony in these plant–ant mutualisms does occur. The different dispersal abilities of the plants and ants under investigation highlight the potential for asynchrony under climate change. Indeed, ants generally disperse seeds 1–2 m from maternal plants (Matlack, 1994; Cain *et al.*, 1998;

Gomez & Espadaler, 1998), whereas winged queens can establish new ant colonies at much larger distances (Holldobler & Wilson, 1990). This discrepancy means that *Aphaenogaster* spp. can shift ranges in response to changing climate much faster than woodland herbs. Notably, many woodland herbs are hardy and can persist long after environmental conditions become suboptimum (Bierzuchudek, 1982; Eriksson, 1996; Vega & Montana, 2004; Whigham, 2004).

The asynchrony between *A. rudis* foraging and *H. nobilis* fruiting may indicate an emerging breakdown in this mutualism due to changing environmental conditions. We note that *H. nobilis* populations are far more patchy and isolated in the WHF region than *H. arifolia* (Harris, 2000; Giladi, 2004; Warren, 2007, 2008), yet transplant studies show that *H. nobilis* tolerates a much wider set of environmental conditions than *H. arifolia* (Warren, 2007, 2008). We need further study to decipher if the patchy distribution of *H. nobilis* is the result of the asynchrony, but it is feasible that phenological synchrony or asynchrony between plants and ant dispersers may favor the persistence of some myrmecochores over others. Indeed, plant and animal communities are not invariant and have shifted species and structure throughout the paleorecord and associated climate shifts (Root *et al.*, 2003; Williams & Jackson, 2007).

Conclusions

We show that the phenologies of seed release and ant foraging in the myrmecochore mutualism is primarily temperature-dependent. Use of transplants suggests that the synchrony of this mutualism is plastic, which may facilitate its persistence as the environment changes. Yet we also find species-specific variation in ant foraging phenology that may lead to seed-dispersal asynchrony for early-timed myrmecochores. If this asynchrony is driven by warming, dispersal failure would leave these species isolated in deteriorating habitat, undermining range adjustments for species already threatened by climate change in the southern parts of their ranges.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mean environmental and phenology values for the beginning (week 1, Feb. 24), midpoint (week 7, Apr. 3) and end (week 14, June 2) of 2010 monitoring at Whitehall Forest (WHF) and Coweeta LTER (CWT).

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