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Upward ant distribution shift corresponds with minimum, not maximum, temperature tolerance

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Abstract

Rapid climate change may prompt species distribution shifts upward and poleward, but species movement in itself is not sufficient to establish climate causation. Other dynamics, such as disturbance history, may prompt species distribution shifts resembling those expected from rapid climate change. Links between species distributions, regional climate trends and physiological mechanism are needed to convincingly establish climate-induced species shifts. We examine a 38-year shift (1974–2012) in an elevation ecotone between two closely related ant species, *Aphaenogaster picea* and *A. rudis*. Even though *A. picea* and *A. rudis* are closely related with North American distributions that sometimes overlap, they also exhibit local- and regional-scale differences in temperature requirements so that *A. rudis* is more southerly and inhabits lower elevations whereas *A. picea* is more northerly and inhabits high elevations. We find considerable movement by the warm-habitat species upward in elevation between 1974 and 2012 with *A. rudis*, replacing the cold-habitat species, *A. picea*, along the southern edge of the Appalachian Mountain chain in north Georgia, USA. Concomitant with the distribution shifts, regional mean and maximum temperatures remain steady (1974–2012), but minimum temperatures increase. We collect individuals from the study sites and subject them to thermal tolerance testing in a controlled setting and find that maximum and minimum temperature acclimatization occurs along the elevation gradient in both species, but *A. rudis* consistently becomes physiologically incapacitated at minimum and maximum temperatures 2 °C higher than *A. picea*. These results indicate that rising minimum temperatures allow *A. rudis* to move upward in elevation and displace *A. picea*. Given that *Aphaenogaster* ants are the dominant woodland seed dispersers in eastern deciduous forests, and that their thermal tolerances drive distinct differences in temperature-cued synchrony with early blooming plants, these climate responses not only impact ant-ant interactions, but might have wide implications for ant-plant interactions.

Keywords: *Aphaenogaster picea*, *Aphaenogaster rudis*, physiological tolerance, regional climate, seed dispersers, southern appalachian mountains, species distributions

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Introduction

Upward and poleward species distribution shifts are consistent with a warming climate as organisms may shift their distributions higher in elevation or further from the poles to remain within suitable thermal habitat (Chen *et al*., 2011; Tewksbury *et al*., 2011). Still, such correlations are not causal; other factors, such as disturbance history, can create similar patterning easily misattributed to climate change (Parmesan *et al*., 2011;; Schwilk & Keeley, 2012). Moreover, regional-scale climate trends can, and do, differ greatly from global climate trends (IPCC, 2007), so the assumption that upward and poleward distribution shifts are caused by changing climate should not be implicit.

Predicting species distributions in a changing climate may depend on the ability to predict species interactions (Urban *et al*., 2012), but empirical evaluation of changes in biotic interactions with climate is lacking (Agrawal *et al*., 2007; Zarnetske *et al*., 2012). Warren *et al.* (2011b) delineated the distribution of several *Aphaenogaster* ant species by climate, and Warren *et al.* (2011a) showed that *Aphaenogaster* species differ in phenology (and therefore ecological roles) by climate, but little is known how *Aphaenogaster* species interact and how their interactions may change with climate. *Aphaenogaster* ants are ecologically important as the central and most effective plant seed dispersers in eastern North American woodlands (Ness *et al*., 2009) and as potential regulators of forest ecosystem dynamics (Warren & Bradford, 2012). *Aphaenogaster* workers are inordinately common in forest habitats where they forage from colonies found under stones, in rotten logs, leaf litter and, occasionally, in the soil (Crozier, 1977; Lubertazzi, 2012). The colonies are highly mobile, and the

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ants appear to colonize microclimates that maximize their preference for local soil moisture and temperature (Smallwood, 1982; Warren *et al*., 2010, 2011a).

At broader scales, eastern N.A. *Aphaenogaster* species have overlapping, but geographically distinct ranges that appear limited by climate. For example, *A. rudis* and *A. picea* often co-occur in the mid-latitudes of eastern N.A., but *A. picea* occurs at considerably more northern latitudes and at much higher elevations than *A. rudis* (Umphrey, 1996; Warren *et al*., 2011b). Warren *et al*. (2011a) found that minimum daily temperatures best predicted when *A. rudis* and *A. picea* break dormancy and begin foraging in spring, but *A. rudis* required ambient temperatures 6 °C higher than *A. picea*. An *A. rudis*/*picea* overlap zone occurs in north Georgia where R.H. Crozier collected Aphaenogaster colonies in 1973–74 for genetic analysis (Crozier, 1977). Crozier noted an elevation gradient where the 'coastal' species (*A. rudis*) gave way to the 'montane' species (*A. picea*). Across nine of his north Georgia study sites, ranging from 473–1050 m, Crozier indicated a shift in the proportion of each species at about 600 m, with *A. rudis* generally occurring at lower elevations and *A. picea* almost exclusively at the higher elevations.

The long-term data needed to establish yearly trends between individual species and climate are largely lacking, and what exists favors less cryptic species such as birds and butterflies (Parmesan, 2006). For these reasons, we utilize historical data intended for a different purpose, genetic analysis (Crozier, 1977), and use relative proportions of each species at fixed sites for long-term comparison. We combine these historical data with regional climate trends in north Georgia to examine shifts in species distributions; however, this pattern remains correlative without a physiological mechanism linking distribution shifts and climate (Helmuth *et al*., 2005) so we also examine physiological thermal tolerance in each species.

There is a growing interest in using physiological ecology to understand large-scale patterns of biodiversity (reviewed in Chown *et al*., 2004). Physiological traits, such as thermal tolerance, can help forecast species climate responses (Kearney & Porter, 2009; Diamond *et al*., 2012). We note, however, that most (see Deutsch *et al*., 2008; Tewksbury *et al*., 2008; Portner *et al*., 2009), but not all (Huey, 2010), physiological climate research only addresses species maximum temperature limits (CT_{max}) and omits the lower thermal limits (CT_{min}). Given that *A. rudis* inhabits lower elevations and latitudes than *A. picea* (Umphrey, 1996; Warren *et al*., 2011b), and that *A. rudis* requires higher minimum temperatures to begin spring foraging (Warren *et al*., 2011a), we expect an upward shift in *A. rudis* colonies if the north Georgia climate has warmed based on its minimum temperature limitations.

Methods

Elevation gradients

Crozier's 1973–74 collection sites ($n = 12$) were re-located using published mileage directions (Crozier, 1977). We spoke with local residents and land managers to verify current roads and landmarks that may have changed during the 35-year interval. We also found that the putative sampling sites coincided with road pull-offs, trailheads, and gated forest roads in the Chattahoochee National Forest and Black Rock Mountain State Park (see S1 for GPS locations). Crozier sampled *Aphaenogaster* ants throughout Georgia, but elevation gradients were not a research priority. As such, a sampling gap occurred in the 600–800 m elevation range. We added six sampling sites in 2012 to capture ant composition in that elevation range and better assess the elevation gradient. An intended 7th site had to be dropped because it was infested with the invasive Asian needle ant *Pachycondyla chinensis*. We dropped three of the original 12 north Georgia sites employed by Crozier in 1973–74 because one essentially overlapped with another, one has become developed with homes and a restaurant, and one only included 1973–74 ants Crozier considered 'intermediate' which did not allow *A. rudis*/*A. picea* assessment. We procured Crozier's 1973–74 *A. rudis* 'coastal' and *A. rudis* 'montane' specimens from the Georgia Museum of Natural History (Athens, GA, USA) to verify consistency with our identifications of *A. rudis* and *A. picea*.

Workers visited the study sites ($n = 15$ total) in May 2012 and collected 4–5 individuals from putative *Aphaenogaster* colonies located by turning over stones and logs for 30 min in woodland habitat. A total of 755 ants from 191 colonies were collected, though 90 ants were later identified as nontarget species, including *A. fulva*, *Myrmica americana* and *Prenolepis imparis*. The ants were placed in numbered alcohol vials and randomly selected with no indication of collection origin to remove any identification bias. Voucher specimens were deposited with the Georgia Museum of Natural History. We analyzed the effect of elevation on the proportion of ant species in 1974 and 2012 using Generalized Linear Models (GLM) with a binomial error distribution (binomial proportion) in the R statistical package (R Development Core Team, 2013). Because the proportion of *A. rudis* levels off at higher elevations in the 1974 data, second order terms were included in the models.

Colonies subsamples from each site were randomly chosen and 10 additional live individuals from these colonies were collected for thermal tolerance testing. Thermal limits, such as CT_{max} and CT_{min}, allow us to determine mechanistic constraints on various populations by using physiological function as an ecologically relevant endpoint. These specimens were kept alive and transported back to the laboratory at Highlands Biological Station where testing began within 8 h of field collection. We analyzed the effect of elevation on

CT_{max} and CT_{min} for each species using linear regression models. We also used linear models to examine whether the slope value for each species CT_{max} and CT_{min} changed similarly with elevation.

Climate trend analysis

We investigated whether regional, long-term climate trends corresponded to observed shifts in *Aphaenogaster* spp. distributions by examining 1974–2011 precipitation and temperature trend data for 11 north Georgia weather stations (136–477 m elev., see S2 for GPS locations). Climate data were downloaded from the National Climatic Data Center (U.S. Department of Commerce, http://www.ncdc.noaa.gov/oa/ncdc.html). We used these data to characterize climate trends for the 11 000-km^2 region. Because idiosyncratic changes in climate collection methods and calibration likely occur during the span of long-term weather measurements, the weather station data were standardized by taking anomalies from the mean of a standard base period (1951–1970) for time series analysis (absolute values are presented in Fig. 2 because they are more intuitive). The 1974–2011 yearly trends were analyzed using Box-Jenkins autoregressive moving average models (ARMA) (Box *et al.*, 1994) using the R software package (R Development Core Team, 2013) 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 assumes that errors are correlated and may have unequal variances without assuming linearity in the data. The model order (degree of autocorrelation) was selected based on the autocorrelation (ACF) and partial autocorrelation (PACF) functions (Shumway & Stoffer, 2006).

Thermal tolerance

We used locomotor ability (loss of righting response) to indicate critical thermal limits in all ant species (Lutterschmidt & Hutchinson, 1997). The loss of righting response is an ecologically important endpoint to assess the thermal limits of an organism prior to mortality. For tolerance testing, individuals were transferred to 16 mm glass test tubes, plugged with cotton to reduce thermal refuges, and were placed in the testing chamber. One vial contained only a copper-constantan Type-T thermocouple (Model HH200A, Omega, Connecticut, USA) to monitor temperature fluctuation inside the test tubes and ensure an accurate temperature reading at which individuals reached their thermal limits. We selected 10 individuals (five for CT_{max}, five for CT_{min}) collected from each colony at each site to undergo thermal tolerance testing. A mean temperature for the loss of righting response served as the index for thermal tolerance for each species at each site.

For CT_{max}, we placed individuals in test tubes haphazardly assigned to a slot in an Ac-150-A40 refrigerated water bath (NesLab, ThermoScientific, Portsmouth, NY, USA) which was prewarmed to 30 °C. Individuals were allowed to equilibrate for 10 min at which point the temperature was increased by 1.0 °C min^{-1}. We checked each tube every minute, rotating them to observe locomotor ability. We characterized heat tolerance as the highest temperature at which an individual could no longer right itself when rotated in the tube. For each CT_{max} and CT_{min} experiment, one individual served as a control and was kept in a separate water bath that was not experimentally heated or cooled. We used the control individuals to confirm that the ants were not incapacitated by confounding factors (e.g., handling stress). In all trials, the control individuals never became incapacitated, nor did they exhibit any behavior indicating distress. We used a similar procedure to determine CT_{min}. Five individuals from each colony at a site were assigned to test tubes and haphazardly placed in slots in an Ac-150-A40 refrigerated water bath. For CT_{min}, the water bath was set to 20 °C. Ants were allowed to equilibrate for 10 min at which point water temperature began to decrease by 1.0 °C min^{-1} until individuals lost righting response. At the conclusion of the testing, all ants were preserved in individual 2.0 ml vials containing 95% ethanol and cataloged at the University of Tennessee.

Results

We found significant incursions of *A. rudis* colonies up to higher elevations (Fig. 1). The proportion of *A. rudis* decreased significantly with elevation in 1974 (*coeff.* = −0.054; SE = 0.012; *z-value* = −4.549; $P < 0.001$), but leveled off (essentially disappeared) at elevations > 900 m (*coeff.* = 0.0003; SE = 0.000008; *z-value* = 3.838; $P < 0.001$). In 2012, the proportion of *A. rudis* also decreased significantly with elevation (*coeff.* = −0.009; SE = 0.001; *z-value* = −12.39; $P < 0.001$), but *A. rudis* did not disappear at elevations > 900 m. The lowest elevation, 473 m, remained exclusively *A. rudis* from 1974, but higher elevation sites (700–800 m) once dominated by *A. picea*, shifted to *A. rudis*. Only locations > 900 m remained predominately *A. picea* (75–85%); notably, in 1974, these locations were 100% *A. picea*.

During this same period (1974–2011), mean (±SD) yearly precipitation (1970s: 41.6 ± 3.8 cm; 2000s: 39.3 ± 5.8 cm) and temperature (1970s: 15.4 ± 0.5 °C; 2000s: 15.6 ± 0.4 °C) remained stable (Table 1, Fig. 2a and b). Maximum yearly temperatures decreased slightly (1970s: 28.0 ± 0.9 °C; 2000s: 28.6 ± 0.6; Fig. 2c), but the significant change in climate in north Georgia between 1974 and 2012 was mean minimum temperatures, which increased significantly (1970s: 0.9 ± 0.7 °C; 2000s: 2.4 ± 0.6 °C; Fig. 2d).

Both species exhibited significant declines in maximum (*A. picea: coeff.* = −0.003; SE = 0.001; *t-value* =

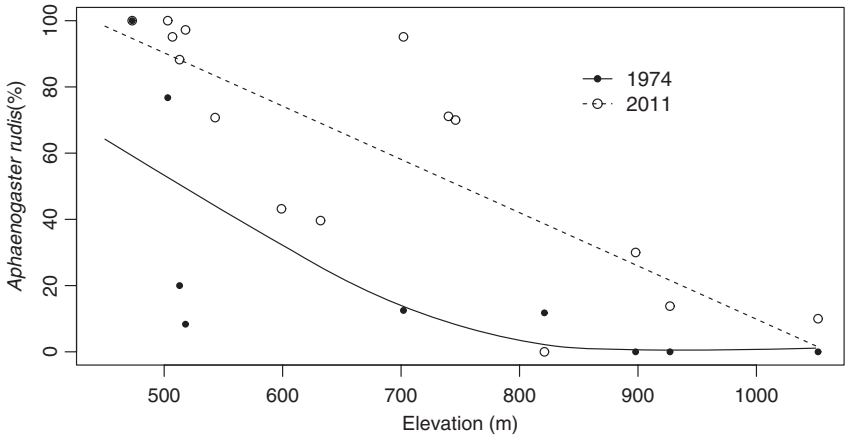

Fig. 1 The percent *Aphaenogaster rudis* ants (vs *A. picea*) by elevation in 1974 and 2012. Only the percent *A. rudis* is shown because *A. picea* = 100 - *A. rudis*. R.H. Crozier collected *Aphaenogaster* spp. in 1974 at the southern edge of the Appalachian Mountains in north Georgia, USA for genetic analysis. The percent *A. rudis* and *A. picea* at each site were culled from the published manuscript (Crozier, 1977) and plotted here. Crozier's nine plots, along with an additional six plots, were re-sampled for *A. rudis* and *A. picea* in 2012. *Aphaenogaster rudis* declined significantly with elevation in both 1974 and 2012 (fitted lines), but no *A. rudis* were found > 900 m in 1974 whereas *A. rudis* was 10–25% of the *Aphaenogaster* ants found > 900 m in 2012.

Table 1 Generalized least squares regressions with maximum likelihood for north Georgia, US, climate trends (1974–2011)

Parameter	*Coefficient*	SE	*t-value*	*p-value*
Mean annual precipitation	−0.363	0.34	−1.067	0.293
Mean annual minimum temperature	0.045	0.016	2.881	0.007
Mean annual maximum temperature	−0.029	0.013	−2.133	0.039
Mean annual temperature	−0.023	0.019	−1.224	0.229

−6.291, $P < 0.001$) and minimum (*A. rudis: coeff.* = −0.009; SE = 0.002; *t-value* = −5.415, $P < 0.001$; *A. picea: coeff.* = −0.011; SE = 0.001; *t-value* = −10.07, $P < 0.001$) thermal tolerances with elevation, except that the decline in *A. rudis* maximum tolerance was not statistically significant (*coeff.* = −0.002; SE = 0.001; *t-value* = −1.588, $P = 0.151$) (Fig. 3). The rate (slope value) of decline with elevation did not differ significantly between species for maximum thermal tolerance (*coeff.* = 0.537; SE = 0.601; *t-value* = 0.894, $P = 0.412$), but *A. picea*'s ability to tolerate cold temperatures increased significantly more with elevation than did *A. rudis* (*coeff.* = 1.285; SE = 0.339; *t-value* = −3.785, $P = 0.013$) thermal tolerances. *Aphaenogaster rudis*, which is much less common > 900 m, maintained a 1–2 °C higher maximum (Fig. 3a) and minimum (Fig. 3b) temperature than *A. picea*, which does not occur < 475 m. Even at mid-elevations (700–900 m) where both species occur, the minimum temperature tolerated by *A. rudis* never dropped below 2 °C whereas *A. picea* tolerated temperatures down to −0.5 °C. Conversely, *A. picea* never tolerated temperatures > 42.5 °C, whereas *A. rudis* tolerated temperatures 1 °C warmer.

Discussion

Aphaenogaster rudis has a higher minimum temperature requirement to break winter dormancy and initiate spring foraging than *A. picea* (Warren *et al*., 2011a), and we show that significant upward shifts in *A. rudis* distributions only coincide with rising minimum temperatures during the period 1974–2012. These results suggest that minimum temperatures limit *A. rudis*, but not *A. picea*–thermal limits that have weakened at the southern end of the Appalachian mountains during the last three decades.

Aphaenogaster picea is adapted to colder temperatures than *A. rudis*, but it can tolerate much higher temperatures than where it is found, which is not uncommon for cold-adapted species (Urban *et al*., 2012). Rather than rising temperatures, what often eliminates cold-adapted species with climate change is competition from colonizing warm-adapted species (Urban *et al*., 2012). Competitive interactions are common between ant species, and these are alleviated by spatial and temporal habitat partitioning (Parr & Gibb, 2010). Typically, habitat segregation among ants is driven by temperature with less competitive species occupying marginal environments (Dunn *et al*., 2007). In southern

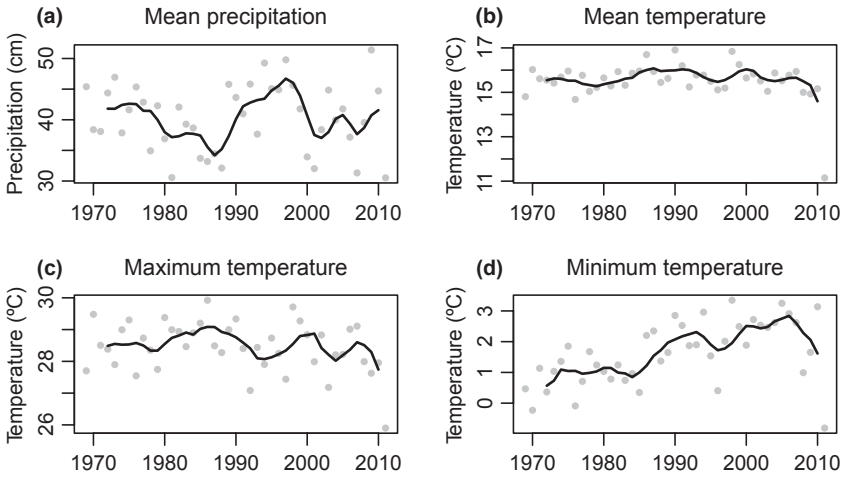

Fig. 2 Climate trends 1974–2012. Climate data compiled from 11 north Georgia weather stations. Shown are absolute values (points) and 5-year running averages (line) for (a) mean precipitation, (b) mean temperature, (c) maximum temperature and (d) minimum temperature.

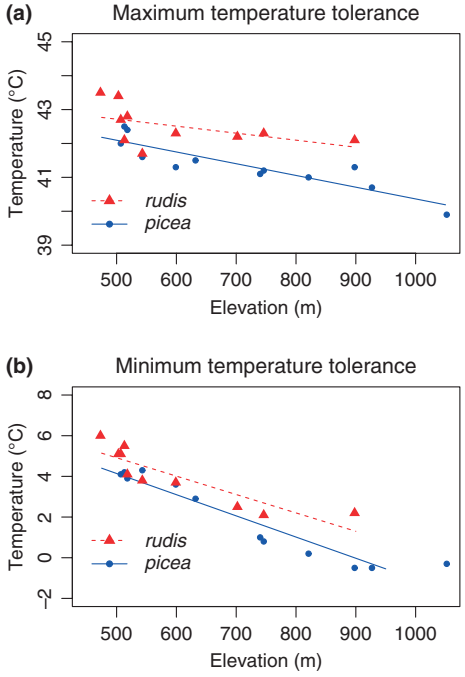

Fig. 3 Thermal tolerance maximum and minimums by elevation for *Aphaenogaster picea* and *A. rudis*. Data for 4–5 individuals of each species pulled from 15 sites along a 473–1050 m elevation gradient.

Appalachian Mountain woodlands, relatively colder habitat appears marginal for ants. Ant diversity decreases with elevation, and the decline is linked with decreasing temperature (Sanders *et al.*, 2007). Given that minimum, not maximum, temperatures coincide with substantial transgressions of *A. rudis* into *A. picea* territory, it appears that the cold-adapted species may be disappearing not through abiotic limitations, but through competition with encroaching warm-adapted species – though additional work, particularly experimental, is required to confirm competition as the mechanism for replacement. One caveat is that, given the limitations of the historical data, we can only compare proportions of each species at each site. It is possible that there are more *A. rudis* individuals at higher elevations along with more *A. picea*. Still, given that *A. rudis* proportions reached 90–100% at the lower elevations (500–700 m), *A. rudis* clearly displaced *A. picea* at those locations.

Aphaenogaster picea occurs far north into eastern Canada, so extinction is unlikely even at the extreme high end of potential temperature change (+5.8 °C) currently predicted for the next century (IPCC, 2007). Both the cold- and warm-adapted *Aphaenogaster* spp. tolerated experimental temperatures > 10 °C warmer than any maximums recorded during the last 40 years in our study region (see Figs. 2 and 3), which is at the southern end of their ranges (Warren *et al.*, 2011b). Given the displacement observed in north Georgia, however, local extirpations may be likely.

A second possibility is that *A. picea* genes rather than individuals are being replaced by *A. rudis*. Crozier found little chromosomal evidence of hybridization where the species overlapped, but did find allelic indication of introgression (Crozier, 1977). We observed that the lowest-elevation *A. rudis* ants are much redder bodied with light legs and uniform antenna coloring than the highest-elevation *A. picea*, which are very dark bodied with darker legs and lighter segments on the antennae end. These phenotypic characteristics blend somewhat at the middle elevations, suggesting hybrid-

ization may occur. The geographical movement of hybrid zones has been implicated in the decline of many species, often the result of more competitive low-elevation species migrating upward (Buggs, 2007). The shifts in thermal tolerance by elevation in both species may indicate physiological acclimatization, gene flow, and/or historical selection. Differentiating between these possibilities will require genetic analysis of the species and populations. Moreover, regional temperature trends do not capture nuances in microclimate that may shift with elevation. Further work is needed to link ant activity, particularly phenology, with microclimate gradients in temperature, and explore how those relationships scale up to regional and continental distributions. As both the cold-adapted *A. picea* and warm-adapted *A. rudis* ants tolerate a wide range of maximum and minimum temperatures, it appears each has ample capacity for acclimatization and/or adaptation; however, the absolute minima and maxima remain distinct for *A. picea* (min: −0.5 °C; max: 42.5 °C) and A. rudis (min: 2 °C; max: 43.5 °C), and *A. picea's* cold tolerance increases more with elevation than *A. rudis*. These results, and previous work (Warren *et al*., 2011a,b), suggest differentiation between species based on temperature, at least in this study region.

A great unknown in climate change science is how species interactions might change with climate (Agrawal *et al*., 2007; Zarnetske *et al*., 2012). Not only does upward *A. rudis* introgression impact *A. picea*, but it also potentially impacts a large guild of understory woodland plants, particularly spring ephemerals. Warming might select against cold-adapted species, but ecosystem function remains stable if that species is replaced by a warm-tolerant congener (Somero, 2010). However, a 'like replaces like' mechanism only maintains function if the replacement species can acclimatize to their newly invaded system (Somero, 2010). We show that even though *A. rudis* migrated upward in the north Georgia mountains, it maintains a considerably lower tolerance for cold temperatures than *A. picea*. The warmer-adapted *A. rudis* likely makes up for lesser cold tolerance by waiting longer to break winter dormancy and begin foraging in the spring–a phenomenon empirically documented by Warren *et al*. (2011a). Phenological shifts often occur much faster in insects than plants (Root *et al*., 2003), and these shifts can cause asynchrony in the timing of interactions, such as between flowers and pollinators (Cleland *et al*., 2007). A shift from *A. picea* to *A. rudis* dominance at mid- to high-elevations, and potentially latitudes, would correspondingly mean a shift from a very early foraging spring species to a later foraging spring species. As such, the delay in availability by the key seed-dispersing ant genera would result in failed dispersal for many spring flowering plants. Potentially then, a contraction of the *A. picea* range northward might cascade into a contraction of early spring woodland plants northward.

Many studies observe species range or elevation shifts and assume an underlying global warming signal without measuring local or regional weather trends (see Parmesan, 2006), but the IPCC called for greater regionalization in climate science assessments (IPCC, 2007). We observe upward species distribution shifts that are not explained by mean climate trends. As such, many observed shifts in species distributions and phenology that assume mean global warming might actually be caused by regional minimum or maximum temperatures, which suggest a far different outlook depending on ecological (e.g., competition, Urban *et al*., 2012) and climate (e.g., airborne particles, Goldstein *et al*., 2009) complexities that interact with changing temperatures. Whereas hotter temperatures may push some cold-adapted species to their physiological limits (Hoffmann *et al*., 2012), the amelioration of colder temperatures may be more insidious in allowing replacement by warm-adapted species.

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Supporting Information

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

Table S1. North Georgia site locations.
Table S2. North Georgia weather stations.