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Climate-driven range shift prompts species replacement

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Abstract Climate change prompts warm-tolerant species upward and poleward to either displace or replace cold-tolerant species. Warm-tolerant species may replace cold-tolerant individuals with upward migration, or cold-tolerant genes if the species hybridize. We examined genetic and morphological differences between low elevation, warm-tolerant (*Aphaenogaster rudis*) and high elevation cold-tolerant (*A. picea*) ant species that form an upward-shifting ecotone in the southern Appalachian Mountains (USA). The *A. picea*/*A. rudis* ecotone shifted upward ca. 200 m between the decades 1970 and 2010, and characteristic morphological traits appeared muddled where the species met, suggesting hybridization. However, we found no evidence of genetic hybridization, and the trait most associated with species identity, pigmentation, remained so across the environmental gradients. Conversely, femur length did not differentiate well between species identities, and it shifted across the environmental gradients. These results suggest that the cold tolerant *A. picea*, associated with high-elevation and high-latitude, was replaced by the warm-tolerant, low elevation *A. rudis* species. As such, these results suggest that less competitive cold-tolerant species may be replaced by more competitive cold-intolerant species with climate warming.

Keywords *Aphaenogaster* · *Rudis* complex · Hybridization · Traits · Phenotypic plasticity · Phylogenetics

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Introduction

Species generally move upward and poleward with climate warming (Brommer 2004; Parmesan et al. 1999; Pelini et al. 2009; Zuckerberg et al. 2009). If all the species move in the same direction at the same rates, their ranges and interactions would simply shift in space without increasing overlap and interaction pressures. However, species move at different rates in response to climate change (Ibanez et al. 2008; Kelly and Goulden 2008; Miller-Rushing et al. 2008; Pelini et al. 2009; Perry et al. 2005; Schweiger et al. 2008; Zhu et al. 2013) so that less competitive (cold-tolerant) species may be replaced by more competitive (cold-intolerant) species with warming (Connell 1975; Menge and Sutherland 1987; Urban et al. 2012). Alternatively, closely related species may interbreed so that genes, rather than species are replaced, and hybrid zones move upward and poleward (Buggs 2007; Harr and Price 2014; Wolf et al. 2001).

Boreal forest communities blanketed the southern Appalachian Mountains during the most recent glacial maximum ~18,000 years ago (Delcourt and Delcourt 1987, 2000). As the Pleistocene ended, species adapted to cold climates migrated northward, and in montane environments, upward. Generally, species that can better tolerate stressful conditions (e.g., cold) are poor competitors (Chase and Leibold 2003; Tilman and Pascala 1993), and

better competitors may replace cold-tolerant species with climate change (Urban et al. 2012). High elevation species not always are replaced, however, and in some cases form hybrid zones with low elevation congeners. For example, ecotones between closely related high- and low-elevation salamander species persist in the Southern Appalachian Mountains (USA), and, though their interactions along elevation gradients generally are competitive, they hybridize where distributions overlap (Bruce 2007; Hairston 1949, 1951; Hairston et al. 1992; Highton and Peabody 2000).

Ant complexes can be very cryptic with plastic morphology that obscures species differentiation across environmental gradients (e.g., darker colors with increased elevation) (MontBlanc et al. 2007; Seifert 2009). For example, in eastern North America, approximately 12 *Aphaenogaster* species are the most abundant arthropods in mesic deciduous forests (King et al. 2013), but eastern North America *Aphaenogaster* species are hard to differentiate based on morphology, including *A. rudis* and *A. picea*; hereafter '*rudis* complex' (Lubertazzi 2012; Ness et al. 2009; Umphrey 1996). The eastern North America *Aphaenogaster* taxonomy remains unresolved, but, genetic, geographic and ecological data suggest discrete species with distinct, albeit overlapping, North America distributions (Creighton 1950; Crozier 1977; De Marco and Cognato 2016; Lubertazzi 2012; Umphrey 1996; Warren et al. 2011b).

Ant species, including *Aphaenogaster*, typically partition habitat (spatially and temporally) by temperature (Dunn et al. 2007; Parr and Gibb 2009; Sanders et al. 2007). In the southern Appalachian mountain region (USA), two *Aphaenogaster* species appear to segregate latitude and elevation by minimum temperatures (Warren et al. 2011a, b; Warren and Bradford 2013; Warren and Chick 2013). The northerly, high-elevation *A. picea* forages at temperatures ca. 6 °C below that of the southerly, low-elevation *A. rudis* (Warren et al. 2011a), and experimental studies indicate that *A. picea*'s physiological heat and cold tolerance is ca. 2 °C lower than *A. rudis* (Warren and Chick 2013). The ecotone between *A. rudis* and *A. picea* shifted upward and northward with rising minimum temperatures in the southern Appalachian mountain region 1974–2012 (Warren and Chick 2013). Ant congeners commonly hybridize (Cahan and Keller 2003; Julian et al. 2002; Shoemaker et al. 1996), and in measuring the *A. rudis*/*A. picea* ecotone across elevation gradients, Warren and Chick (2013) noted that the species were difficult to differentiate at mid-elevations based on morphological characters alone, and suggested that the two closely related species might hybridize. However, in investigating the same elevation gradients, Crozier (1977) found little chromosomal evidence of hybridization.

We used morphometric analysis of ants collected along an *A. rudis*/*A. picea* elevation ecotone in northern Georgia in 1974 (Crozier 1977) and 2014 (Warren and Chick 2013) to investigate whether the shift in species appeared consistent with replacement or hybridization. We also used ants collected ca. 75 km north and 75 km south of the elevation ecotone to capture morphology in non-overlapping *A. rudis* and *A. picea* colonies. Moreover, we used ants collected with the 2014 ecotone samples, along with ants collected throughout eastern North America (De Marco and Cognato 2016), for genetic analysis of *A. rudis* and *A. picea*. If replacement occurred, we would expect no genetic evidence of hybridization and a discrete 'step' in species traits with transition between cold-intolerant, low-elevation *A. rudis* and cold-tolerant, high-elevation *A. picea*. If hybridization occurred, we would expect evidence of genetic introgression and a continuous shift in traits across the species boundary. We also investigated links between morphological traits that potentially differentiate the *Aphaenogaster* species and their thermal tolerances.

Methods

Specimen collections

In 2011, *A. rudis* was collected at Whitehall forest in Athens, GA, and *A. picea* was collected at Coweeta Hydrologic Laboratory (CWT) in Otto, NC (for methodology and GPS locations see King et al. 2013) (Fig. 1). In 2012, *A. rudis* (low elevation) and *A. picea* (high elevation) ants were collected in northern Georgia (NGA) in Chattahoochee National Forest and Black Rock Mountain State Park (for methodology and GPS locations see Warren and Chick 2013). The ant samples were dried and stored frozen at −4 °C until 2013 when they were pinned and mounted for morphometric analysis. A total of 290 ant specimens were used for morphometric analyses: 163 specimens from the 2011 collections and 52 specimens from the 2012 collections. Voucher specimens are stored at the Georgia Museum of Natural History and at SUNY Buffalo State. Location data and morphometric measurements also were taken from 75 voucher specimens collected by Crozier (1977) and stored at the GMNH. An additional 52 specimens (S2) were used for phylogenetic analysis, six of which were collected at the same sites as those used for the morphometric analysis.

Morphometrics

We used three morphometric measurements commonly used for ants, and possibly distinctive between
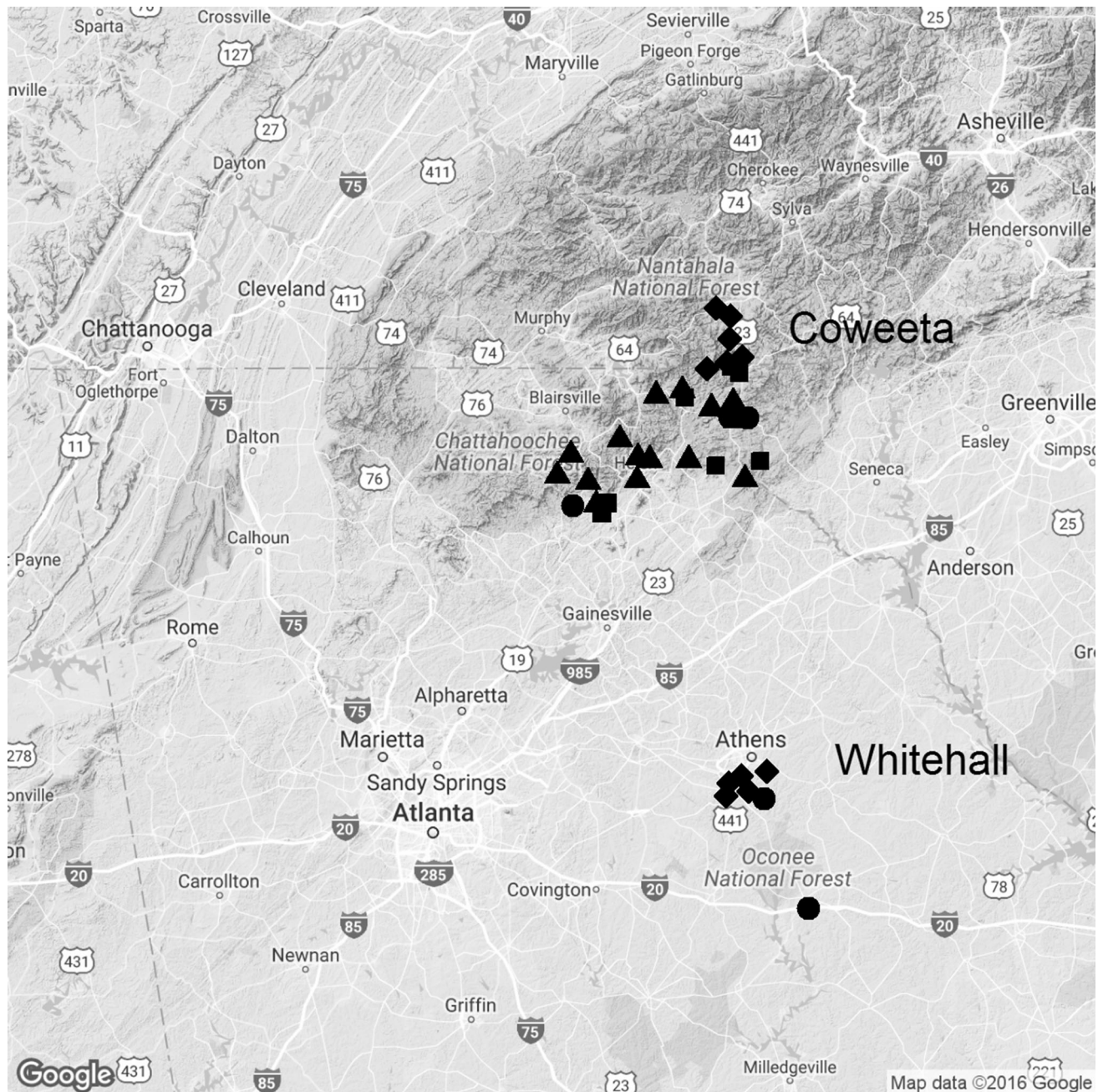
Fig. 1 Site map of the main study region (not including greater sampling area for genetic analysis) in northern Georgia and western North Carolina (USA). Ant specimens analyzed in this study were collected in 1974 for a genetic gradient study (*circle*, Crozier 1977), in 2011 to examine social insects (*diamond*, King et al. 2013), and in 2012 for gradient (*triangle*, Warren and Chick 2013) and genetic (*square*, De Marco and Cognato 2016) studies. A small amount of 'jitter' was added to the *symbols* to reduce overplotting. For *scale*, the distance between Coweeta and Whitehall is 125 km

Aphaenogaster species (De Marco and Cognato 2016; Umphrey 1996): relative eye length (maximum eye length/maximum head width including outer edges of eyes × 100), maximum femur length (posterior view) and pigmentation. Moreover, these traits correspond with functional abilities as larger relative eye length corresponds with greater night foraging (Greiner et al. 2007), greater femur length corresponds with greater speed/foraging

success (Pearce-Duvet et al. 2011) and darker color corresponds with cold tolerance (Kaspari et al. 2015). We digitally measured relative eye metrics and femur lengths using a Leica M125 stereomicroscope with DFC295 digital camera and Leica Application Suite V4. Two traits were measured: Given that *A. rudis* legs typically are lightly colored and reddish and *A. picea* legs darker black, and that *A. rudis* antennal segments are of uniform color whereas the

last four segments of *A. picea* antennae are lighter (Ellison et al. 2012), color and antennae pigmentation indices were generated. Leg pigmentation was coded as 1 = light, 2 = medium, 3 = dark; antennae pigmentation was coded as 1 = segments uniform, 2 = last four segments somewhat lighter than rest, 3 = last four segments clearly lighter than rest. The leg and antennae data were added to create a pigmentation score. Two technicians not involved with Warren and Chick (2013) independently coded specimens.

Phylogenetic analysis

Field-collected *Aphaenogaster* specimens were sent using an overnight mail carrier to the A. J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan from northern Georgia (*A. rudi*s) and western North Carolina (*A. picea*). Six of these specimens from NGA and CWT were included in a phylogenetic analysis using DNA data from five genes including the mitochondrial gene cytochrome oxidase subunit 1 (CO1), and nuclear genes: carbamoylphosphase synthase (CAD), elongation factor 1-alpha (EF1αF2), long-wavelength rhodopsin (LWR) and wingless (WG). These loci were included in a broad analysis of North American *Aphaenogaster* phylogeny (De Marco and Cognato 2016) that also included a larger number of specimens, and are phylogenetically informative for intraspecific and intergeneric relationships (Brady et al. 2006; Ward et al. 2010). All methods for DNA extraction, amplification and PCR (polymerase chain reaction) were followed using methods from De Marco and Cognato (2016). Primers used in PCR came from Brady et al. (2006) and Ward et al. (2010). After PCR, unincorporated deoxyribonucleotide triphosphates (dNTPs) and oligonucleotides were removed from PCR with Exo-SAP (http://www.usbweb.com/category.asp?cat=pcr&id=78200) and directly sequenced on an ABI 3700 automated sequencer using a BigDye (Applied Biosystems, Inc., Foster City, CA) fluorescent chemistry reaction. Both sense and anti-sense strands were sequenced for all individuals. This phylogeny was inferred with Bayesian analysis with Mr. Bayes via the CIPRES Gateway (Huelsenbeck and Ronquist 2001; Miller et al. 2010). Data were partitioned by gene and codon position (Castoe et al. 2004), with models of evolution applied independently to each partition (Nylander et al. 2004), with a best-fit GTR + I + G model, 20 million generations and a burn-in of 5,000,000 generations.

Samples of *A. carolinensis* and *A. miamiana* were included in the phylogeny due to an overlap of geographic locations and some morphological characters. *Aphaenogaster carolinensis* and *A. miamiana* can be found in North Carolina, along with *A. rudis* and *A. picea*. *Aphaenogaster miamiana* was previously known only from Florida (De

Marco and Cognato 2016), but can be distinguished from the others based on heavier sculpturing.

Climate and thermal tolerance

Mean maximum and minimum temperatures for the period June 2011–June 2012 were calculated for each ant collection site (based on GPS coordinates) using PRISM climate data (http://www.prism.oregonstate.edu). For ant thermal tolerance, we used the minimum and maximum physiological temperature tolerances for *A. rudis* and *A. picea* ants collected in NGA in 2012 as part of Warren and Chick (2013). In that study, we transferred individuals to 16 mm glass test tubes that were plugged with cotton to reduce thermal refuges and placed the test tubes in an Ac-150-A40 refrigerated water bath (NesLab, ThermoScientific). 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 measured thermal tolerance for 10 individuals (5 for CT_{min}, 5 for CT_{max}) from each colony at each site. We estimated thermal tolerance by determining the loss of righting response as the index for thermal tolerance using a ramping rate of 1 °C min^{-1}. We calculated the mean tolerance temperature for each species at each site. See Warren and Chick (2013) for full methodology.

Data analysis

We examined variation among ant morphological traits (pigmentation, femur length and relative eye length), physiological traits (minimum and maximum temperature tolerance), elevation and temperature (minimum and maximum) with principal component analysis (PCA) using the "prcomp" method and "scale" option (standardizes all variables to unit length) in the "R" statistical package (R Development Core Team 2016). There was a large drop in variance explained after the first principal component, which explained 61 % of the variance, but the second principal component explained more variance (16 %) than one variable (12 %), so we examined the first two components, which explained 77 % of the variance. We used the minimum contribution if all variable loadings contributed equally (35 % here) to determine the most important loadings for each principle component.

We used elevation to represent environmental variation as it was the main gradient in the field studies and it correlated with maximum temperature, and ant maximum and minimum temperature tolerances (PCA axis 1). We examined morphological trait values by elevation (1974 and 2012 data) and by species—as determined by karyotype (Crozier 1977)

and genotype (De Marco and Cognato 2016) using generalized linear models (GLM) assuming Poisson error distributions. The fitted models were over dispersed, so quasi Poisson error distributions were used. We examined the effect of elevation and species identity on relative eye length, femur length and pigmentation. Given that a shift in species occurred between low-elevation *A. rudis* and high-elevation *A. picea* at ca. 750 m elevation (Warren and Chick 2013), we included second-order terms to capture any nonlinear patterning. We considered coefficients with a *p* value <0.05 'significant' and those with a *p*-value <0.10 'marginally significant' (sensu Hurlbert and Lombardi 2009).

Results

Phylogenetic analysis

The phylogenetic analysis produced a mostly resolved Bayesian tree with strong support for the outgroups, including *Camponotus pennsylvanicus*, *Formica glacialis*, *Stenamma diecki*, *Novomessor cockerelli*, *Veromessor julianus* and *Solenopsis invicta* (S1). There also was strong support for the *A. fulva* and *A. picea* clades, however, *A. picea* was separated into two smaller clades. The sample from North Carolina was in the smaller clade. *Aphaenogaster carolinensis* and *A. miamiana* clades each showed strong support; however, they were within the less supported *A. rudis* clade. *Aphaenogaster carolinensis* and *A. miamiana* were distinguished from *A. rudis* due to a missing intron in the gene CAD.

Principal component analysis

Principal component analysis on ant morphological and physiological traits, elevation and temperature indicated that most variation occurred across elevation and temperature gradients and correlated well with femur length and temperature tolerance, but not pigmentation or relative eye length (Fig. 2). The most important variables for PC1, which explained most of the variance, were elevation, femur length, minimum and maximum temperature tolerance and maximum temperatures (S3). The most important variables for PC2 were pigmentation and relative eye length, suggesting that elevation and temperature did not explain trait variation well.

Trait variation with elevation and species identity

Elevation correlated strongly with ant maximum ($r = 0.92$) and minimum ($r = 0.97$) temperature tolerances, and with maximum ambient temperature ($r = 0.97$), but poorly with minimum ambient temperature ($r = 0.31$). The ant pigment was significantly higher in *A. picea* than *A. rudis* (Fig. 3a), but did not change with
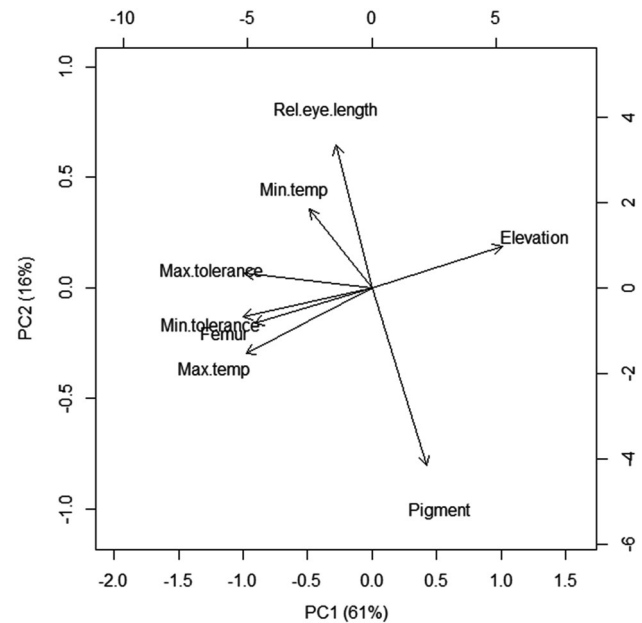

Fig. 2 Principal component analysis of ant morphological traits [pigment, femur (femur length) and relative eye length], physiological traits (minimum and maximum temperature tolerance), elevation and temperature (minimum and maximum). *Arrows* pointing in the *same direction* indicate positive covariation and those pointing in *opposite directions* indicate negative covariation

elevation (species: coef. = −0.052, SE = 0.003, *t*-value = −13.996, *p*-value <0.001; elevation: coef. = 0.001, SE = 0.007, *t*-value = 0.515, *p*-value = 0.607). These results indicated that, although the ants became darker in leg color and last four antennal segments at higher elevations, these patterns were better explained by species identity than by geographic location (Fig. 4a). Relative eye length did not change with species identity or elevation (species: coef. = 0.006, SE = 0.014, *t*-value = 0.446, *p*-value = 0.656; elevation: coef. = −0.001, SE = −0.001, *t*-value = −0.526, *p*-value = 0.600) (Figs. 3b, 4b). Femur length was significantly longer in *A. rudis* than *A. picea* (Fig. 3c), and it decreased significantly with elevation (species: coef. = −0.024, SE = 0.015, *t*-value = −1.689, *p*-value = 0.092; elevation: coef. = −0.001, SE = 0.001, *t*-value = −5.406, *p*-value <0.001) (Fig. 4b). Variance partitioning indicated that elevation explained 54 % of the variation in femur length whereas species identity only explained 3 %. These results indicated that *A. picea* had slightly shorter femurs than *A. rudis*, but more importantly, femur length decreased with elevation.

Discussion

Upward movement of an ant ecotone in the southern Appalachian mountain region appears better explained by species replacement than hybridization. Pigmentation best

Fig. 3 Species-level
differences in pigment (**a**),
relative eye length (**b**) and femur
length (**c**) trait values for
Aphaenogaster picea ($n = 94$)
and *A. rudis* ($n = 196$). Shown
are mean ± SE
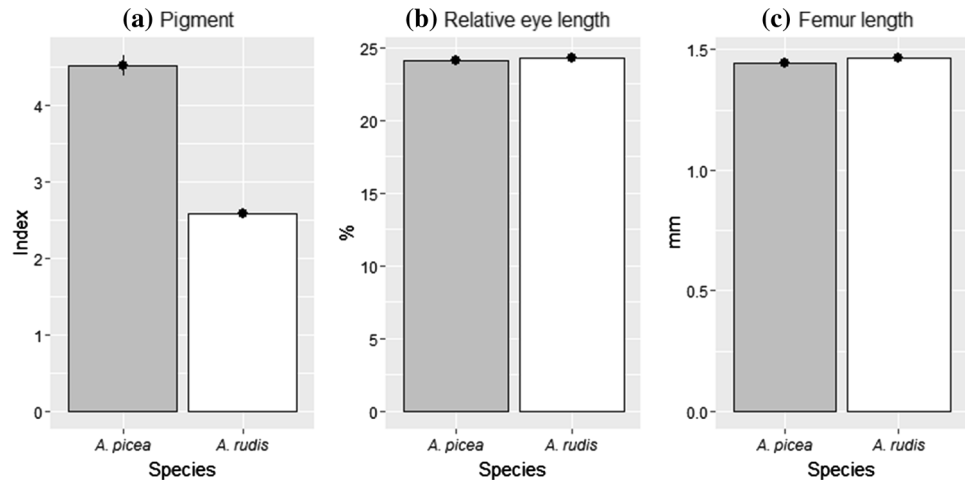
Fig. 4 Changes in
Aphaenogaster ant pigmentation
(**a**), the relative eye length
(**b**) and femur length (**c**) along
elevation gradients. The *fitted
line* includes both species, and
the *legend* indicates the residual
contribution of *A. picea* and *A.
rudis*. A small amount of 'jitter'
was added to the residuals to
reduce overplotting
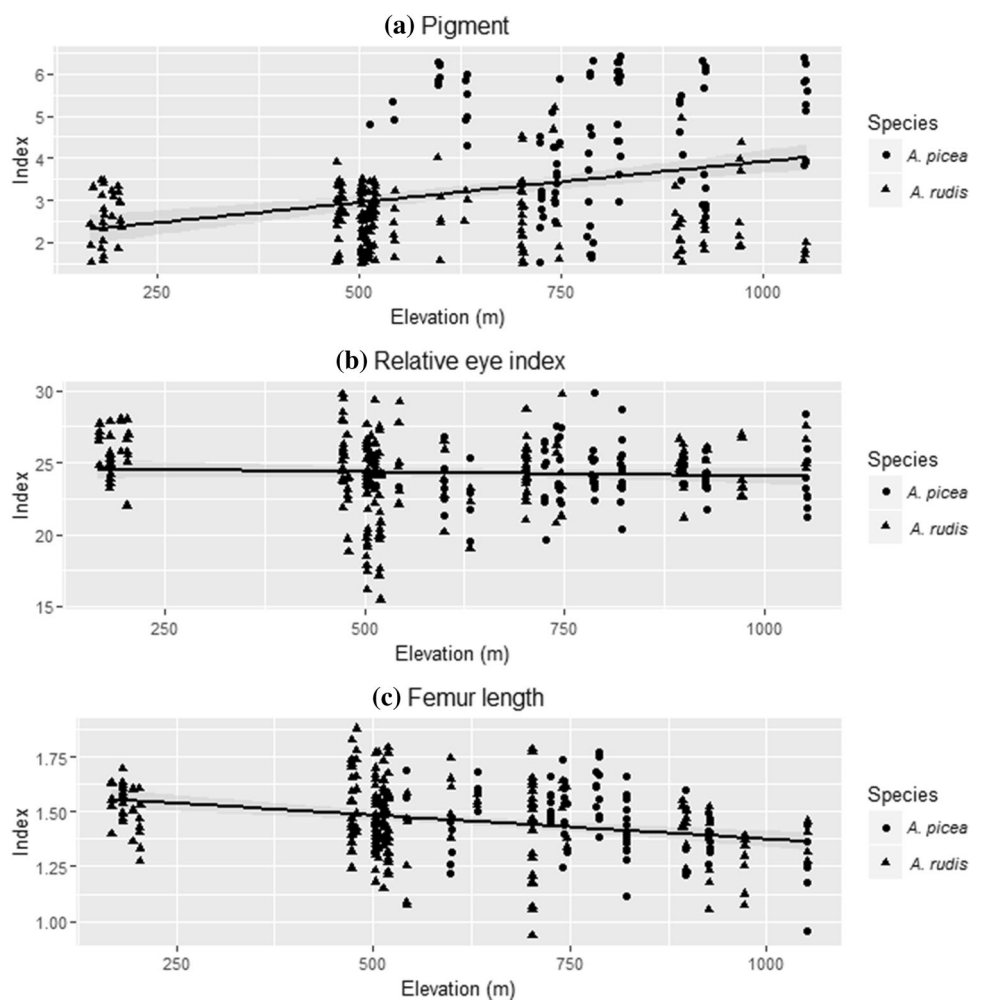
distinguishes between *A. picea* and *A. rudis*, and ants get
darker with higher elevation, but the change is better
explained by species identity than the environmental gra-
dient. Conversely, ant femur lengths get shorter with higher
elevation, and the shift is better explained by phenotypic
plasticity than species identity.

Crozier ([1977](#)) identified an ecotone in the Southern
Appalachian Mountains where low elevation *Aphaenoga-
ster rudis* shift to high elevation *A. picea* populations—
species, he differentiated based on chromosome number and
color. Warren and Chick ([2013](#)) re-sampled his gradient and
found that the *A. rudis*/*A. picea* ecotone had shifted ca.

200 m upwards to ca. 750 m elevation due to an increase in minimum temperatures, but they noted that mid-elevation ant morphology appeared muddled between the species, suggesting hybridization. In the current study, we found no evidence of genetic hybridization, nor did Crozier (1977), and the morphological shift in pigmentation at ca. 750 m was consistent with species rather than gene replacement. However, color was highly plastic, relative eye length essentially was invariant, and femur length was more dependent on environment than species. Overall, we found *Aphaenogaster* spp. morphology highly plastic and somewhat indistinguishable at local scales, but clearly genetically distinct and morphologically differentiated at broader scales.

Ant species in the *rudis* complex are widespread in North America, hard to morphologically differentiate, and are distributed in a manner that appears linked with post-glacial climates (King et al. 2013; Lubertazzi 2012; Warren and Bradford 2013; Warren and Chick 2013; Warren et al. 2011b). Based on morphology, Creighton (1950) identified six species/subspecies in the *rudis* complex (*A. miamiana*, *A. picea*, *A. rudis*, *A. fulva*, *A carolinensis* and *A. texana*) and suggested that color was a poor trait for distinguishing between them. Crozier (1977) questioned whether there were more cryptic species hiding in the *rudis* complex, and used chromosomal and isozyme variation to distinguish light colored coastal plain (*A. rudis*) and dark colored montane (*A. picea*) species, but suggested that color differences were too slight to be useful. Umphrey (1996) examined morphometrics in the *rudis* complex based on species identified with cytogenetic and electrophoretic markers and proposed nine species (four previously undescribed) with geographic location and coloring included as identifying characteristics. Subsequent direct and indirect testing of temperature requirements among the species supported ecological differentiation among the six identified species, particularly *A. rudis* and *A. picea* (Warren et al. 2011a, b; Warren and Bradford 2013; Warren and Chick 2013).

Our genetic analyses suggest, as did Umphrey (1996), that additional cryptic species may be hidden within the six identified species. The two *A. picea* clades that have darker legs and the last four antennal segments lighter in color correspond to the DNA data that separates them from other samples in the *A. rudis* clade. Morphologically, there is a tremendous amount of variability within the *A. rudis* clade. We found that pigmentation best distinguished between *A. picea* and *A. rudis* as identified by haplo- and genotypes (Crozier 1977; De Marco and Cognato 2016), whereas relative eye length was not useful and femur length appeared more responsive to environment than species. Given that our genetic analysis was based on samples collected at a continental scale and morphological analysis based on

samples collected at a regional scale, these results are not conclusive falsification of hybridization between *A. picea* and *A. rudis*. A more intensive genetic sampling across the ecotone/environmental gradient is required for greater insight into genetic differentiation at this scale. Moreover, based on the differences in thermal tolerance, traits and distributions, the assumption is that *A. picea* is a poor competitor that tolerates colder climes better than *A. rudis*; however, this assumption is not well tested.

The overlap in morphology between species may be explained by the linkage between the color, size and shape traits with physiological temperature tolerance; the strongest link possibly between darker pigmentation and higher elevation. Darker pigmentation (melanization) with higher elevation and latitude is a common inter- and intraspecific difference for many species as an adaptation for cold tolerance (Ellers and Boggs 2004; MontBlanc et al. 2007; Parkash and Munjal 1999; Robinson 2001). The blurring in pigmentation between *A. rudis* and *A. picea* at mid elevations may indicate some phenotypic plasticity in melanization, but the species generally remained distinct across the environmental gradient. Moreover, shorter femur length with higher elevation may reflect a plastic response to the higher temperatures at lower elevations so that longer legs are a heat ameliorating advantage.

Both the genetic work of Crozier (1977) and the results presented here show no evidence of hybridizing between sympatric *A. rudis* and *A. picea* populations. As such, the movement of *A. rudis* colonies upward appears to be replacing *A. picea* colonies. Whether structured by competition or habitat selection, or some combination of both, high-elevation ant species appear replaced by low-elevation congeners.

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