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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 seed-collecting ants and mean dispersal distance for each depot. Collection was defined as displacement of a seed \geq 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 \approx 10 workers to baits within 10 min in invaded habitats. Depots were separated by \geq 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

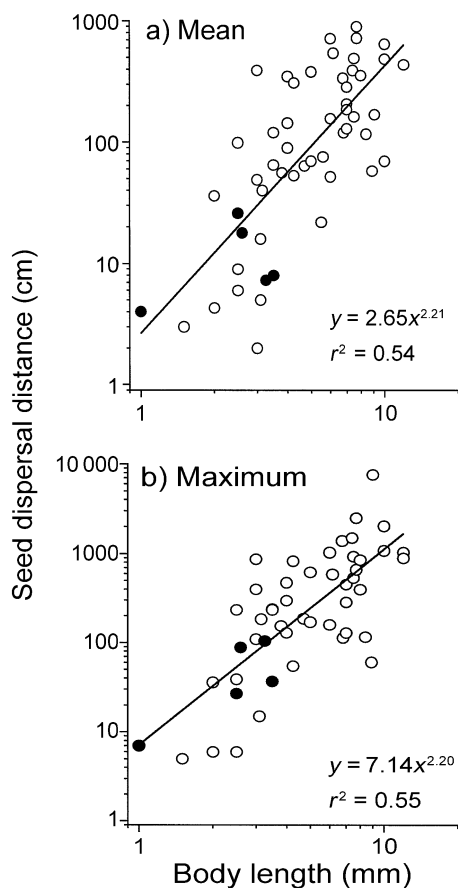


FIG. 1. (a) Mean and (b) maximum seed dispersal distances of plants adapted to ant–seed dispersal as a function of mean body length of worker ants carrying the seeds. Each point indicates an ant species: solid circles, invasive; open circles, noninvasive.

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 $y = ax^{2.2}$, 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

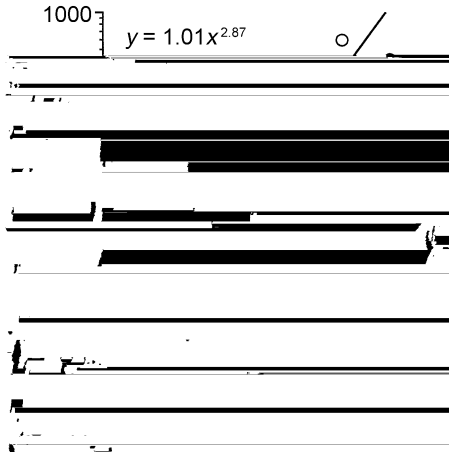


FIG. 2. Mean seed dispersal distances of plants adapted to ant-seed dispersal as a function of mean body length of worker ants carrying the seeds. Each point indicates an ant community: solid circles, communities with invasive ants; open circles, communities without invasive ants.

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 given by the equation $y = 1.01x^{2.87}$, where y is the mean seed dispersal distance (m) and x is the mean body length of worker ants (mm).

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, cross-study 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 (Kaspary 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 non-invaded 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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