Environmental Heterogeneity and Interspecific Interactions Influence Nest Occupancy By Key Seed-Dispersing Ants

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ABSTRACT The complex interplay between species along environmental gradients ultimately shapes their distributions and additional community interactions. Ant-mediated seed dispersal fails in the wettest habitat of deciduous forest in eastern North America, and we examine whether this pattern corresponds with colony distributions for seed-dispersing ants and associated heterogeneity in abiotic and biotic variables. Specifically, we used spatial variation in soil moisture, temperature and diffuse light along natural habitat gradients and experimentally manipulated soil moisture gradients to examine ant habitat selection. We also examined niche segregation between effective (*Aphaenogaster* spp.) and ineffective (*Lasius alienus* Foerster) seed-dispersing ants across these environmental gradients. Whereas most research links ant foraging and nesting with temperature gradients, we find niche segregation between *Aphaenogaster* spp. and *L. alienus* by soil moisture along naturally occurring gradients and in experimentally irrigated upland habitat. The failure of *Aphaenogaster* spp. to occupy the wettest habitats, where *L. alienus* is present, is consistent with observed seed dispersal failure in these habitats. These results indicate that environmental heterogeneity drives niche segregation between effective (*Aphaenogaster* spp.) and ineffective (*L. alienus*) seed dispersers so each occupies distinct habitat. Most forest understory plants rely on ants for seed dispersal. Our research implies that climate-mediated interactions between effective and ineffective seed dispersing ant species may structure the microhabitat distributions for woodland herbs.

KEY WORDS *Aphaenogaster picea*, *Aphaenogaster rudis*, biotic interactions, community ecology, *Lasius alienus*

Species interactions influence the composition and structure of ecological communities (Connell 1975), and these dynamic relationships shift with habitat heterogeneity in space and time (Thompson 1994, Leathwick and Austin 2001, Warren et al. 2010, Wiescher et al. 2011). Understanding the biotic and abiotic mechanisms driving variation in species interactions is essential to assess species responses in current (Pulliam 2000) and changing environments (Agrawal et al. 2007). The interaction between woodland herbs and seed-dispersing ants structures understory plant communities in eastern North American deciduous forests (Ness et al. 2009, Warren et al. 2010, Sorrells and Warren 2011, Zelikova et al. 2011), but this mutualism inexplicably fails in the wettest habitat resulting in undispersed, aggregated plants (Warren et al. 2010). The underlying mechanism limiting seed dispersing ants in these habitats is unknown.

What makes the soil moisture pattern unexpected is that ant community diversity and species segregation (temporally and spatially) typically are associated with temperature, not moisture, gradients (Fellers

1987, Hölldobler and Wilson 1990, Retana and Cerda, 2000, Albrecht and Gotelli 2001, Dunn et al. 2007, Sanders et al. 2007) as the result of competitive interactions (Lynch et al. 1980, Fellers 1987) and niche segregation (see Parr and Gibb 2010). Ants commonly exhibit environmental trade-offs that generate seasonal and landscape segregation among co-occurring species (e.g., Wiescher et al. 2011), making it reasonable to suspect such abiotic partitioning may include soil moisture.

Ant-mediated seed dispersal (myrmecochory) is a prevalent mutualism occurring in diverse habitats worldwide (Gorb and Gorb 2003, Rico-Gray and Oliveira 2007), and in North America (N.A.) several ant *genera* disperse understory herb seeds (Beattie and Hughes 2002, Rico-Gray and Oliveira 2007). All seed dispersers are not created equal, however. One genus, *Aphaenogaster*, picks up >75% of myrmecochorous seeds, delivers them the greatest distance and generally keeps the seed intact (Giladi 2006, Ness et al. 2009, Warren et al. 2010), making *Aphaenogaster* spp. the most effective seed dispersers in N.A. Woodland *Aphaenogaster* species are associated with mesic forest habitat (Culver 1974, Lynch 1981, Gotelli and Ellison 2002, Ness et al. 2009, Warren and Bahn 2011) so that seed dispersal failure in wet microhabitats may not be caused by the ant absence, but by a habitat-

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specific interaction, such as competition with seed predators, that limits their foraging success. For this reason, it is important to determine what drives *Aphaenogaster* spp. microhabitat distributions to understand what drives seed dispersal dynamics.

We investigate *Aphaenogaster* spp. distributions in woodland habitat by placing artificial ant nests in the same plots used by Warren et al. (2010) for seed removal research. We used spatial variation in soil moisture along natural and experimentally manipulated gradients to examine ant colony site selection. We examine the abiotic drivers (soil moisture, temperature, and diffuse light) of nest site selection by *Aphaenogaster* spp. as well as potential biotic drivers. *Aphaenogaster* spp. and *Lasius alienus* (Foerster) ants share similar foraging and nesting preferences (Talbot 1934, Beattie 1978, Lynch et al. 1980), but *L. alienus*, nicknamed the 'moisture' and 'cornfield' ant for its association with high moisture environments and irrigated agricultural fields (e.g., Peck et al. 1998), may inhabit wetter conditions. If so, the observed spatial patterning in seed dispersal along soil moisture gradients may reflect niche partitioning between effective (*Aphaenogaster* spp.) and ineffective (*L. alienus*) seed-dispersing ants.

Materials and Methods

Study Sites and Design. In February 2010, we placed artificial ant nests at three sites, all dominated by the mature (60–80 yr), oak–maple–hickory stands characteristic of the deciduous forests of the region. At two of the sites, the work was observational. These sites (observational, OBS) were established by Warren et al. (2010) in 2008–2009 to examine seed dispersal by ants along environmental gradients perpendicular to streams. The first was located in the Middle Oconee River (OBS1) watershed within a natural area of the State Botanical Garden of Georgia, Clarke County, GA (33° 54′08″ N, 83° 22′58″ W, 190–210 m elevation) (Fig. 1). The second was in the Betty's Creek (OBS2) watershed in the Cowee Mountains of Jackson County, NC (35° 17′10″ N, 85° 17′27″ W, 777–790 m elevation) (Fig. 1). The two sites were selected for their macroscale divergence in precipitation and temperature as the southern Appalachian Mountain site (OBS2) is generally wetter and cooler than the Georgia piedmont site (OBS1). At each OBS site, we established five, 20-m transects at 100-m intervals perpendicular to a small stream. Along each transect, we placed a nest at each 5-m interval ($n = 5$ per transect, $n = 25$ per site) in contact with the soil and within the forest litter layer.

The third site was used for soil moisture manipulation (experimental site: EXP). It was established in relatively drier upland habitat (35° 16′18″ N, 83° 17′52″ W) *ca.* 400 m from OBS2. We used drip irrigation to increase the soil moisture in treatment plots in the EXP grids to mimic the soil moisture gradient found in the OBS sites. At the experimental site, we established two 4 × 6 m grids (giving 24 1-m² cells per grid). Untreated water was delivered via drip irrigation
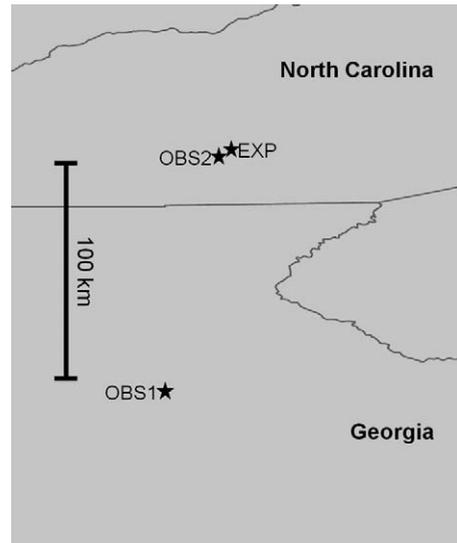

Fig. 1. Map of study sites. The OBS1 and OBS2 sites were perpendicular to forested stream corridors. The EXP site was located in upland forest habitat.

(Dripworks, Inc., Willits, CA) to half ($n = 12$) of the cells in each grid weekly (for 2 h) across March to July 2010. Drip irrigation has a limited moisture shadow (<10 cm) and does not impact nontarget cells (see Warren 2010). Ant nests were placed randomly in a stratified design so they were equally assigned to irrigated ($n = 6$) and nonirrigated cells ($n = 6$) in each grid (giving 12 per grid).

Overall, we placed 50 ant nests at the OBS sites and 24 in the EXP site ($n = 74$ total). The rectangular artificial ant nests (15 × 12 × 2 cm) were constructed with untreated white pine and capped with 1.5 mm Plexiglas. Nest chambers were created by routing 1.5 cm deep grooves into the wood with a 10 × 4 mm chamber entrance. The nests were placed Plexiglas side up for observation, but covered with ceramic tiles (16 × 16 cm) to block sunlight and secure the nests in the leaf litter. The nests were constructed with openings and cavities larger than the minimum required for occupation by *Aphaenogaster* spp. This permitted use by other aboveground nesting species that use rocks, leaves and coarse woody debris for nest sites (Talbot 1934, Beattie 1978, Lynch et al. 1980, Smallwood 1982a).

Study Species. *Aphaenogaster rudis* (Enzmann), found at the Georgia sites, and *A. picea* (Wheeler), found at the North Carolina sites, are widespread and abundant ants in N.A. (Umphrey 1996, Warren and Bahn 2011). They also are the predominant species (77% of ants identified) removing seeds in the study sites (Warren et al. 2010). These *Aphaenogaster* spp. are behaviorally subordinate, individually foraging ants (Lynch et al. 1980, Fellers 1987). They specialize in fast discovery of food resources and are quantitatively and qualitatively the most efficient seed-dispersing ants in deciduous forests in the eastern United

States (Ness et al. 2009). Another species, *L. alienus* (Foerster), did not remove seeds (Warren et al. 2010), but occupied the artificial nests as did *Aphaenogaster* spp. *L. alienus* is a relatively behaviorally dominant species (Fellers 1987). Notably, both *Aphaenogaster* spp. and *L. alienus* establish shallow, transient nests beneath rocks and logs (Talbot 1934, Beattie 1978, Lynch et al. 1980) and scavenge for similar food resources (Fellers 1987), though *Lasius* spp. are only occasionally and inconsistently interested in myrmecochorous seeds (Ness et al. 2009, Warren et al. 2010, Warren et al. 2011).

Measurements. We focused our analysis on the spring season as it coincides with peak myrmecochore seed release, ant foraging and ant colony brood development (Smallwood 1982b, Ruhren and Dudash 1996, Warren et al. 2011). We placed the artificial ant nests at all sites in February 2010, before the fruiting of spring ephemeral myrmecochores, and checked for occupation in June by lifting the ceramic tile cover and peering through the Plexiglas top without upsetting the actual nest box. We considered a nest occupied if it contained >10 ants along with larvae.

We used mean weekly abiotic measurements ($n = 4$) in June 2010 to assess relative soil moisture, temperature, and diffuse light at the sites. Volumetric soil moisture percentage was measured with a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT); we used the average of five points within 1 m^2 of each nest in our data analysis. Ambient soil temperature was measured next to each nest with a T-shaped digital thermometer inserted 8 cm into the soil; we used the average of five points per nest for data analysis. Percent photosynthetically active radiation (diffuse light) was calculated as the difference between nest-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). Measurements were taken during early morning (8–9 a.m.) to minimize relative error in diffuse light.

Data Analysis. The presence of *Aphaenogaster* spp. and *L. alienus* ant colonies in artificial nests at the OBS sites was analyzed with a logistic regression using generalized linear mixed models (GLMMs) assuming binomial error distributions using the Laplace approximation in the 'lme4' package for the 'R' statistical program (R Development Core Team 2009). Generalized liner mixed models allow robust analysis of observational and experimental ecological data that often violate classical statistical assumptions of normality and independent variance among units (Bolker et al. 2009). Soil moisture, diffuse light, and temperature, along with interaction terms, were included in the OBS models as fixed effects, and second-order terms were included to account for unimodal responses. Subsequent inclusion or exclusion of the fixed effects, their interactions and second-order terms was based on Akaike's Information Criterion (AIC) values

Table 1.   Mean (±SD) soil moisture (Moist), temp (Temp), and diffuse light (Light) for the study locations, June 2010

Site	Moist	Temp	Light
Middle Oconee	21.3 ± 5.5%	19.2 ± 0.2°	3.6 ± 1.9%
Betty's Creek	22.0 ± 5.6%	17.6 ± 0.5°	3.0 ± 1.6%
Experimental (ambient)	18.8 ± 7.0%	17.0 ± 1.9°	3.2 ± 4.0%
Experimental (irrigated)	24.5 ± 8.4%	17.0 ± 1.9°	3.2 ± 4.0%

Middle Oconee is located in the north Piedmont region of Georgia; Betty's Creek and the experimental site are located in the southern Appalachian Mountain region of North Carolina.

(Akaike 1973). AIC rewards models for goodness-of-fit, but penalizes them for the number of parameters (Burnham and Anderson 2002). Because of the clustering of nests in transects (OBS) and grids (EXP), these 'blocks' were included as random effects. No collinearity was detected across soil moisture, temperature and diffuse light (variance inflation factors for all models <1.5), and the overdispersion parameter in the OBS models was ≤1.2.

The presence of *A. picea* and *L. alienus* ant colonies in the artificial nests in the experimental grids was analyzed with a logistic regression using GLMMs assuming binomial error distributions. The combination of the irrigation treatment, and natural heterogeneity in background soil moisture, generated in the EXP site a soil moisture gradient comparable to that in the OBS sites. This experimental gradient was used to evaluate the relationships between soil moisture and occupation in that site. The overdispersion parameter in the experimental models was ≤2. In all models, we considered coefficients with P value <0.05 significant and coefficients with P value <0.10 marginally significant (sensu; Hurlbert and Lombardi 2009).

Results

Site Conditions. Mean soil moisture was similar (21–22%) between the observational sites (OBS1 and OBS2), but 3–4% lower at the EXP site (Table 1). Irrigation raised soil moisture in EXP treatment plots by *ca.* 6% so they resembled the soil moisture at the observational sites. Mean temperature at the mountain sites (OBS2 and EXP) was *ca.* 2°C cooler than the piedmont site (OBS1). Mean diffuse light was similar across all sites. *Aphaenogaster* spp. nest occupation was highest (*ca.* 41%) in the nests located at OBS1 and in the ambient EXP plots, whereas *L. alienus* occupation was highest (25%) in the irrigated EXP plots.

Nest Occupation. Using the AIC-based model selection procedure for the observational data (OBS sites), we found that temperature and soil moisture best corresponded with *Aphaenogaster* spp. nest occupancy without any interaction or second-order terms. *Aphaenogaster* spp. nest occupation decreased significantly with higher soil moisture (coeff. = −0.197; SE = 0.082; $z = -2.396$; $P = 0.017$) but the increase associated with temperature was not significant (coeff. = 0.611; SE = 0.409; $z = 1.494$; $P = 0.135$). Soil moisture, temperature, and diffuse light predicted nest occupancy by *L. alienus* best without interaction or second-order
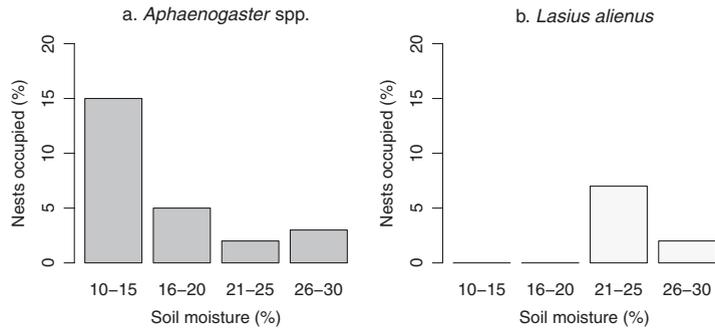
a. *Aphaenogaster* spp.

b. *Lasius alienus*

Fig. 2. Barplots for artificial nest occupation (%) by *Aphaenogaster* spp. (*A. picea* and *A. rudis*) and *L. alienus* binned into four classes of soil moisture availability generated by natural and experimental soil moisture gradients. The classes volumetric soil moisture in mesic forest, ranging from drier (10–15%) to wetter (26–30%) microhabitat conditions. Shown is the percentage of total nests occupied in each soil moisture class, where the total number of nests per class was 30 (10–15%), 16 (16–20%), 13 (21–25%), and 14 (26–30%). Nest occupation by *Aphaenogaster* spp. was negatively correlated, and by *L. alienus* positively correlated, with soil moisture (see text).

terms. *L. alienus* nest occupation increased with increasing soil moisture (marginal significance: coeff. = 0.200; SE = 0.110; z = 1.817; P = 0.069), but the increases associated with temperature (coeff. = 0.749; SE = 0.735; z = 1.019; P = 0.308) and diffuse light (coeff. = 0.142; SE = 0.128; z = 1.106; P = 0.269) were not significant.

Artificial nest occupation at the experimentally irrigated site (EXP) confirmed the observed soil moisture-mediated segregation between ant species in nest occupation. In the experimental grid, *Aphaenogaster* spp. nest occupancy decreased marginally significantly with increasing soil moisture (coeff. = −0.131; SE = 0.073; z = −1.795; P = 0.073) whereas *L. alienus* occupation increased marginally significantly with higher moisture (coeff. = 0.203; SE = 0.114; z = 1.784; P = 0.075).

At the OBS sites, *Aphaenogaster* spp. occupied the artificial nests where mean soil moisture (±SD) was 15.0 ± 4.1%, whereas *L. alienus* occupied artificial nests where mean soil moisture was 23.7 ± 2.0%. These relationships with soil moisture were similar to those at the EXP site as occupation at the EXP site occurred at mean soil moisture values of 16.8 ± 7.6% for *A. picea* and 24.4 ± 2.2% for *L. alienus.* When the OBS and EXP data were pooled, *Aphaenogaster* spp. nest occupation remained negatively and significantly correlated with soil moisture (coeff. = −0.114; SE = 0.045; z = −2.514; P = 0.012) and *L. alienus* remained positively and significantly correlated with soil moisture (coeff. = 0.160; SE = 0.061; z = 2.613; P = 0.009) so that *Aphaenogaster* spp. mostly occupied nests at the drier end of the gradient (Fig. 2a) and *L. alienus* only occupied nests at the wetter end (Fig. 2b).

Discussion

Ant community assemblages vary with spatial and temporal heterogeneity in the environment (Lynch et al. 1980, Smallwood 1982a, Fellers 1987, Hölldobler and Wilson, 1990, Cerdà et al. 1997, Sanders et al. 2007). The major influence on the structure of these

assemblages, at macro- and microscales, appears to be temperature (Lynch et al. 1980; Sanders et al. 2007; Smallwood 1982a,b; Smallwood and Culver, 1979). However, Warren et al. (2010) found ant seed dispersal services corresponding with soil moisture. We investigate whether this microhabitat variation in dispersal services is linked with ant community structure (e.g., *Aphaenogaster* distributions). We find moisture a primary driver of microhabitat occupation, both in observational and experimental grids (Fig. 2). The ant distribution patterning does not appear solely the product of habitat selection by the key N.A. seed disperser, *Aphaenogaster,* but more likely niche segregation with an ineffective seed disperser, *L. alienus.*

Both *Aphaenogaster* spp. and *L. alienus* occur in mesic N.A. woodlands (Talbot 1934, Herbers 1985). Because *Aphaenogaster* spp. and *L. alienus* relocate nests every 20–30 d (Smallwood and Culver 1979; Smallwood 1982a,b; Herbers 1985, 1989), nest location is indicative of current environmental preferences. We find that *Aphaenogaster* spp. generally occupy sites where mean soil moisture is 1.6 times lower than where *L. alienus* nests. However, *Aphaenogaster* spp. can and do occupy nests in the same soil moisture range as *L. alienus,* just far less frequently, whereas *L. alienus* ants never occupy a nest where soil moisture <20% (Fig. 2). Previous to our findings, there was little evidence (see Lynch et al. 1980) for microsite differentiation in nest location across soil moisture gradients, though some effects attributed to temperature may covary with moisture (see Sanders et al. 2007). Although our results suggest niche segregation (i.e., resource partitioning), which is common in ant species, it is difficult to discern whether these patterns arise from current or past competition (Connell 1980), or whether discrete abiotic tolerances explain the patterns (Parr and Gibb 2010). Competitive interactions between ant species include avoidance by subordinate species and aggressive biting and formic acid attacks by dominant species (Lynch et al. 1980, Fellers 1987). These encounters usually occur when ants forage (Lynch et al. 1980, Fellers 1987), but territorialism by

dominant species also reduces the persistence and location of subordinate species' nests (Carroll and Janzen 1973, Levings and Traniello 1981, Herbers 1989). There is no indication that *Aphaenogaster* spp. form and protect territories; however, *Lasius* spp. are noted as possibly territorial (see Levings and Traniello 1981 and references therein). Because both *Aphaenogaster* and *Lasius* spp. exhibit highly mobile colonies and appear flexible in nest substrate (Talbot, 1934, Beattie 1978, Lynch et al. 1980), it is unlikely that forest floor nest sites are limiting.

Whereas several ant species collect myrmecochore seeds in eastern N.A., ants in the genera *Aphaenogaster* are the key dispersers of myrmecochorous plants across eastern N.A. This is because of their widespread distribution and high abundance in eastern N.A. deciduous forests (Culver 1974, Lynch 1981, Gotelli and Ellison 2002, Warren and Bahn 2011), and their strong tendency to collect and disperse myrmecochorous seeds (Giladi 2006, Ness et al. 2009, Warren et al. 2010). Combined, these traits render this group the keystone seed-dispersing mutualist (Ness et al. 2009). Based on its even nest distribution, colony density ($\approx$1 colony m^{-2}), colony size ($\approx$600 workers colony^{-1}), and foraging distance ($\approx$60–120 cm), *Aphaenogaster* spp. cover >100% of the forest floor (Giladi 2004, Ness 2004, Ness et al. 2009, Lubertazzi 2012). Therefore, elucidating the factors that control the distribution of *Aphaenogaster* spp. is paramount for understanding the ecology of a large guild of understory plants.

Our findings suggest that the most effective seed dispersers, *Aphaenogaster* spp., occupy relatively drier microhabitats; whereas a much less effective seed disperser, *L. alienus*, (Beattie 1978, Ness and Morin 2008, Ness et al. 2009), occupies the wetter areas (Fig. 2). Although myrmecochorous plants can use the entire moisture gradient that we studied (see Warren 2010, Warren et al. 2010), the segregation of *Aphaenogaster* spp. and *L. alienus* nest occupation coincides with reduced seed removal and consequently clumped plant distribution in the wetter microhabitats (Warren et al. 2010). This clumping may decrease plant fitness (Gorb and Gorb 2003, Handel and Beattie 1990, Giladi 2006, Ness and Morin 2008) and highlights that *Aphaenogaster* spp. and *L. alienus* are not interchangeable as plant mutualists. Indeed, the microhabitat distributions that we report for *Aphaenogaster* spp. and *L. alienus* directly relate to myrmecochore distributions and fitness (Smallwood 1982a, Ness et al. 2009, Warren et al. 2010). These myrmecochores include many early flowering, spring ephemerals that comprise an important component of woodland diversity (Beattie and Hughes 2002, Ness et al. 2009).

Acknowledgments

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