# REPORTS

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# ANT BODY SIZE PREDICTS DISPERSAL DISTANCE OF ANT-ADAPTED SEEDS: IMPLICATIONS OF SMALL-ANT INVASIONS

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Abstract. The services provided within a community can change as the species composition of that community changes. For example, ant-seed dispersal mutualisms can be disrupted in habitats dominated by invasive ants. We propose that this disruption is related to changes in mean ant body size, given that invasive ants are smaller than most native seed-dispersing ants. We demonstrate that the mean and maximum distances that ants transport seeds adapted for ant dispersal increase with worker body size, and that this relationship is an accelerating power function. This pattern is consistent among three ant subfamilies that include most seed-dispersing ants as well as most invasive ant species, is generalizable across ant species and communities, and is independent of diaspore mass. Using a case study, we demonstrate that both the mean body size of seed-collecting ants and seed dispersal distances are decreased in sites invaded by Solenopsis invicta, the imported red fire ant. Furthermore, we demonstrate that the mean size of seed-collecting ants at a seed depot or within a community is a useful predictor of mean seed dispersal distances at those sites. Last, we show that small seed-collecting ants and decreased seed dispersal distances are common features of sites occupied by invasive ants. The link between ant body size and seed dispersal distance, combined with the dominance of invaded communities by typically small ants, predicts the disruption of native ant-seed dispersal mutualisms in invaded habitats.

Key words: ants; biodiversity; diaspore; exotic species; invasion; Linepithema; macroecology; mutualism; myrmecochory; power function; scaling; seed dispersal; Solenopsis.

#### INTRODUCTION

Ecologists have long sought to link the traits of individual species to their influences on communities and ecosystems (Jones and Lawton 1995). This challenge becomes more urgent as an increasing array of exotic species disrupts processes within invaded communities. Ants are among the most damaging invaders of terrestrial habitats worldwide, altering the plant and animal compositions of those invaded communities (Bond and Slingsby 1984, Porter and Savignano 1990, Holway 1998, Hoffman et al. 1999, Christian 2001, Holway et al. 2002), although they can also engage in mutually beneficial interactions with diverse taxa (Beattie 1985). Here, we offer a framework that links ant traits with mutualistic services, one that both clarifies the role of individual species within communities and demonstrates how communities are affected by the species replacement that accompanies invasion.

We focus on seed dispersal, an important ecosystem service provided by ants. More than 3000 plant species have seeds adapted for dispersal by ants (Beattie 1985). Ants collect these seeds to ingest an attached food body, the elaiosome, and subsequently discard the intact seeds some distance from the parent plant (see Plate 1). These seeds are unlikely to be dispersed by other organisms, such as birds, due to poor matching of phenology, small energetic reward per unit mass, color, presentation (seeds are dropped to the ground, or actively presented near ground level), and chemistry of the reward (Thompson 1981, Davidson and Morton 1984, Westoby et al. 1990). Collection by ants also reduces seed consumption by granivorous mammals (Beattie 1985). As a result, the ant-seed interaction is of great importance to the plant. Any ant that encounters these seeds could theoretically participate in this generalized ant-plant mutualism. However, striking interspecific and intercommunity differences in the suitability of ant partners have been reported. For example,

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PLATE 1. A *Rhytidoponera aurata* worker transporting an *Acacia dunnii* seed in tropical savanna woodland outside Darwin, northern Australia. The worker is dragging the seed by the elaiosome. This is a large ant (8 mm length) and a large seed (12 mm length, 302 mg). Photo credit: M. Nielsen.

seeds in habitats dominated by the invasive Argentine ant, *Linepithema humile*, rarely escape the parental canopy and remain vulnerable to small-mammal predators (Bond and Slingsby 1984). Perhaps as a result, seedlings in invaded habitats are poorly dispersed and less than 1/10 as abundant (Bond and Slingsby 1984), in some cases even leading to local extinctions of plant species (Christian 2001). Why these problems occur, and whether we might expect similar disruption of this ant-plant mutualism after invasions by other exotic ants, is not yet well understood.

Our attempt to link ant traits, plant benefits, and invasion ecology to answer these questions was prompted by three observations. First, several researchers have noted that larger ant species at their study sites disperse seeds further than do smaller ants (e.g., Pudlo et al. 1980, Davidson and Morton 1981, Horvitz and Schemske 1986, Gomez and Espadaler 1998), although these comparisons were limited to a few ant species. Second, invasive ants are typically smaller than the native ants they exclude (Porter and Savignano 1990, Holway 1998, McGlynn 1999, Holway et al. 2002). Third, plants in invaded habitats interact most often with invasive ants, as these ants frequently constitute >90% of surface-foraging ant abundance in invaded habitats, and can decrease the species richness of native ants in those habitats by >70% (e.g., Bond and Slingsby 1984, Porter and Savignano 1990, Holway 1998, Hoffman et al. 2000, Holway et al. 2002). Insofar as small ants are poor dispersers, and invasive ants are both small and dominant, this could explain how seed dispersal is disrupted in invaded sites.

We first asked whether ant body size was a consistent predictor of mean and maximum seed dispersal distance across numerous ant and plant species throughout the world, then whether invasive ants disperse seeds as far as other similarly sized species. We also addressed whether the relationship between ant body size and seed dispersal distance is influenced by diaspore mass. Second, we used a case study to examine whether the mean body size of a seed-collecting ant assemblage is a useful predictor of mean seed dispersal distance, and whether the body size of seed-collecting ants differs in invaded and noninvaded sites. Lastly, we compared ant body size and mean and maximum seed dispersal distances between communities occupied by invasive ant species and those occupied by other ants.

#### MATERIAL AND METHODS

# Global analysis of ant species

We compiled data on ant sizes and seed dispersal distances from the primary literature, museum specimens, field observations, and unpublished data provided by other researchers. We used mean body lengths for dimorphic and polymorphic ant species in cases where worker size was not recorded. The full data set included 57 ant species from 23 genera, 24 ant-dispersed plant species, and 24 sites across six continents (see Appendix A). Five ant species were identified as invasive based on their capacity to dominate and disrupt natural communities outside their native range (Holway et al. 2002): *Linepithema humile* (Argentine ant), *Solenopsis geminata* (tropical fire ant), *S. invicta* (imported red fire ant), *Paratrechina longicornis* (black

crazy ant), and *Wasmannia auropunctata* (little fire ant). This capacity distinguishes these ants from other nonnative species that are simply "exotic." We include data from both the native and invaded ranges of those five species when available. As a result, we classify the ant species included in this study as either "invasive" or "other," rather than "exotic" vs. "native."

We used simple linear regression to address the extent to which ant body length predicts mean and maximum seed dispersal distances. Because the dispersal distances of more than one plant species are known for some ant species, we analyzed these data in two ways. The first treated each combination of ant, plant, and site as independent data. The second used the average dispersal distances among those plant species and communities, thereby both avoiding pseudoreplication at the ant species scale and minimizing the influence of individual plant species or sites on the ant-specific measurements. Dispersal distances were log-transformed prior to analysis due to heteroscedasticity.

We used a general linear model to evaluate whether the utility of ant body length as a predictor of mean seed dispersal distance changed with diaspore (seed + elaiosome) mass. Data were taken from nine studies that included 32 ant species and six plant species (see Appendix B). The median ant body length in that data set was 5 mm (range, 2-10 mm), and median diaspore mass was 13.7 mg (range, 11.5-40 mg). Ants and diaspores smaller or lighter than those median values were classified as "small" rather than "large." Small ants and diaspores were less than half the size of their larger counterparts (mean sizes, 3.0 vs. 7.3 mm and 11.8 vs. 26.5 mg, respectively). Our model included ant size, seed mass, and a size  $\times$  mass interaction term as categorical variables, and log-transformed seed dispersal distances as the dependent variable.

We performed two additional tests to evaluate whether any observed differences between small and large ants could be attributable to ant phylogeny or sample size. Most seed-dispersing ants belong to the subfamilies Dolichoderinae, Formicinae, or Myrmicinae, as do the invasive ants included in this study. We used simple linear regressions to address whether ant body length predicts the mean and maximum seed dispersal distances within subfamilies, and whether that pattern was qualitatively similar among subfamilies. Because the maximum dispersal distance observed could increase with sample size, we used a two-sided *t* test to compare the number of observed dispersal events for invasive and noninvasive ants.

#### Case study

We monitored seed dispersal events in five forests partially invaded by *S. invicta* to further examine the body size-seed dispersal relationship. We compared body sizes of ants that collected myrmecochorous seeds (*Sanguinaria canadensis*) at 72 depots in five pine-oak forests in northeastern Georgia, USA. (For details on these forests and ant communities, see Ness [2004].) Each depot included five seeds, and was observed for 60 min. We noted the identity of each ant that collected seeds and dispersal distance of each collected seed, and subsequently computed the mean body size of seedcollecting ants and mean dispersal distance for each depot. Collection was defined as displacement of a seed >1 cm. Subsequent to our observations, we used processed meat baits to attract ants. Areas with baits dominated by S. invicta within 90 min were identified as "invaded." This duration should be sufficient to classify depots regarding invasion, as Porter and Savignano (1990) found that S. invicta typically recruited >10workers to baits within 10 min in invaded habitats. Depots were separated by >20 m and, as a result, were encountered by distinct ant colonies and assemblages. Because these depots are independent from an ant's perspective, we treated each as an independent replicate. We used two-tailed t tests to test the hypotheses that the mean ant body size and seed collection rates differed among invaded and noninvaded sites. We used a simple linear regression to test whether the mean dispersal distance increased with mean ant body size.

## Global analysis of ant communities

We compiled data on ant sizes and seed dispersal distances in communities occupied by the five invasive ant species and communities occupied by other ants (see Appendix C). We estimated the mean size of the seed-collecting ants in each community if those data were available (n = 18 communities; see Appendix C). We used mean sizes of the seed-removing ant species, weighted by the proportion of seeds removed by that species. We used simple linear regression to address the extent to which mean ant body length predicts mean dispersal distances of collected seeds within those communities. We also tested the hypothesis that the mean size of seed-collecting ants differed in communities with and without invasive ants, using a one-tailed *t* test that assumed unequal variances.

We used the larger data set of 43 communities (see Appendix C) to compare mean and maximum seed dispersal distances in sites with and without invasive ants. The hypothesis that dispersal distances would be longer in sites lacking invasive ants was evaluated with a one-tailed Wilcoxon test. We used a two-tailed t test to compare the number of observed dispersal events in sites occupied by invasive ants vs. other ants.

## RESULTS

#### Global analysis of ant species

The mean and maximum distances that ants transported seeds increased with ant body length. These relationships were significant (P < 0.0001) both when each combination of ant, plant, and site was treated as independent (mean,  $F_{1.74} = 48.24$ ; maximum,  $F_{1.58} = 39.51$ ) and when only the mean response of individual



FIG. 1. (a) Mean and (b) maximum seed dispersal distances of plants adapted to ant-seed dispersal as a function of mean body length of worker ants carrying the seeds. Each point indicates an ant species: solid circles, invasive; open circles, noninvasive.

ant species pooled across plant species and sites was included (mean,  $F_{1,51} = 43.40$ ; maximum,  $F_{1,47} =$ 38.97). The best-fit lines for the latter relationships took the form of a power relationship  $y = \alpha x^{2.2}$ , and explained >50% of the >100-fold variation observed among seed dispersal distances (Fig. 1). Dispersal distances increased with ant body length, both when ant subfamilies were pooled (Fig. 1) and when subfamilies were considered separately (Dolichoderinae, mean,  $F_{1,9}$ = 21.99, P = 0.002; maximum,  $F_{1,7} = 10.78$ , P =0.011; Formicinae, mean,  $F_{1,9} = 8.37$ , P = 0.018; maximum,  $F_{1,7} = 3.86$ , P = 0.090; Myrmicinae, mean,  $F_{1,18}$ = 19.62, P = 0.0003; maximum,  $F_{1,18} = 16.31$ , P =0.0008).

The importance of ant size as a predictor of seed dispersal distance was also demonstrated in the general linear model. Ant size (small vs. large) was a significant predictor of mean seed dispersal distance ( $F_{1,31} = 15.61$ , P = 0.0004). Lighter seeds were typically dispersed farther than heavier seeds, but that difference was not significant ( $F_{1,31} = 2.84$ , P = 0.102). The ant–

seed size interaction was not significant ( $F_{1,31} = 0.05$ , P = 0.817).

Invasive ants were smaller than most seed-dispersing species, and dispersed seeds shorter distances (Fig. 1). The mean dispersal distances of invasive and noninvasive ants did not differ, however, when comparisons were limited to similarly sized ants (<3.5 mm; two-sided t test; t = 1.72, df = 14, P = 0.11). The number of seed dispersal events observed for all invasive and noninvasive ants was indistinguishable (mean  $\pm 1$  SD: 22.0  $\pm$  28.2 and 22.8  $\pm$  28.5, respectively; t = 0.08, df = 9, P = 0.94), suggesting differences were not merely attributable sampling artifacts.

#### Case study

The mean body size of ants collecting seeds at depots placed in invaded habitats was significantly less than in other depots (mean  $\pm 1$  sE: 4.0  $\pm 0.3$  and 5.3  $\pm 0.3$ mm, respectively; t = 3.30, df = 51, P = 0.002). Mean seed dispersal distance observed at each depot increased with mean ant body size ( $F_{1,51} = 35.99, P <$ 0.0001), and that relationship was best described by a power function ( $y = 0.07x^{4.1}$ ;  $r^2 = 0.59$ ). Ants collected seeds from 54 of the 72 case study depots, and S. invicta removed most (68%) of the collected seeds in invaded sites. Nineteen percent of the depots had seeds collected by multiple ant species, and the numbers of seeds collected at invaded and noninvaded depots were indistinguishable (mean  $\pm$  1 sE: 4.1  $\pm$  0.3 seeds and 3.9  $\pm$  0.2 seeds, respectively; t = 0.62, df = 52, P = 0.54). Ant body sizes ranged from 3.1 to 8.9 mm (see Ness 2004; also see Appendix A).

#### Global analysis of ant communities

The mean dispersal distance of ant-collected seeds increased with the mean size of the ants collecting seeds in those communities ( $F_{1,16} = 22.75$ , P = 0.0002). That relationship is best explained by the power relationship  $y = \alpha x^{2.87}$  ( $r^2 = 0.71$ ; Fig. 2). The mean body length of the seed-collecting ants in communities with invasive ants was less than that in communities without invasive ants (t = 3.10, df = 15, P = 0.004).

Mean seed dispersal distance in communities occupied by invasive ants was only approximately onethird that in other sites (mean  $\pm 1$  sE: 38.6  $\pm 16.7$  cm vs.  $124.3 \pm 20.8$  cm; Z = 2.42, P = 0.008). Maximum reported seed dispersal distances did not differ among sites with and without invasive ants (Z = 1.52, P =0.065). This lack of a difference is primarily due to an anomalously large maximal dispersal distance observed in a Mexican rain forest. That community included native W. auropunctata and S. geminata, but was not dominated by them. Maximum dispersal distances in the remaining communities with invasive ants (outside their native range) were less than one-fourth that observed in other communities (mean  $\pm$  1 sE:  $134.3 \pm 70.2$  cm vs.  $617.5 \pm 105.8$  cm). The number of dispersal events observed at sites occupied by in-



FIG. 2. Mean seed dispersal distances of plants adapted to ant-seed dispersal as a function of mean body length of worker ants carrying the seeds. Each point indicates an ant community: solid circles, communities with invasive ants; open circles, communities without invasive ants.

vasive ants and sites with other ants was indistinguishable when all sites were compared (mean  $\pm 1$  sD: 59.8  $\pm$  35.6 events and 84.9  $\pm$  74.9 events, respectively; t = 1.31, df = 14, P = 0.21), although there was a marginally significant difference when comparisons were limited to the subset of studies that reported maximum dispersal distances (t = 2.15, df = 17, P = 0.05). However, sample size was a poor predictor of maximum dispersal distance observed within a community (simple linear regression,  $F_{1,31} = 0.26$ , P = 0.62).

#### DISCUSSION

This study demonstrates that the distance ants transport seeds adapted for ant dispersal increases with ant body size. Dispersal distances can be predicted from ant body size, a pattern generalizable across ant species and communities. The relationship between ant body size and seed dispersal distance is remarkably strong, given numerous factors influencing the residual error, including worker polymorphism, differences in seed mass, foraging environments, habitat disturbance, and research methodologies. The relationship is also consistent across ant taxa and ecological communities. Below, we discuss why ant body size and seed dispersal distance are ecologically meaningful variables, and why their functional relationship has implications for the persistence of this widespread ant-plant mutualism in the face of ant invasions.

Ant body size incorporates many of the variables known to influence seed dispersal distance, including group vs. solitary foraging, foraging range, and ant nest distribution (Horvitz and Schemske 1986, Andersen 1988, Christian 2001). Large ants may also carry seeds farther due to a more favorable worker-to-seed mass ratio, relative to smaller ants, although that hypothesis was not well supported by our analyses. Also, ant size can influence the likelihood that ants will drop seeds in midtransport (Gorb and Gorb 1999).

The ecological importance of this relationship rests upon seed dispersal distances having broad and general effects on ant-dispersed plants. Many of the benefits plants receive from this mutualism increase with dispersal distance. Such benefits include reduced competition between related plants, patch colonization, access to different microhabitats, and escape from highdensity patches where seeds are vulnerable to densitydependent natural enemies (e.g., small mammals and pathogens; Beattie 1985). The functional relationship between each of these benefits and dispersal distance likely differ (e.g., linear, asymptotic, or perhaps even unimodal if more distant microhabitats are less suitable for seedling establishment). Similarly, the relative importance of these benefits is expected to differ across the diversity of plants and their environments. In some instances, the dispersal of the average (or median) seed may be even less important than are the rare, "maximal" dispersal events experienced by a few seeds. Bearing this in mind, we offer the following observations. Because dispersal beyond the maternal plant's canopy reduces parent-offspring competition, the canopy radius can be considered a minimal distance for seeds to benefit from the interaction. The mean canopy radius of most myrmecochorous plants is <1 m in the southern hemisphere (e.g., Bond and Slingsby 1984, Westoby et al. 1990) and <50 cm in the northern hemisphere (e.g., Pudlo et al. 1980, Horvitz and Schemske 1986). Kjellsson (1991) found that the life expectancy and fecundity of myrmecochorous seedlings dispersed 51-215 cm from their parent plant was more than a seven times that observed for seedlings dispersed within 50 cm. Should seeds escape the maternal canopy, farther dispersal decreases seed aggregation size and the likelihood that individual seeds have a sibling as a nearest neighbor, while increasing the number of sites at which a plant's progeny arrive (Kalisz et al. 1999). Environmental heterogeneity is sufficiently pronounced at the one-meter scale to influence the growth rates of small plants (Antonovics et al. 1987). Thus, dispersal exceeding this distance also allows plants to sample distinct environments. Whether long-distance ("maximum") dispersal events well beyond this distance are also important to plants may depend on safesite density (Green 1983) and the presence of suitable patches that are unoccupied due to dispersal limitation. Many ant-dispersed plants colonize new sites by establishing isolated individuals rather than by expanding along a wave front (Matlack 1994, Brunet and Von Oheimb 1998), and ants can transport seeds >50 m (Davidson and Morton 1981). Thus, these dispersal events can be important despite their rarity.

Seed dispersal is preceded by seed collection and concludes with seed deposition, two behaviors that can provide their own benefits to plants. Might small and large ants engage in these behaviors differently? We

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did not analyze whether seed collection rates differed with ant size for two reasons. First, the definition of "collection" differed greatly among studies, ranging from a minimum seed displacement of 1 cm (Beattie et al. 1979) to 20 cm (Christian 2001). Second, crossstudy differences in seed presentation methods, such as number of seeds per depot, depot distribution, or duration of observations, make it difficult to compare ant encounter rates, seed collection rates, and any effects of seed satiation. We note, however, that other researchers have shown that larger ants are more likely to collect seeds (Beattie et al. 1979, Garrido et al. 2002) or collect a broader range of seed sizes (Kaspari 1996), and less likely to drop seeds in midtransport (Gorb and Gorb 1999). Seed removal rates can be decreased in sites with mostly small (Pudlo et al. 1980) and/or invasive ants (Bond and Slingsby 1984, Horvitz and Schemske 1986, Christian 2001), although this is not always the case (Quilichini and Debussche 2000; this study). Whether nominally "dispersed" seeds that are only transported very short distances (e.g., <20 cm) receive any benefits relative to nontransported seeds is unclear. These short dispersal events typically conclude with aril robbing (elaiosome consumption), thereby decreasing the likelihood that subsequent ants will disperse the seeds. Aril robbing appears to be particularly common in sites with mostly small (Pudlo et al. 1980) and/or invasive ants (Horvitz and Schemske 1986, Andersen and Morrison 1998; Ness 2004). Long-distance dispersal events typically conclude with the seed arriving at the forager's nest, a site that may offer additional benefits including greater soil nutrients and protection from fire and/or predators. In contrast, foragers that transport seeds very short dispersal distances typically abandon seeds on or just below the soil surface (Bond and Slingsby 1984, Horvitz and Schemske 1986; Ness 2004), sites that afford little protection or new access to nutrients.

In speciose ant communities, the mean dispersal distance of a cohort of seeds reflects encounters with both small and large ants. Invasive ants disperse seeds in a manner typical of small ants, but invaded habitats are unusual in being dominated by these small workers. Invasive ants frequently constitute >90% of total ant abundance in invaded habitats (e.g., Porter and Savignano 1990, Holway 1998, Hoffman et al. 1999, Holway et al. 2002), and they can repel larger ants that otherwise act as effective seed dispersers (Horvitz and Schemske 1986). As a result, seeds tend to be encountered by smaller ants. The accelerating power relationship between ant size and seed dispersal distance (Figs. 1 and 2) suggests those changes in mean ant body size can engender an abrupt alteration in dispersal distances. Differences in mean ant size among invaded and noninvaded habitats may seem negligible (4.0 vs. 5.3 mm in our case study, and 3.4 vs. 5.5 mm in the communities shown in Fig. 2), but such a change in ant community composition can decrease mean and maximum

seed dispersal distances by greater than half (Figs. 1 and 2). This study suggests that mean dispersal distances in sites occupied by invasive ants fall short of the minimum distances typically necessary to escape competition with the maternal plant, and maximum dispersal distances in these sites are perhaps also decreased relative to those observed in sites lacking these ants. Many of the benefits associated with dispersal distance, such as reduced competition, access to different microhabitats, patch colonization, and predator avoidance, are diminished in invaded habitats (Bond and Slingsby 1984, Christian 2001). That these effects are linked with reduced dispersal distance, and the reduced body size of ants within those invaded communities, is a well-based, testable hypothesis.

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#### APPENDIX A

A table showing mean and maximum seed dispersal distances and mean body lengths of 54 ant species is available in ESA's Electronic Data Archive: *Ecological Archives* E085-030-A1.

#### **APPENDIX B**

A table showing the mean distance that ants differing in body length disperse diaspores that differ in mass is available in ESA's Electronic Data Archive: *Ecological Archives* E085-030-A2.

#### APPENDIX C

A table showing mean and maximum seed dispersal distances and mean body lengths of seed-collecting ants in different communities is available in ESA's Electronic Data Archive: *Ecological Archives* E085-030-A3.