RESEARCH ARTICLE

Ecological differentiation among key plant mutualists from a cryptic ant guild

R. J. Warren II · P. McAfee · V. Bahn

Abstract As key dispersers of herbaceous seeds, *Aphaenogaster* ants strongly influence the distribution of woodland plants in eastern North America. Ants within this genus are difficult to distinguish and often are identified by subgroup, but emerging research suggests they occupy species-specific ecological niches. As such, distinct climatic requirements among *Aphaenogaster* spp. might result in transient plant interactions with climate change. We examine whether there are ecological and distributional differences among *Aphaenogaster* species that coincide with current taxonomic differentiations. We use occurrence records for six *Aphaenogaster* spp. that occur in deciduous forests in eastern North America. We associate the geographic patterning of species occurrence with temperature and precipitation data, and we examine whether unique climatic niches characterize each species. We then predict habitat suitability throughout eastern North America using species distribution models. For verification, we test how well the predicted ranges fit observed occurrences using novel data sets for each species. We find that *Aphaenogaster* species within this cryptic genus demonstrate unique ecological and geographic signatures. Each species within the subgroup generally responds differently to temperature, and somewhat differently to precipitation and seasonal variance, suggesting unique ecological niches for each species. Our results indicate that each ant species may respond uniquely to changes in climate.

Such shifts could disrupt current community associations and biotic interactions with ant-dispersed plants.

Keywords *Aphaenogaster* · Climate change · Deciduous forest · Facilitation · Myrmecochory · Species distribution

Introduction

Ant-mediated seed dispersal (myrmecochory) occurs worldwide (Gorb and Gorb, 2003; Rico-Gray and Oliveira, 2007), and it is a major facilitative interaction in understory woodland communities in eastern North America (N.A.) with direct influence on a substantial part of plant diversity (Beattie and Hughes, 2002; Ness et al., 2009). Myrmecochorous plants benefit from ant-mediated dispersal through seed predator avoidance, decreased intraspecific competition and placement in nutrient-rich environments (see Gorb and Gorb, 2003; Giladi, 2006; Rico-Gray and Oliveira, 2007 and references therein), and the ants benefit by receiving nutrition for larvae from lipid-rich seed appendages (Carroll and Janzen, 1973; Marshall et al., 1979; Morales and Heithaus, 1998; Gammans et al., 2005). The benefits of this interaction are mutual, but the plants depend far more on the ants than vice versa, making the interaction facultative for ants and obligate for plants (Pudlo et al., 1980; Ness et al., 2009; Warren et al., 2010).

Myrmecochory long was considered a diffuse mutualism between a host of scavenging ants and spring-flowering plants (Berg, 1966; Handel, 1976; Beattie et al., 1979; Beattie and Hughes, 2002; Garrido et al., 2002), but researchers increasingly identify specific ant genera as dominant specialists in myrmecochorous interactions worldwide (Anderson, 1988; Espadaler and Gomez, 1996;

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Garrido et al., 2002; Gorb and Gorb, 2003; Rico-Gray and Oliveira, 2007). Indeed, the timing of propagule release may correspond with peak foraging in certain seed-dispersing ant genera and these genera appear far more effective as seed dispersers than other seed-gathering ants (Giladi, 2006; Boulay et al., 2007; Gove et al., 2007; Zelikova et al., 2008; Bas et al., 2009; Manzaneda and Rey, 2009; Ness et al., 2009). In eastern deciduous forests (USA), members of the ant genus *Aphaenogaster* dominate these mutualist interactions (Ness et al., 2009).

The *Aphaenogaster* genus is cosmopolitan (Bolton, 2010) with approximately a dozen species occurring in eastern N.A. (Creighton, 1950; Smith, 1979; Umphrey, 1996). *Aphaenogaster* spp. colonies typically are found below rocks and logs in mesic deciduous forests in the eastern USA (Talbot, 1934; Beattie, 1978; Lynch et al., 1980; Smallwood, 1982a). Given the high diversity of ant species worldwide, there are many challenges in species identification and taxonomic revisions are common. These considerations make genus-based ant classification a relatively useful way to approach ant research (Fisher and Cover, 2007; Ward, 2007; Bolton, 2010; Guénard et al., 2010). In addition, the taxonomic status of several *Aphaenogaster* species in the eastern USA remains unsettled, and members of this complex can be difficult to distinguish (Creighton, 1950; Umphrey, 1996). For these reasons, workers studying ant-mediated seed dispersal generally identify *Aphaenogaster* spp. to genus, particularly members of a species/sub-species known as the *fulva-rudis-texana* complex (hereafter 'rudis complex'), which also contains the majority of seed-dispersing species (see Ness et al., 2009 and references therein).

The *rudis* complex includes six identified species in eastern N.A. (Umphrey, 1996). For *Aphaenogaster* species, and ants in general, habitat partitioning appears to be driven by temperature (Brian, 1956; Bernstein, 1979; Lynch et al., 1980; Smallwood, 1982a; Cerdà et al., 1997; Retana and Cerda, 2000; Dunn et al., 2007; Sanders et al., 2007), but moisture also plays a role (Cerdà et al., 1997; Warren et al., 2010). Whereas spatial and temporal habitat partitioning is common among ant species (see Parr and Gibb, 2010), little is known about species partitioning within genera (e.g., Brian, 1956). Workers have demonstrated segregation between *Aphaenogaster* spp. and sympatric ant genera (e.g., Lynch et al., 1980; Fellers, 1987), but only limited, mostly anecdotal, information exists surrounding habitat segregation by species within the *rudis* complex (Talbot, 1934; Crozier, 1977; Mitchell et al., 2002). Previous taxonomic work on the *rudis* complex has differentiated species by morphology and genetics (Creighton, 1950; Crozier, 1977; Umphrey, 1996), but the species ranges are not well established and ecological differentiations are relatively unknown. As a result, most ecological research involving

the *rudis* complex, particularly seed-dispersal studies, makes no discrimination among members within this sub-group (also noted by Ness et al., 2009). However, Warren et al. (2011) demonstrated that differences exist in the foraging phenology of two members of the *rudis* complex, suggesting species-specific ecological roles in seed dispersal. *Aphaenogaster picea* began foraging early enough in the spring to overlap with seed set by all local myrmecochorous plants, whereas *A. rudis* began foraging too late in the spring to disperse early flowering species (Warren et al., 2011).

If individual *Aphaenogaster* spp. respond dissimilarly to rapid climate change, Warren et al. (2011)'s results indicate that the ant–plant mutualism may become disrupted. Myrmecochores comprise a large portion of understory plant diversity, and a potential disruption of the ant mutualism would entail great consequence for forest diversity. It is unfortunate, then, that little is known about how climate impacts the current distributions of individual *Aphaenogaster* spp. We explore the climatic niches of individual *Aphaenogaster* ant species to examine ecological and distributional differences among *Aphaenogaster* species within the *rudis* complex that coincide with their current taxonomic status. We associate the geographic patterning of species occurrence (from collection localities) with temperature and precipitation data, and we examine whether unique climate associations occur for each species. We then use these climatic niche models to predict habitat suitability throughout eastern N.A. using species distribution models (SDMs). For verification, we test how well the predicted ranges fit observed occurrences using novel occurrence data sets. In doing so, we generate probability distribution maps for each species and, more importantly, assess whether members of the *rudis* complex are ecologically equivalent or require greater effort for species-specific ecological investigations. These insights will help elucidate the interactions between the ants and the plants, the seeds of which they disperse, and how these relationships may vary under climate change.

Methods

Records of *Aphaenogaster* species and climate variables were obtained from published literature (Umphrey, 1996) and online databases to investigate the climatic niche and create species distribution models (SDMs) for each member of the *rudis* complex. Climate layers were obtained from the WorldClim Version 1.4 data set (www.worldclim.org). WorldClim provides gridded high-resolution monthly temperature and precipitation data and derivate variables that are thought to be biologically significant, such as means, seasonality and extremes (Hijmans et al., 2005). The climate

data are interpolated from weather stations worldwide and averaged for the years 1950–2000. We downloaded the data in a 2.5 arc-minute (4.65 km^2) generic grid format. We used this scale instead of a finer resolution to reflect the probable scale of error in digitizing Umphrey's (1996) data. Because the targeted study species are not known to occur outside of the eastern portions of the USA and Canada, a mask of eastern North America climate layers limited the spatial data to a target area from Florida to Nova Scotia, North Carolina to Arizona (e.g., Peterson et al., 2007; but see Phillips, 2008; and Van Der Wal et al., 2009). The data were converted to formats conducive for spatial analysis using ArcMap 9.3 (www.esri.com) and DIVI-GIS 7.2.1 9 (www.diva-gis.org).

Worldclim provides 19 climate layers derived from temperature and precipitation records. Because collinearity among climate variables undermines the reliability and interpretation of model output, we examined collinearity between the selected climate variables using a Pearson correlation matrix and a principal component analysis (PCA) using the "prncomp" method and "scale" option (standardizes all variables to unit length) in the "R" statistical package (R Development Core Team 2005). The PCA axes could be used for bioclimatic modeling, but we preferred to use a sensible selection of the original variables for ease of interpretation and prediction. Based on the correlation matrix and PCA, we selected a suite of basic climate variables that is a compromise between capturing most information contained in the 19 original variables, parsimony and ease of interpretation: BIO1—annual mean temperature (Tavg); BIO4—temperature seasonality (standard deviation × 100, Tvar); BIO5—maximum temperature of the warmest month (Tmax); BIO6—minimum temperature of the coolest month (Tmin); BIO12—annual precipitation (Tavg); BIO13—precipitation of the wettest month (Pmax); BIO14—precipitation of the driest month (Pmin); and BIO15—precipitation seasonality (coefficient of variation, Pvar) for bioclimatic analysis. The PCA analysis indicated that Tavg and Tmin were essentially identical (Fig. 1), so Tmin was omitted from the next step in the analysis.

As is often the case with species data (Phillips et al., 2004), we only had access to *Aphaenogaster* presence data, and the individual species sample sizes were small (Table 1). Therefore, we used the maximum entropy algorithm, Maxent 3.3.3a (Phillips et al., 2006), which has been demonstrated as a relatively robust approach for SDM from small presence-only data sets (Phillips et al., 2004; Elith et al., 2006; Hernandez et al., 2006; Phillips et al., 2006; Pearson et al., 2007; Wisz et al., 2008). Maxent is a general purpose method that estimates probability distributions from incomplete information by finding the probability distribution closest to maximum entropy (closest to uniform)
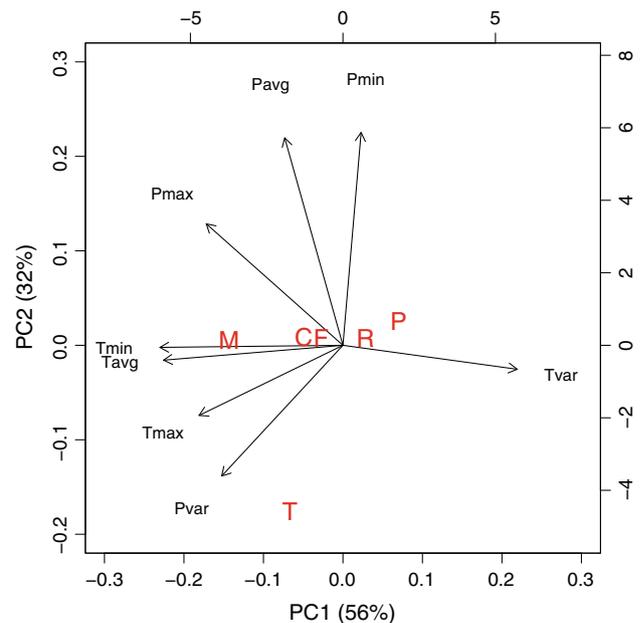
Fig. 1 Principal component analysis of ant species and climate variables. The biplot represents covariation among temperature (T) and precipitation (P) means (avg), extremes (max, min) and variation between seasons (var). Also shown is associated covariation between *Aphaenogaster miamiana* (M), *picea* (P), *rudis* (R), *fulva* (F), *carolinensis* (C) and *texana* (T). The *length of the lines* in the biplot indicates the degree of variation in a component (relatively *longer lines* indicate relatively higher variation). *Lines* that point in the *same direction* indicate a positive correlation between components; *opposite directions* indicate negative correlation and *perpendicular lines* indicate no relationship. Principal component analysis indicates that the first principal component (PC1), which corresponds with temperature, explains 56% of the variance and the second principal component (PC2) corresponds with precipitation and accounts for 32% of the variance

constrained only by associations between species presences and predictor variables (see Phillips et al., 2004; Phillips et al., 2006 for full explanations). The logistic output gives a spatially explicit suitability value ranging from 0 (unsuitable habitat) to 1 (optimal habitat) (Phillips and Dudik, 2008). We used the recommended default settings for Maxent to examine potential species distributions and associated climate drivers.

In the absence of independent validation data, the best method is to build models on one portion of the data ('training data') while withholding a portion of the same data for validation ('testing data') (Araujo et al., 2005; Phillips et al., 2006; Phillips and Dudik, 2008). A better approach, especially in cases where data are limited, is to train and test the models with independent data sets (Elith et al., 2006; Pearson et al., 2007). We derived training data from Umphrey (1996) for six *Aphaenogaster* species within the *rudis* complex: *A. carolinensis* Wheeler, *A. fulva* Roger, *A. miamiana* Wheeler, *A. picea* Wheeler, *A. rudis* Enzmann and *A. texana* Wheeler. Umphrey (1996) collected

Table 1 Summary data from *Aphaenogaster* species distribution models

Aphaenogaster	Train	Test	AUC (±SD)	Tavg	Tmax	Tvar	Pavg	Pmax	Pmin	Pvar
Carolinensis	23	12	0.921 ± 0.008	26.7	5.6	10.8	4.1	0.0	52.6	0.2
Fulva	37	25	0.855 ± 0.032	45.1	11.3	0.9	3.0	1.4	38.0	0.2
Miamiana	11	9	0.993 ± 0.002	35.2	0.0	7.8	0.5	56.4	0.0	0.0
Picea	25	19	0.904 ± 0.019	21.1	35.4	3.1	9.7	0.0	6.2	24.5
Rudis	31	7	0.905 ± 0.029	44.8	16.9	0.2	0.0	0.6	0.0	37.4
Texana	3	9	0.966 ± 0.007	0.1	63.0	0.0	2.5	0.0	23.3	11.1
				28.8	22.0	3.8	3.3	9.7	20.0	12.2

The number of presence records used for training (train) and testing (test) each species distribution model. Model performance was evaluated using the area under curve (AUC). The relative percent contribution for each climate variable is given for each species and mean contribution is given below each column. The climate variables were temperature (T) and precipitation (P) mean (avg) and variability between seasons (var)

Aphaenogaster spp. at >76 locations throughout the eastern N.A. to generate the most recent and comprehensive taxonomic revision of the *rudis* complex. We georeferenced the collection localities by associating spatial directions given in the manuscript with digitized maps to generate GPS coordinates. We then generated an independent testing data set by obtaining *Aphaenogaster* spp. data reported (along with GPS coordinates) via AntWeb (www.antweb.org), Antbase (www.antbase.org) and Discover Life (www.discoverlife.org). These databases contain records from individual researchers and research institutions identified by species and GPS coordinates for collection location. We evaluated the performance of the species distribution models using independent location data and the area under receiver operator characteristic (ROC) curves (AUC). The AUC gives the probability that a randomly chosen presence site is predicted to be a better fit by the model than a randomly chosen absence site (Phillips and Dudik, 2008). As such, a random fit would have an AUC = 0.5, and a perfect fit would result in AUC = 1.0. When using Maxent, which is based on presence-only data, background data ("pseudo-absence") are sampled at random locations from the study area. In our models, AUC represents the fit of the testing data to the model generated by the training data, which are independent data sets. The AUC can be inflated, however, by species with narrow distribution ranges relative to the study area (Phillips, 1996). The final models were used to create habitat suitability maps of the predicted geographic distributions.

Results

Principal component analysis

Principal component analysis on the full set of 19 bioclimatic variables indicated that seven principal components can account for 97% of the variability in the 19 variables. Whereas our selected variables are not fully orthogonal and

thus cannot account for exactly 97% of the variability in the full climate data set, we are confident that they represent the contained information very well and in a much more parsimonious and less intercorrelated way. Plotting the selected variables on a graph of the first two principal components using the seven selected variables shows that the variables are well selected in terms of maximizing the information (the first two PCA axes explain 88% of the climate variability) covered minimizing correlation (Fig. 1). The ant species, except *A. carolinensis* and *A. fulva,* sort apart distinctly along the PC1 axis, which explains 56% of the climate variability and mostly represents temperature and its temporal variance. Most of the species did not sort out as well along the PC2 axis, which explains 32% of the variability and mostly represents annual precipitation and its temporal variance, with only *A. texana* inhabiting unique precipitation space and *A. picea* somewhat different from the rest. The most similar species in abiotic associations were *A. carolinensis* and *A. fulva*, which were almost identical along both PCA axes. *Aphaenogaster texana* was the most distinct and was differentiated most from the others by precipitation.

Maxent algorithm

The AUC values for all species models except one were >0.900, with the exception being 0.855, making all models adequate for interpretation (Table 1). The probability of occurrence for the *rudis* complex species typically peaked around 54–77% across eastern North America (Fig. 2), and the highest probabilities (>90%) only occurred at the southern tip of Florida for *A. miamiana* (Fig. 2a) and at the highest elevations of the Appalachian Mountains for *A. picea* (Fig. 2b). *Aphaenogaster rudis* (Fig. 2c) and *A. picea* had similar ranges in northeastern N.A. from the Atlantic Coast to the Great Lakes, but *A. picea* was projected to occur at more northern extremes and at high elevations in the Appalachian Mountains, whereas *A. rudis* was projected most likely to occur in the lower elevations
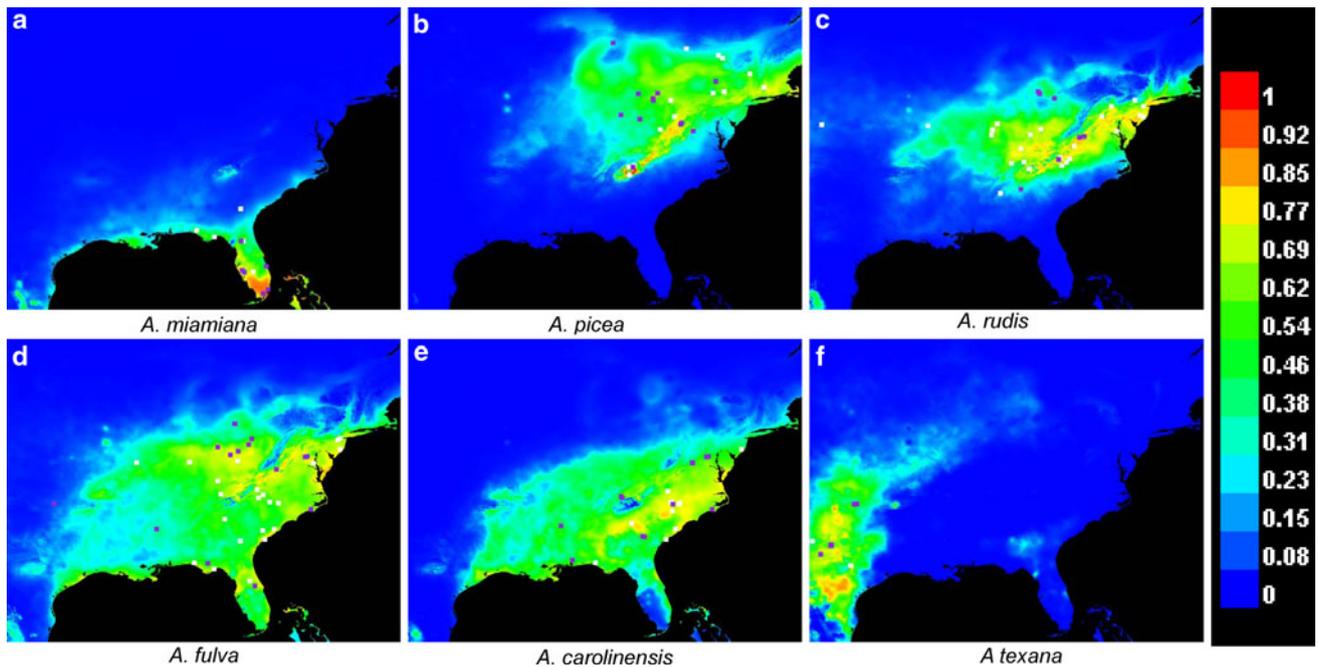
Fig. 2 Maxent projections of current suitable habitat for species in the *Aphaenogaster rudis* complex. The range probabilities are based on species occurrence data and the associated temperature and precipitation. *Dark squares* indicate species occurrences used to generate the model (training data) and *white squares* indicate locations used to test it (testing data). The *lighter shades* indicate higher probabilities for finding suitable habitat

surrounding the Appalachian Mountains. *Aphaenogaster fulva* (Fig. 2d) and *A. carolinensis* (Fig. 2e) were projected to occur throughout eastern N.A. from the Gulf Coast to Nova Scotia, east of the Mississippi River, though the *A. carolinensis* range did not extend as far northwest in the Great Lakes region or throughout southern Florida. *Aphaenogaster texana* was projected to only occur with substantial probability in the Texas–Oklahoma region, though this is truncated on the western edge by the projection range (Fig. 2f).

In all models, the temperature variables generally were the most important component of AUC (percent contribution), but some precipitation variables also weighed heavy as predictors of species distributions (Table 1). Mean temperature best predicted *A. fulva* and *A. rudis* distributions, although minimum precipitation was almost as important for *A. fulva* and precipitation variability between seasons was almost as important for *A. rudis*. Maximum temperature was the best predictor of *A. texana* distribution, by far, with minimum precipitation also considerable. Temperature variability between seasons and average precipitation contributed relatively little to any of the species models. None of the species distributions corresponded at all with maximum precipitation except *A. miamiana*, which was best predicted by maximum precipitation. Seasonal variation in precipitation also predicted *A. picea* and *A. rudis* distributions.

Discussion

We used PCA analysis to infer large-scale climate niche requirements for six *Aphaenogaster* ant species and SDMs to validate the climate associations and geographic distributions. At this coarse scale, the climatic variables were capable of accurately predicting the distribution of these species as verified by independent collection data. We use this framework to show that *Aphaenogaster* species within the cryptic *rudis* complex demonstrate unique ecological and geographic signatures as all six species generally respond to different features and limits of temperature and precipitation. *Aphaenogaster texana* and *miamiana* exhibit very distinct geographic ranges and have little overlap with the other species, whereas *A. fulva* and *A. carolinensis* appear to have considerable overlap in ecology and distribution (Figs 1, 2). *Aphaenogaster rudis* and *picea* overlap with *A. fulva* and *A. carolinensis* in the northeastern portion of N.A., but appear to have inverse distributions with *A. picea,* which has habitat requirements that appear more northerly and at higher elevations than *A. rudis*. Taxonomic distance does not appear equivalent to ecologic distance as Umphrey (1996) identified *A. fulva* as the most morphologically and genetically different from others in the *rudis* complex, yet it is almost identical in climate associations and projected range with *A. carolinensis*.

Whereas we only used seven distal (sensu Austin, 2002) variables, namely temperature, precipitation and their variability over time and space, to evaluate and predict *Aphaenogaster* spp. habitat suitability, we believe this approach was useful for two reasons: (1) a large body of literature on ant distributions and assemblies indicates that temperature and, secondarily, precipitation are the key environmental factors (Lynch et al., 1980; Smallwood, 1982a, b; Herbers, 1985; Fellers, 1987; Fenner, 1987; Hölldobler and Wilson, 1990; Mitchell et al., 2002; Sanders et al., 2007; Warren et al., 2010) and (2) employing only a few factors in niche-type investigations is most useful for hypothesis formation and testing and, if the factors are appropriate, simplifies the analysis and interpretation to the core limiting requirements (Chase and Leibold, 2003). The sample sizes are large enough to examine ecological and geographic differences across the target species (see Pearson et al., 2007; Wisz et al., 2008), but we feel they are not large enough to choose a climate projection and make predictions about potential *Aphaenogaster* spp. distributions under warming scenarios.

These models should be considered as projecting geographic regions with habitat similar to regions where the species occur rather than as delineating the actual range limits for each species (see Pearson et al., 2007). The collection and assembly of more data linking the distribution and ecology of these species with relevant habitat parameters would be useful to advance such projections. As such, there is high similarity between our projections and previous range estimates for members of the *rudis* complex (Creighton, 1950; Umphrey, 1996), though our projections place *A. carolinensis* further inland than previous reports and *A. texana* is projected, with very low probability, further eastward (Fig. 2). It is interesting to note that these two species once were considered the same species with a range that included both current distributions. An additional consideration is that, because *Aphaenogaster* is a cryptic genus, collection location could influence collectors in species identification. Whereas this bias would reduce the independence of the test data sets, it is likely most relevant to *A. carolinensis* and *A. texana*. We suggest searching Antweb (www.antweb.org), Antbase (www.antbase.org) and Discover Life (www.discoverlife.org) for further information on collecting sites and collectors responsible for species identification.

Crozier (1977) found shifts between sympatric *rudis* complex species—though these were not identified by accepted species names or those delineated by Umphrey (1996)—within 1 km along elevation gradients in the Appalachian Mountain foothills of north Georgia, USA. In such mountainous terrain, shifts in temperature and moisture equivalent to 100 km of latitude can occur across 1 km of elevation (Warren, 2008; Warren, 2010a; Warren, 2010b).

Microhabitat ecological differences among species in the *rudis* complex cannot be captured at the scale measured here, but the demonstrated associations with unique portions of broad-scale temperature and precipitation gradients also may occur at the microscale, particularly where the species distributions overlap. Such climate segregation likely influences their role and effectiveness as seed dispersers and, ultimately, as facilitators of woodland plants. At macroscales, our data suggest that each species (except possibly *A. fulva* and *A. carolinensis*) may respond uniquely to changes in climate. Seed set phenology differs among ant-dispersed plant species (e.g., Radford et al., 1968) and foraging phenology differs between at least two species in the *rudis* complex (Warren et al., 2011). Species-specific climate responses could result in the disruption of current community associations (Root et al., 2003; Williams and Jackson, 2007) and co-evolved mutualisms (Leathwick and Austin, 2001; Parmesan, 2007; Brook, 2009; Cavender-Bares, 2009). Warren et al. (2011) found that *A. picea* and *A. rudis* exhibited differing foraging phenologies, so that *A. rudis* activity did not overlap with early fruiting plant species. We demonstrate here that *A. picea* and *A. rudis* are not ecologically equivalent so that shifts in their distributions could result in asynchronous phenology with early blooming plant species if, for example, *A. rudis* replaces *A. picea*.

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