

Cryptic indirect effects of exurban edges on a woodland community

R. J. WARREN II,^{1,†} S. M. PEARSON,² S. HENRY,³ K. ROSSOUW,² J. P. LOVE,⁴ M. J. OLEJNICZAK,¹ K. J. ELLIOTT,⁵
AND M. A. BRADFORD⁶

¹SUNY Buffalo State, 1300 Elmwood Avenue, Buffalo, New York 14222 USA

²Department of Natural Sciences, Mars Hill University, Mars Hill, North Carolina 28754 USA

³Department of Environmental Studies, University of North Carolina at Asheville, Asheville, North Carolina 28804 USA

⁴Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602 USA

⁵USDA Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, Otto, North Carolina 28763 USA

⁶School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511 USA

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Abstract. Exurban development (e.g., second homes) in woodlands spreads urban land use impacts beyond suburbs, but because exurban developments often retain many components of original ecosystem structure—such as a forest canopy rather than open lawn—their ecological impacts may be underestimated. Changes in seed-dispersing ant behavior prompted by exurban land use, such as edge avoidance, may pose deleterious impacts on the woodland plants (myrmecochores) they disperse, and hence the floristic diversity of exurban forests. We examined the effects of exurbanization on seed-dispersing ant nesting and foraging, seed retrieval, dispersal direction and subsequent impact on myrmecochores. We used a matrix of forested and exurbanized habitats to test whether (1) exurban edges decrease ant nest colonization and seed foraging, (2) ants disperse seeds away from exurban edges, and (3) consequently, there is lower ant-dispersed plant abundance nearer exurban edges. We found that exurban development poses little impact on keystone seed-dispersing ants because they foraged, colonized and thrived in fragmented woodland habitats as well as they did in intact forests. Exurban edges changed ant behavior, however, so that they generally moved seeds toward forest interiors, and, hence, away from edges. Corresponding to this behavioral change, we found that ant-dispersed plants declined with proximity to edges, whereas other woodland herbs with dispersal modes other than ants were unaffected. Exurbanization poses little threat to seed-dispersing ant viability, but, by changing foraging patterns (specifically, limiting the directionality of dispersal), it indirectly threatens the plants they disperse. Edge effects on biota commonly are associated with cascades through abiotic resources, but we show a deleterious biotic cascade between exurban edge, keystone ants and herbaceous plants. Species-mediated services, such as seed dispersal and pollination, are key resources, and assessing the full consequences of land use change therefore necessitates evaluation of impacts on biotic interactions.

Key words: *Aphaenogaster*; biotic interactions; dispersal; edge effects; fragmentation; land use; mutualism; myrmecochory; niche.

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† **E-mail:** hexastylis@gmail.com

INTRODUCTION

Anthropogenic land use alters ecosystem structure, which changes ecological community composition and species diversity (Mitchell et al. 2002, Foley et al. 2005, Flynn et al. 2009). Land-use alteration imposes obvious direct effects by changing the availability of abiotic resources, such as light and soil moisture, which, in turn, cause shifts in ecological communities (e.g., Whigham 2004). Land-use alteration also may impose indirect effects on ecological communities by altering biotic interactions, such as pollination and dispersal (Weiner et al. 2014). These ‘biotic resource’ interactions may be as important for species persistence as abiotic resources (Bronstein 1989, Pauw 2013, Warren II et al. 2014), but their disruption by land use-change is much more cryptic than immediate and direct extirpation.

Exurbanization is the fastest growing and most extensive form of anthropogenic development in North American (N.A.) natural areas (Theobald 2005, Clark et al. 2009, Kirk et al. 2012). Exurban development is characterized by low-density housing developments in rural areas for long-distance commuting or second homes (Kirk et al. 2012, Glennon and Kretser 2013). Exurbanization extends urban impacts beyond suburbs, but, because exurban developments often retain their original ecosystem structure—such as a forest canopy rather than open lawn—their ecological impacts may be underestimated (Maestas et al. 2001, Glennon and Kretser 2013). Still, such development may fragment natural habitat enough to undermine ecological integrity (Maestas et al. 2001, Heilman et al. 2002, Irwin and Bockstael 2007, Glennon and Kretser 2013).

Aphaenogaster ants are exceedingly abundant in N.A. woodlands (King et al. 2013), and they are the most effective herbaceous seed dispersers in these habitats (Ness et al. 2009). Where *Aphaenogaster* dispersal fails, ant-dispersed plants (myrmecochores) become moribund (Warren II et al. 2010, Zelikova et al. 2011, Warren II and Bradford 2013). Unlike the plants they disperse (mean dispersal 1–2 m, Gomez and Espadaler 2013), ants can migrate 50–100 m year⁻¹ through aerial mating flights (Hölldobler and Wilson 1990) and *Aphaenogaster* re-colonize forest habitats relatively rapidly (within 15 years after

disturbance; Wike et al. 2010). In contrast, anthropogenic forest disturbance generally causes long-term reductions in woodland herbaceous abundance and diversity (Matlack 1994a, Mitchell et al. 2002, Harrelson and Matlack 2006)—particularly for poor colonizers (Matlack 1994a, Singleton et al. 2001, Bellemare et al. 2002) such as myrmecochores, which are limited in younger forests (Cain et al. 1998, Gomez and Espadaler 1998, Mitchell et al. 2002, Oberrath and Boehning-Gease 2002).

Exurban development in forested landscapes results in forest edges that fall somewhere between “hard” (e.g., utility line cuts, roads) and “soft” (e.g., forests of different ages; see Ness 2004). Ant-dispersed plants are uncommon along hard forest edges (Matlack 1994b, Jules 2000, Ness and Morin 2008) and appear relatively dispersal limited across soft forest edges (Brunet and von Oheimb 1998, McLachlan and Bazely 2001). Given that seed-dispersing *Aphaenogaster* ants appear to forage less along forest edges, and may predominantly move seeds away from them (Ness 2004, Ness and Morin 2008), the dearth of myrmecochores may reflect a change in their interaction with ants from forest interior to edge. We tested whether: (1) exurban edges affect *Aphaenogaster* spp. nest colonization and seed foraging and retrieval; (2) *Aphaenogaster* spp. disperse seed proxies away from exurban edges; and if so, (3) there is decreased ant-dispersed plant (myrmecochores) abundance nearer exurban edges than interior forests.

METHODS

Study sites

The Southern Blue Ridge Province of the Southern Appalachian Mountains, in the southeastern U.S., contains large expanses of protected public lands, but the region faces increased urbanization and exurbanization (Gragson and Bolstad 2006, Kirk et al. 2012). We established six sites each in two regional locations (in Macon and Madison Counties, North Carolina) in 2012. All of the sites in both study locations were within forested habitat: half of the sites were in continuous forest (relatively intact) and half were exurban forest (fragmented with housing development). The exurban sites differ from suburban developments in that they contained a matrix of

disturbed (roads, lawns, houses) and relatively undisturbed forest habitat. We used forested plots within each of the twelve sites to analyze ant and plant abundance (hereafter, “habitat plots”). We used a second group of transects at the same sites that bisected exurban-intact forest edges, but did not overlap with the habitat plots, to analyze edge effects on seed dispersal direction (hereafter, “edge plots”). We used bait stations located along the edge transect so that half fell within intact forest patches and half fell outside the patches in exurban habitat (which had canopy cover but not forest floor).

Habitat plots

We established 12 habitat plots in forest patches at each site ($n = 72$ habitat plots per location, 36 forested, 36 exurban; 144 habitat plots total across both locations). The two locations were approx. 100 km apart, sites approx. 2–20 km apart and habitat plots 0.2–1 km apart. Within each of the 144 10×10 m habitat plots, we identified and estimated the percent cover of herbaceous plants with three 1×1 m subplots spaced 2 m apart and arranged perpendicular to the slope. Surveys were conducted in early summer to identify spring ephemerals. Nomenclature follows Weakley (2011).

Ants in the *Aphaenogaster rudis* complex (hereafter, *A. rudis*) dominate understory habitats in eastern N.A. (Lubertazzi 2012, King et al. 2013), and these ants are the keystone seed dispersers (they disperse 75% of myrmecochore seeds; Ness et al. 2009, Warren II et al. 2010). For these reasons, we only targeted *A. rudis* in assessing ant-plant seed dynamics. *Aphaenogaster rudis* ants generally forage approx. 60–120 cm from their nests (usually located under rocks or in coarse woody material), but nest locations also are largely transient (Talbot 1951, Pudlo et al. 1980, Giladi 2004, Ness et al. 2009, Lubertazzi 2012). Given that *A. rudis* colonies move among multiple nests, we assessed *A. rudis* colony abundance by placing an artificial ant nest in every habitat plot ($n = 144$ nests), 4 m from the herb subplots, in June 2012. Each nest consisted of $12 \times 14 \times 1.7$ cm wooden pine board with a $25 \times 2 \times 1$ cm “G”-shaped chamber routed out and opening to the outside. The chamber was topped with Plexiglas and a ceramic tile, following

established protocols (Warren II and Bradford 2012, Bradford et al. 2014). In September 2013, the nests were retrieved and ant colonies freeze-killed. Nest midden material was removed, dried and sorted by insect, seed and unidentified material. Ants were identified and counted, and colony health assessed by total fat storage. Fat storage indicates the nutritional status of the colony (Tschinkel 1999) and was measured by colony dry biomass before and after lipid removal using Soxhlet extraction (Smith and Tschinkel 2009).

We assessed *Aphaenogaster* foraging via artificial bait stations placed in each habitat plot ($n = 144$ stations, one per plot) within 1 m of the artificial nests. The bait stations were 5×5 cm weighing trays held in place by a metal nail. The stations were baited with small amounts of tuna, which contains a chemical signature similar to dead insects and seed elaiosomes and is a common attractant used to study seed-dispersing ants (Mitchell et al. 2002, Ness and Morin 2008). Tuna bait can overestimate the diversity of effective seed dispersers, and it can cause ants to recruit in greater numbers than usual (Sanders and Gordon 2000, Ness et al. 2009, Warren II and Giladi 2014). We used tuna, however, because we targeted a single species (*A. rudis*) as the keystone seed disperser and measured its relative abundance as a function of exurbanization rather than ant community diversity.

Soil temperature and moisture were measured at each bait station during ant monitoring. Soil temperature was measured using a temperature probe (5 cm depth); soil moisture was measured using a Hydrosense soil moisture sensor with 20-cm stainless steel rods (Campbell Scientific, Logan, UT, USA) at three points near the stations and values were averaged. Such spot measures effectively resolve spatial variation in soil temperature and moisture at the spatial scale of our study (Warren II and Bradford 2011).

All coarse woody material (CWM) ≥ 1 m in length and ≥ 10 cm in diameter was measured in each habitat plot, given its importance as nest habitat for *Aphaenogaster* (King et al. 2013). Only CWM that was downed and/or suspended within 2 m of the forest floor was measured; snags were not included in the survey. The length of CWM was measured to the nearest centimeter with a measuring tape until the CWM tapered to

<10 cm diameter. The diameter of both ends was measured using calipers to the nearest 0.1 cm to determine volume; if the CWM was ≥ 3 m in length, a third diameter was taken in the middle of the CWM.

Distance to forest edge (m) was measured using 2012 aerial photographs (NAIP 2013) and a geographic information system. Non-forest habitats created by agricultural land uses, houses, and paved roads were used to designate hard edges. Two-track, unpaved forest roads (e.g., for logging) and trails were considered soft forest edges and not measured because they do not impede ant movement. We note that these edge data were used to evaluate habitat suitability for ants and plants, and the effect of edge on seed dispersal distance and direction were measured in the “Edge Plots.”

Edge plots

We advanced investigation into ant edge dispersal from previous work by investigating dispersal distance and direction across edge boundaries. Edge experiments were conducted at the six exurbanized (as opposed to intact forest) sites. The edge plots were separate but adjacent to the habitat plots. Bait stations were placed along transects perpendicular to the forest edges so the bait stations were -10, -7, -4, -1, 0, 1, 4, 7 and 10 m from the forest edge (i.e., -10 was 10 m within the forest patch; 10 was 10 m outside the forest patch). Bait stations -10 to -4 m from the edge were ‘interior’ points for *Aphaenogaster*, given their limited foraging distance. Bait stations at -1 to 1 m were considered ‘edge’ and 4 to 10 m were considered ‘exterior’.

We again used tuna bait as *Aphaenogaster* spp. are incapable of trophallaxis (transporting liquid food; Lorinczi 2014) so they must immediately transport food back to their colony. Hence, the type of food should in no way affect dispersal direction as they immediately transport any food directly to their nest. All edge plot stations were baited and ants inventoried after 50 min, three times in June and July 2012. To make it easier to track after being retrieved by *Aphaenogaster* ants, tuna bait was marked with fluorescent dye, which has no impact on food desirability for ants (e.g., Zelikova et al. 2008). Ants were tracked to their natural nests after retrieving tuna, and distance and angle from edge to nest were recorded using

polar coordinates. This approach is independent of true compass points and is used only so that directionality can be analyzed using a full 360° window (Warren II and Bradford 2013). For our analysis, “northerly” directions represented dispersal toward the forest exterior and “southerly” directions represented dispersal toward the forest interior.

Data analysis

Generalized linear mixed models (GLMM) were used to evaluate *Aphaenogaster* artificial nest use (binomial error distribution) and colony size (Poisson error distribution). The Laplace approximation in the lme4 package (Bates and Maechler 2009) in the R statistical program (R Core Team 2015) was used to evaluate the GLMM models. Overdispersion (ϕ) was < 2 in the ant presence model, but $\phi > 20$ in the colony size model. An individual-level random effect was included in the colony size GLMM to account for the overdispersion. A linear mixed model (LMM) was used to evaluate *Aphaenogaster* lipid content (Gaussian error distribution) in colonies with > 100 individuals ($n = 52/66$ colonies). We included ant abundance, soil moisture (%), soil temperature (°C), CWM (m³), distance to edge (m), total herbaceous cover (%) and myrmecochore cover (%) as fixed effects in the mixed models. We used the car package (Fox and Weisberg 2011) in R to test for collinearity among fixed effects and found none (variance inflation < 2). The inclusion or exclusion of fixed effects was based on Akaike’s information criterion (AIC) values calculated using maximum likelihood with the best-fitting parameters ($\Delta\text{AIC} < 2$) retained. We evaluated the slope value of retained fixed effects and considered coefficients with p -value < 0.05 significant and coefficients with p -value < 0.10 marginally significant (sensu Hurlbert and Lombardi 2009).

Mixed models also were used to evaluate ant nest midden contents as a function of the distance to forest edges: arthropod mass (Gaussian error distribution), seed abundance (Poisson error distribution) and oak gall abundance (Poisson error distribution) with site as a random effect. We also examined lipid content as a function of midden contents (arthropod, seed, gall and unidentified midden material weights) using an LMM with site as a random effect. In the

GLMMs, ϕ was <1.5 , and variance inflation was <2 in all models. Seed size can be a proxy for elaiosome size, but the ratio varies greatly between and within species, and geographically (Rico-Gray and Oliveira 2007). Most of the seeds collected here were <2 mm with miniscule elaiosomes (e.g., *Viola* spp.), and we generally found elaiosomes uneaten on the larger seeds (e.g., *Sanguinaria canadensis*). Moreover, as there is no literature about oak gall dispersal by ants, the ratio of gall size to food benefit, if any, is unknown. For these reasons, we also investigated ant lipid content as a function of the presence or absence of seeds and oak galls in artificial nests using *t*-tests. Given that seed elaiosomes may provide food when better sources are unavailable (Carroll and Janzen 1973), we also observed the relationship between arthropod parts and seeds, expecting a negative relationship if seeds act as a surrogate food.

For ant foraging activity at bait stations, the software PRESENCE (version 6.1, <http://www.mbr-pwrc.usgs.gov/software/presence.shtml>) was used to model the occupancy of plots assessed during multiple sampling dates. This modeling framework estimates the probability that ants are present in the area around the bait station (i.e., “occupancy”) as a function of habitat characteristics. However, ant foraging activity during any given sampling period may be influenced by weather or other conditions (i.e., detection covariates). That is, the model estimates occupancy while accounting for detection factors that would generate false negatives (MacKenzie et al. 2005). The Macon County habitat plots were sampled three times, and the Madison County plots were sampled twice. In PRESENCE, a series of models using detection covariates were analyzed first. Then, occupancy models were analyzed using the important detection covariates. This suite of models included a separate model containing each occupancy covariate alone and all the combinations of these variables. Model fit and parsimony were assessed using AIC (MacKenzie et al. 2005). The top models had $\Delta AIC < 2$. Detection and occupancy covariates were normalized prior to analysis $[(x - \mu)/\sigma]$ to allow direct comparison of their beta coefficients. A larger coefficient value indicated a stronger influence of that covariate. A county-level study location parameter was in-

cluded to account for any biogeographic patterns or unmeasured habitat factors that were systematically different between Macon and Madison Counties. The detection covariates were study site, soil moisture (%) and ambient air temperature ($^{\circ}\text{C}$). Air temperature was included as a detection covariate because it could vary over time in response to weather conditions. Occupancy covariates were CWM, distance to forest edge, soil moisture, total herb percent cover, myrmecochore percent cover, and forest vertical structure.

The volume of CWM for each plot was quantified by measuring the length and diameter of woody debris on the forest floor. Distance to edge (meters) was measured using 2012 aerial photographs (NAIP 2013) and a geographic information system. Non-forest habitats created by agricultural land uses, houses, and paved roads were used to designate edges. Two-track, nonpaved forest roads (e.g., for logging) or trails were not considered significant enough to create a forest edge. These distances were square-root transformed prior to analysis.

Forest vertical structure within a 100-m radius of the bait stations was represented by three variables derived from LiDAR data (NCDEM 2006). These variables quantified the relative amount of vegetation in the herbaceous (<0.5 m above ground), shrub (0.5–2.0 m) and canopy/subcanopy (>2 m) layers by recording the proportion of LiDAR returns in these three strata. Furthermore, the canopy/subcanopy variable provided a fine-scale measurement of the relative extent and density of the forest canopy around each bait station. Only LiDAR first returns were used; the mean density was 1209 returns ha^{-1} . We excluded returns from roofs of buildings. Although the LiDAR data were collected prior to our field study (2005), we verified the validity of these data with ground-truthing and examination of recent aerial photographs.

For edge experiments, we converted polar coordinates to Cartesian coordinates where positive y values equaled ant movement away from forested patches, negative y values equaled movement toward forested patches and zero y values equaled movement along the forest edge. We used analysis of variance (ANOVA) models to test whether dispersal direction and dispersal distance differed between interior, edge and

exterior bait stations.

Linear mixed models (LMM) were used to evaluate herbaceous cover and ant-dispersed herbaceous cover as a function of distance to nearest forest edge with site as a random effect. We also analyzed plant cover as a function of soil moisture and soil temperature to account for any difference in habitat requirements between ant-dispersed and other-dispersed plant types.

RESULTS

Nest colonization

Ants colonized 45% (ants directly observed) to 57% (ants and/or midden material observed) of the artificial nests placed in the habitat plots. The vast majority of nest colonization (95% when ants were directly observed) was by *A. rudis*. Nest colonization was best predicted by soil temperature and myrmecochore cover ($\Delta\text{AIC} < 2.0$), but the slope value of the coefficients did not differ significantly from zero: soil temperature, coeff. = -0.295 , SE = 0.252 , z -value = -1.169 , p -value = 0.242 ; myrmecochore cover, coeff. = 0.181 , SE = 0.129 , z -value = 1.405 , p -value = 0.160 . *Aphaenogaster* ant colony size (count) was also best predicted by soil temperature and myrmecochore cover ($\Delta\text{AIC} < 2.0$), and the positive slope value of myrmecochore cover differed marginally significantly from zero: soil temperature, coeff. = -1.300 , SE = 1.085 , z -value = -1.199 , p -value = 0.231 ; myrmecochore cover, coeff. = 0.777 , SE = 0.417 , z -value = 1.862 , p -value = 0.063 .

Most of the nest midden material was unidentifiable (71.5% by dry weight), 19.6% was arthropod exoskeleton parts, 5.9% seeds and 3.1% oak galls. There were 139 plant seeds total in 18 nests and 27 oak galls in 14 nests. Neither arthropod part weight nor oak gall abundance were impacted by distance to edge: arthropod, coeff. = -0.003 , SE = 0.003 , t -value = -1.180 , p -value = 0.242 ; oak galls, coeff. = -0.0001 , SE = 0.0001 , z -value = -0.122 , p -value = 0.903 . Seed number increased significantly with greater distance from edge, coeff. = 0.012 , SE = 0.002 , z -value = 5.718 , p -value < 0.001 .

Fat content of the colonies (and hence colony health) was best predicted by ant abundance and CWM ($\Delta\text{AIC} < 2.0$). Specifically, mass lipids ant^{-1} increased significantly with colony size (abundance of individuals; coeff. = 0.001 , SE =

0.001 , t -value = 6.567 , p -value < 0.001), but the slope value of CWM did not differ significantly from zero (coeff. = -0.006 , SE = 0.014 , t -value = -0.418 , p -value = 0.683). When we looked at fat content by midden material, we found that it was best predicted by arthropod exoskeleton weight ($\Delta\text{AIC} < 2.0$), and the positive slope differed significantly from zero, including a second-order term: coeff. = -1.334 , SE = 0.518 , t -value = -2.577 , p -value = 0.0167 , coeff.² = 13.381 , SE = 4.306 , t -value = 3.108 , p -value = 0.005 (Fig. 1A). Mean lipid content did not differ between colonies with and without oak galls ($t = -0.381$, $df = 5.628$, p -value = 0.717), but colonies without seeds had significantly greater colony lipid content ($t = 2.774$, $df = 29.865$, p -value = 0.009 ; Fig. 1B). Arthropod midden mass increased significantly with colony size (coeff. = 0.001 , SE = 0.001 , t -value = 2.047 , p -value = 0.044) but seed abundance did not (coeff. = -0.001 , SE = 0.004 , t -value = -0.166 , p -value = 0.868).

Bait station foraging

Aphaenogaster rudis was the most common species found at the bait stations in the habitat plots, but other genera also foraged for tuna, including *Camponotus*, *Formica*, *Lasius*, *Myrmica*, *Pheidole*, *Prenolepis* and *Tapinoma*. *Aphaenogaster*'s presence was influenced by habitat conditions. In the occupancy models, detection probability of *A. rudis* at bait stations was influenced by soil moisture, which was the only covariate included in the top model of detection probability and it had a negative effect on ant activity (beta coefficient mean $\pm$ SE, -1.51 ± 0.52). Air temperature was not useful in predicting foraging activity during the morning sampling periods of our study, presumably because the work was conducted in the summer when temperatures did not fall low enough to diminish ant activity (in contrast to early spring).

The top four models ($\Delta\text{AIC} < 2$) included occupancy parameters describing habitat differences between the habitat plots (Appendix). The availability of CWM, distance to forest edge and soil moisture were positively related to *A. rudis* presence at bait stations. The magnitude of the soil moisture coefficient was much greater than coefficients for CWM and edge distance (Table 1), suggesting that soil moisture was a more important habitat feature. Herbaceous plants

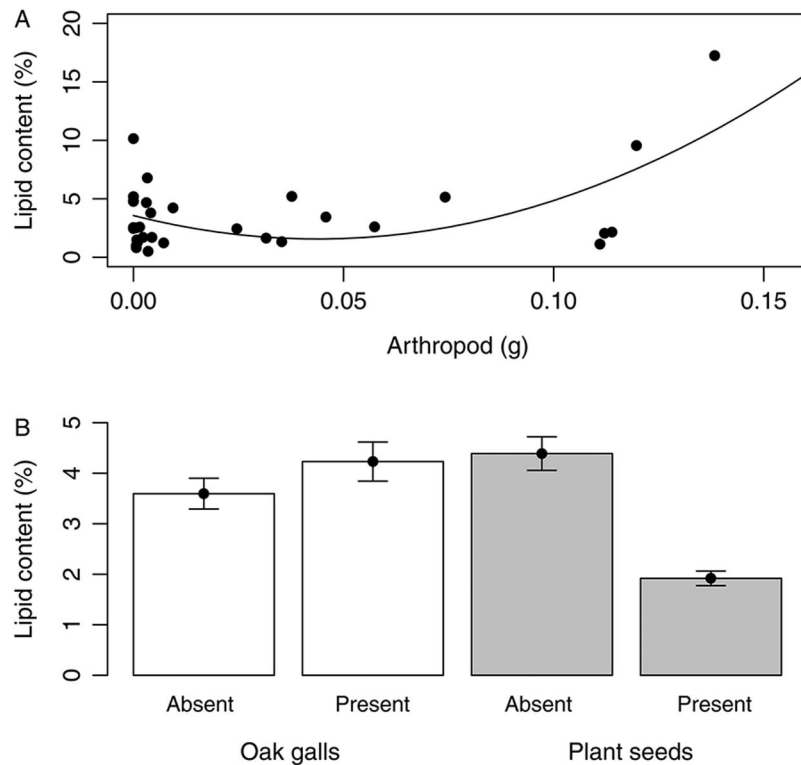


Fig. 1. Percent lipid content (fat proxy for colony health) in colonies as a function of the accumulated weight of arthropod parts in nests (A) and the presence (Ps) or absence (Ab) of oak galls and herbaceous seeds (B). In (A) Colony health dipped slightly with increased arthropod remains but increased significantly at the highest levels of arthropod mass. In (B), colony health did not vary with the presence of retrieved oak galls, but it was significantly lower in colonies that retrieved seeds. The mean (line) $\pm$ SE (shade) of lipid content for all ant colonies in the study is included.

and myrmecochores were included in the top four models, but the coverage of these woodland plants did not have a strong influence on *A. rudis* presence. Indeed, their parameter estimates were small relative to the other covariates, and the 95%

Table 1. Beta parameter estimates for occupancy covariates from the four top ranked models (see Appendix: Table A1). Covariates are standardized for direct comparison. Given are AIC weighted mean values along with 95% CI.

Covariate	Mean	Lower	Upper
Study site	1.76	-3.97	0.45
Coarse woody material	3.10	-0.38	6.58
Distance to edge	3.99	0.95	7.03
Soil moisture	6.56	1.25	11.88
Herbaceous cover	0.00	-0.004	0.004
Myrmecochore cover	-0.21	-0.62	0.19

CI of both covariates included 0 (Table 1). Forest vertical structure was not included in any of the top models. After accounting for detection probability and habitat factors, occupancy rates, as estimated from the best model, were slightly greater at the Madison County (0.839 ± 0.010) than Macon County sites (0.753 ± 0.064). However, the confidence interval for the location coefficient, averaged across the top four models, included 0.

Edge dispersal distance and direction

Overall, dispersal direction by *A. rudis* was toward forest interiors (mean $\pm$ SE, -5.02 ± 2.31 Cartesian y coordinate; negative values indicate dispersal toward forest interior). Specifically, a greater magnitude of negative Cartesian y -axis values indicates greater preponderance of forest interior-directed dispersal, highlighting that *A.*

rudis moved food more directly toward forest interiors at exterior as compared to interior stations (forest exterior = -11.15 ± 3.59 , edge = -3.20 ± 3.79 , forest interior = -0.89 ± 5.57 ; $SS = 2510$, $MS = 2510$, $f\text{-value} = 3.167$, $p\text{-value} = 0.078$; Fig. 2). Despite these differences in directionality, mean ($\pm$ SE) dispersal distance did not significantly differ between exterior (33.79 ± 4.64 cm), edge (36.15 ± 3.14 cm) or interior (38.11 ± 3.81 cm) forest habitat.

Herb abundance by forest edge

Distance to the forest edge did not have a significant effect on total herbaceous cover (coeff. = -0.045 , $SE = 0.018$, $t\text{-value} = -0.501$, $p\text{-value} = 0.627$), but myrmecochore plant cover increased significantly with greater distance from forest edge (coeff. = 0.002 , $SE = 0.001$, $t\text{-value} = -2.210$, $p\text{-value} = 0.059$; Fig. 3). Soil moisture did not have a significant effect on herbaceous (coeff. = 0.316 , $SE = 0.214$, $t\text{-value} = 1.476$, $p\text{-value} = 0.142$) or myrmecochore cover (coeff. = 0.031 , $SE = 0.030$, $t\text{-value} = 1.063$, $p\text{-value} = 0.290$). Soil temperature also did not have a significant effect on herbaceous (coeff. = 2.453 , $SE = 2.738$, $t\text{-value} = 0.896$, $p\text{-value} = 0.374$) or myrmecochore cover (coeff. = 0.204 , $SE = 0.264$, $t\text{-value} = 0.774$, $p\text{-value} = 0.442$).

DISCUSSION

Exurban edges did not influence ant nesting or colony health, but did modify ant nest location and foraging behavior. It seems plausible that this behavioral shift helps explain edge impacts on woodland myrmecochore abundance and distribution. Specifically, the woodland ants occupied nests in exurban forest patches regardless of distance to edge, but did not live in exurban habitats outside edges. As a result, food retrieval was directed away from edges toward forest interior so that seed flow would move away from the edges. This behavior near forest edges appears consistent with our finding that myrmecochore abundance declined near edges whereas other woodland herbs were unaffected. Moreover, plant seed abundance in ant nests declined with closer proximity to edges. Hence, exurbanization seems to pose little threat to *A. rudis* viability, but, by changing the structure of an animal-plant mutualism, has a cryptic indirect

effect that may inhibit ant-dispersed woodland herbs, which can be a large part of the floristic diversity in eastern N.A. woodlands (Beattie and Culver 1981, Handel et al. 1981).

Ness (2004) found similar foraging and seed-dispersal distance results for ants along hard forest edges (i.e., roads), where approximately 75% of the ants he surveyed were *A. rudis*. Specifically, he found ant foraging activity and seed dispersal distance were unaffected by edge proximity, but the dispersal direction was significantly biased away from the edges. Ness and Morin (2008) also found that *A. rudis* visitations to bait-stations decreased nearer forest edges, as did Pudlo et al. (1980) and Banschbach et al. (2012), but none of these studies measured dispersal dynamics and disperser identities outside of the forest edges (across the edges and in the exteriors). Also consistent with our findings are observations that myrmecochorous plant species are less common in younger forests (Pearson et al. 1998, Mitchell et al. 2002, Flinn and Vellend 2005) and near forest edges (Jules and Rathcke 1999, Jules 2000, Ness and Morin 2008). Although ants disperse via aerial mating flights (Hölldobler and Wilson 1990), they do not carry seeds during aerial dispersal, so myrmecochorous plant dispersal is constrained by worker ant-foraging behavior. Observations that myrmecochore plants progressively move toward forest interiors (see Matlack 1994a, b) are then consistent with our findings of interior-directed seed dispersal.

We found that the abundance of seeds in ant nests also increased with distance to edge – again suggesting an accumulation of myrmecochore seeds directed away from edges (or reflecting the increase in myrmecochore density with distance to edge). There is some indication that myrmecochores may be able to cross edge boundaries via alternate dispersal mechanisms (Bale et al. 2003, Myers et al. 2004); however, these events have only involved *Trillium* spp., and successful recruitment has not been demonstrated, questioning whether the findings can be generalized to infer population viability of species-rich myrmecochore assemblages. An alternate possibility is that woodland plants dispersed by ants have different habitat requirements (i.e., more dependent on forest interior conditions) than woodland herbs with other dispersal mecha-

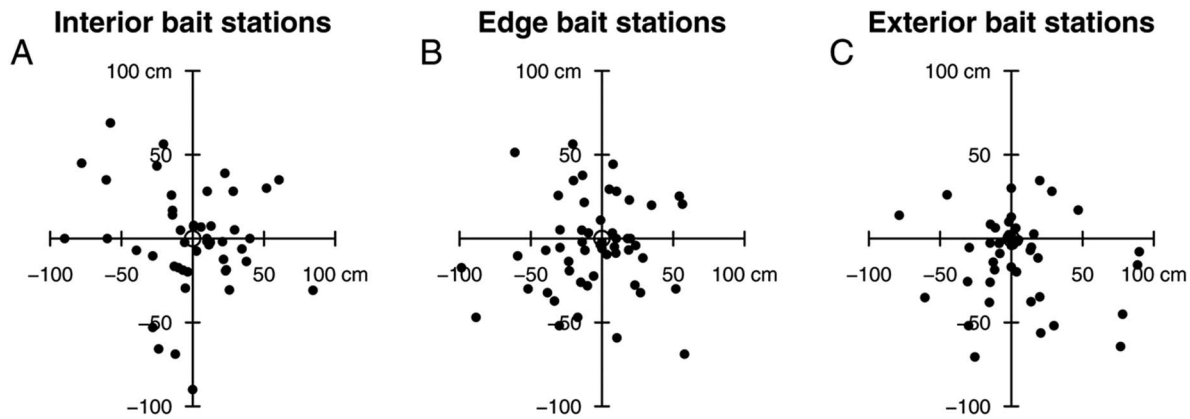


Fig. 2. Cartesian coordinates for *Aphaenogaster* ant dispersal distances and directions from tuna bait stations (points) placed in (A) forest interior, (B) forest edge and (C) forest exterior habitats. Negative y -values represent dispersal toward the forest interior whereas positive y -values indicate dispersal toward forest exterior. Overall, dispersal direction became more and more focused toward forest interiors as the bait stations were located systematically from interior to edge to forest exterior.

nisms. We found no published literature suggesting this alternate possibility, and we note that the patterning of ant-dispersed plants in these forest systems appears more structured by ant rather than plant habitat requirements (Giladi 2004, Warren II et al. 2010, 2014, Warren II and Bradford 2011, 2013). Here, we found that, within the forest patches, neither soil moisture nor temperature predicted plant cover of either type.

These results suggest that, as with the aforementioned studies, ants appear most influential in structuring myrmecochore communities. Most importantly, we show that presence of a dispersal partner does not necessarily translate to a functional mutualism if the partner's dispersing behavior is dependent on habitat structure.

Although exurban forest patches contained similar ant abundance and colony health to

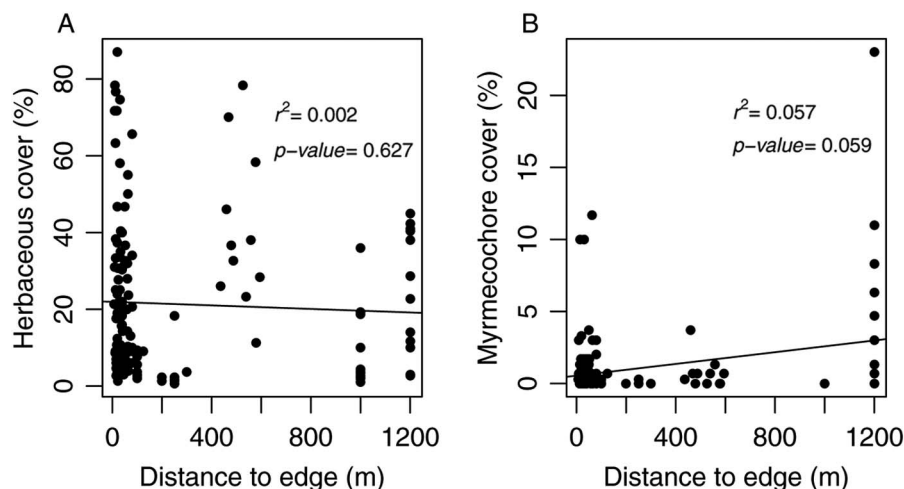


Fig. 3. Distance to edge from forest interior for (A) woodland herbaceous plant coverage and (B) myrmecochore (ant-dispersed) plant coverage. Myrmecochore abundance increased significantly the further the plots were located from forest edges, whereas other understory plants were unaffected. Note the difference in y -axis scales as myrmecochores were far less common than other herbs.

continuous forests, ant abundance did increase with myrmecochore cover. Clark and King (2012) demonstrated that ants fed elaiosomes can increase lipid content, but we found that neither myrmecochore cover nor seeds found in nests corresponded with improved colony health (though we note that seeds collected in Spring may have been discarded from the nests by the time of ant colony collection in Fall). Instead, we found that ant colonies containing seeds were significantly less healthy than those in which we found no seeds. These results are unexpected if we follow the conventional wisdom that ants benefit in the interaction because the elaiosome is an important food (but see Warren II and Giladi 2014). One possibility is that ant colonies in resource-poor locations depended on seeds in lieu of higher-quality food, but arthropod parts and seeds were positively correlated, suggesting that seed elaiosomes did not act as a surrogate food in the absence of preferred foods. Interestingly, colony health improved with colony size, and arthropod midden increased with colony size, but seeds did not. It may therefore be the case—at least within our study system—that ants do not benefit from elaiosomes, and, instead, the correlation between ant abundance and myrmecochore cover is causal in the opposite direction. That is, we might have found more myrmecochores where there were more ants to disperse them.

A second unexpected finding was the presence of oak galls in the ant nests, and this paper is the first reporting of gall retrieval to ant nests. Given that we found the galls in 14 different nests, ca. 120 km apart, gall retrieval to the nests was not idiosyncratic. Oak gall wasps (Cynipidae) oviposit eggs into plant tissue, resulting in a diverse variety of gall formations depending on Cynipid species and gall location (e.g., bud, twig, leaf, etc.; Felt 1940). Several gall types are seed-like, and they detach from the tree and fall to the forest floor (Felt 1940). Some galls excrete a honeydew substance that attracts hymenoptera and may even induce Cypinid larvae protection by ants (Inouye and Agrawal 2004). The commonness and prevalence of gall retrieval/dispersal by ants, as well as any potential chemical inducement/reward, requires further investigation.

Overall, our findings suggest that exurbaniza-

tion alters plant communities by shifting the behavior of seed-dispersing ants, a biotic cascade. These cryptic indirect effects on woodland communities indicate that snapshot assessments of land use patterns may miss long-term degradation of biotic interactions and, hence, communities. For example, we see no edge impact on ant nesting and colony health but evidence for degradation of the plant communities they disperse. Most notable from our study is that changes in habitat structure cascaded through the ecological community by altering ant behavior which, in turn, altered plant distributions. Edge effects on biota commonly are associated with cascades via abiotic variables, but we show a biotic cascade between exurban edge, keystone ants and herbaceous plants—highlighting that accurate prediction of edge effects requires assessing key biological interactions along with abiotic parameters.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES15-00318.1.sm>