Quantitative analysis of the effects of the exotic Argentine ant on seed-dispersal mutualisms

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Although it is increasingly clear that exotic invasive species affect seed-dispersal mutualisms, a synthetic examination of the effect of exotic invasive species on seed-dispersal mutualisms is lacking. Here, we review the impacts of the invasive Argentine ant (Linepithema humile) on seed dispersal. We found that sites with L. humile had 92 per cent fewer native ant seed dispersers than did sites where L. humile was absent. In addition, L. humile did not replace native seed dispersers, as rates of seed removal and seedling establishment were all lower in the presence of L. humile than in its absence. We conclude that potential shifts in plant diversity and comitant changes in ecosystem function may be a consequence of Argentine ant invasions, as well as invasions by other ant species. Because very few studies have examined the effects of non-ant invasive species on seed-dispersal mutualisms, the prevalence of disruption of seed-dispersal mutualisms by invasive species is unclear.

Keywords: Argentine ants; exotic invasive species; seed-dispersal mutualisms; meta-analysis

1. INTRODUCTION
Seed-dispersal mutualisms influence seedling recruitment, population dynamics, species distributions, plant-community composition and gene flow (Howe & Smallwood 1982; Nathan & Muller-Landau 2000). However, the spread of exotic invasive species (invasive species hereafter) threatens seed-dispersal mutualisms, with potential consequences for native populations and communities (Traveset & Richardson 2006; Tylianakis et al. 2008).

Although a growing number of studies have examined whether invasive species disrupt seed-dispersal mutualisms, by affecting either the dispersal agent or the plant (e.g. Bond & Slingsby 1984; Kelly et al. 2006), a quantitative examination of the effect of invasive species on seed-dispersal mutualisms is lacking (Traveset & Richardson 2006). Here, we report the results of a meta-analysis aimed at determining the magnitude of the effect of the invasive Argentine ant (Linepithema humile) on seed-dispersal mutualisms. Linepithema humile has become established in Mediterranean climates globally. Importantly, some of these regions are biodiversity hot spots and harbour a number of unique and endemic plant species, which may rely on native ants to disperse their seeds. Seed dispersal by ants (i.e. myrmecochory) is particularly important in that it involves hundreds of ant species and thousands of plant species across many terrestrial ecosystems (Beattie & Hughes 2002; Rico-Gray & Oliveira 2007). Our focus is on the invasive Argentine ant, a species known to have dramatic effects on native communities and ecosystems (Holway et al. 2002). Specifically, we ask three questions: (i) do Argentine ants reduce the abundance of seed dispersers? (ii) do invasive Argentine ants disrupt seed-dispersal mutualisms by reducing the number of seeds removed? and (iii) do Argentine ants reduce seedling recruitment?

2. MATERIAL AND METHODS
On 31 January 2009, we searched Web of Science to locate publications that included the keywords ‘dist* seed dispersal’, ‘predation seed dispers*’, ‘competition seed dispers*’, ‘disrup* mutual*’ and ‘inva* or introduced or alien or exotic or non-native or non-indigenous’. We also used our knowledge of the literature and scanned the references of any relevant papers to obtain additional sources from the primary literature. To be included in our meta-analysis, a study had to be either an observational or experimental study on seed dispersal in both the presence and absence of an invasive species in the same area.

In total, we found 14 publications focusing on 31 plant species that met our criteria. Eleven out of the 14 articles focused on the impact of invasive ants on seed-dispersal mutualisms, and of these 11, 10 were concerned with the effect of L. humile and one with the effect of Solenopsis invicta. Because of the low number of publications dealing with species other than L. humile, we report only the results of a meta-analysis quantifying the effect of this species on seed-dispersal mutualisms.

Nine of the 10 publications used in the meta-analysis examined seed removal, three examined seedling establishment and four examined the abundance of seed dispersers (appendix A). From each of these publications, we extracted quantitative estimates of the mean number of seed dispersers, seeds removed and/or seedlings established in the presence and absence of the invasive species. Several publications contained information for more than one plant species or seed-dispersal agent, in which case we treated each as distinct data points in our analyses if the species were analysed separately by the author(s) of the original study. If the data were not available in the text, table or online appendix, we used GetDataGraph Digitizer (v. 2.22, copyright S. Fedorov, 2002–2006) to extract data from figures in the original manuscript.

We calculated the effect of invasive species on seed-dispersal mutualisms (effect size) as the log-response ratio (ln R),

\[
\ln R = \ln \left( \frac{X_v}{X_A} \right)
\]

where \( X_v \) is the mean of the response variable in the presence of the invasive species and \( X_A \) is the mean of the response in the absence of the invasive species (Hedges et al. 1999; Osenberg et al. 1999). A negative effect size indicates that the invasive species reduced the number of seed dispersers, seeds removed or seedlings established. We performed a meta-analysis using a random effect model and calculated the weighted mean effect size and 95% bootstrap CI for the three response variables using MetaWin (Rosenberg et al. 2000).

3. RESULTS AND DISCUSSION
Invasive species can affect diversity, modify ecosystem function and alter interactions among native species (Mack et al. 2000; Traveset & Richardson 2006; Tylianakis et al. 2008). In our study, sites with L. humile contained 92 per cent fewer native seed dispersers than did sites without L. humile (figure 1). Moreover, it seems unlikely that L. humile replaces...
native seed dispersers, as overall rates of seed removal and seedling establishment were lower in the presence of invasive ants than in their absence: sites with *L. humile* had, on average, 47 per cent fewer seeds removed and seedling establishment was 76 per cent lower, than when *L. humile* was present (figure 1).

Our quantitative analysis supports previous studies that have documented the effects of invasive ants on seed-dispersal mutualisms (Horvitz et al. 2002; Ness & Bronstein 2004). Indeed, our study suggests that the major impact of invasive Argentine ants results from their dramatic reduction of the abundance of native seed-dispersing ants (figure 1). This is not surprising, as Argentine ants clearly alter the composition of native ant communities (Christian 2001; Carney et al. 2003; Gómez & Oliveras 2003; Gómez et al. 2003; Rowles & O’Dowd 2007).

Seed dispersal by ants has been hypothesized to benefit plants by reducing competition and predation, minimizing the effects of fire, and depositing seeds in nutrient-rich sites (Bond & Slingsby 1984; Christian 2001; Ness & Bronstein 2004). Plants that depend on ants as seed dispersers often disproporionately rely on a single ant species (Gove et al. 2007), making them especially vulnerable if the behaviour or abundance of the keystone mutualist is altered (Giladi 2006). Our meta-analysis and the studies that did not meet our criteria for inclusion in the meta-analysis suggest that invasive ants, such as *L. humile* and *S. invicta*, are typically poor seed dispersers relative to the native ants they displace. Invasive ants may find seeds more slowly or collect fewer seeds per unit of time than do natives (Bond & Slingsby 1984; Horvitz & Schemske 1986; Carney et al. 2003; Gómez et al. 2003; Ness 2004; Oliveras et al. 2007; Rowles & O’Dowd 2009). Additionally, invasive ants often bury seeds less frequently than do native ant species (Bond & Slingsby 1984; Christian 2001; Zettler et al. 2001; Gómez & Oliveras 2003; Gómez et al. 2003). These invasive ants may also act as seed predators (Horvitz & Schemske 1986; Zettler et al. 2001) or consume elaiosomes without moving seeds (Quilichini & Debussche 2000; Gómez et al. 2003; Ness 2004). However, it is important to note that native ants may also consume seeds and the relative importance of seed predation among native ants may influence the ultimate impact of invasive ants.

Body size in ants plays a crucial role in seed dispersal (Ness & Bronstein 2004), an important fact, as invasive ants are sometimes smaller than the native species that they exclude (McGlynn 1999; Holway et al. 2002). As a result, invasive ants frequently fail to disperse large elaiosome-bearing seeds while readily dispersing small native and exotic seeds (Ness 2004; Witt et al. 2004; Rowles & O’Dowd 2009). However, the ultimate impact of Argentine ants on seed dispersal in a community may be mediated by seed size. For example, Rowles & O’Dowd (2009) showed that Argentine ants removed large as well as small diaspores but this was influenced by elaiosome mass. Additionally, when they do remove seeds, dispersal distances by invasive ants are often shorter than those of native species (Bond & Slingsby 1984; Horvitz & Schemske 1986; Ness 2004; Rowles & O’Dowd 2009). Finally, not only do invasive ants disrupt seed-dispersal mutualisms between native species but they also successfully disperse seeds of exotic plants (Rowles & O’Dowd 2009).

As with any meta-analysis, our results could be biased by the failure to publish studies that show no effects of invasive species. In addition, there may be a research bias, whereby researchers tend to study sites or species (such as *L. humile*) where the effects are likely to be found. We would encourage publication of any results showing non-negative effects of invasive ants on seed-dispersal mutualisms.

Finally, we would like to highlight the fact that we found few studies on species other than *L. humile*. In our opinion, this paucity of studies suggests a clear need for ecologists to examine the effects of invasive species on seed-dispersal mutualisms. We also suggest that long-term studies are needed to understand the population-level consequences of the disruption of seed-dispersal mutualisms by invasive species. Nevertheless, our results at least suggest that Argentine ants have strong negative effects on the dispersal of seeds and the establishment of seedlings, but it is unclear how these effects influence population dynamics of native plant species or the structure of native plant communities.

We thank J. K. Bailey, R. R. Dunn, and T. J. Zelikova and two anonymous reviewers for providing advice that greatly improved this manuscript.
Table 1. Results of the search of peer-reviewed studies that quantified the effects of the invasive Argentine ant on seed-dispersal mutualisms. (For each study, the identity of stage(s) examined, native seed dispersers and plants are shown.)

<table>
<thead>
<tr>
<th>references</th>
<th>stage(s) examined</th>
<th>native seed dispersers</th>
<th>plant species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bond &amp; Slingsby (1984)</td>
<td>seeds removed–seedlings</td>
<td>Anoplolepis custodiiens, Pheidole capensis, Dorymyrnx insignus, Messor sp., Pogonomyrnx submitidus</td>
<td>Mimetus cucullatus (Proteaceae)</td>
</tr>
<tr>
<td>Carney et al. (2003)</td>
<td>seed dispersers–seeds removed</td>
<td>Anoplolepis custodiiens, Meranoplus peringueyi, Pheidole capensis, Tetramorium quadrispinosum</td>
<td>Dendromecon rigida (Papaveraceae)</td>
</tr>
<tr>
<td>Christian (2001)</td>
<td>seed dispersers–seed removed</td>
<td>Anoplolepis custodiiens, Cataglyphis pulicicapsus, Messor barbarus, Messor bouvieri, Myrmica sabuleti, Pheidole pallidula, Tapinoma nigerrimum, Tetramorium semilaeve</td>
<td>Leucospermum concarpodendron (Proteaceae), Leucospermum truncatum (Proteaceae), Mimetus cucullatus (Proteaceae), Serruria phylloides (Proteaceae), Spatalla racemosa (Proteaceae), Serruria inconstipica (Proteaceae)</td>
</tr>
<tr>
<td>Gómez et al. (2003)</td>
<td>seed dispersers–seeds removed</td>
<td>Aphaenogaster subterrana, Crematogaster scutellaris, Formica cunicularia, Messor bouvieri, Pheidole pallidula, Tapinoma nigerrimum, Tetramorium semilaeve</td>
<td>Rhamnus alaternus (Rhamnaceae)</td>
</tr>
<tr>
<td>Gómez &amp; Oliveras (2003)</td>
<td>seed dispersers–seeds removed</td>
<td>Aphaenogaster subterrana, Crematogaster scutellaris, Formica cunicularia, Messor bouvieri, Pheidole pallidula, Tapinoma nigerrimum, Tetramorium semilaeve</td>
<td>Euphorbia characias (Euphorbiaceae), Euphorbia biumbellata (Euphorbiaceae), Genista linifolia (Fabaceae), Genista triflora (Fabaceae), Genista monspessulana (Fabaceae), Sarothamnus arbores catalaucinus (Fabaceae)</td>
</tr>
<tr>
<td>Oliveras et al. (2005)</td>
<td>seedlings</td>
<td>Aphaenogaster subterrana, Crematogaster scutellaris, Formica cunicularia, Messor bouvieri, Pheidole pallidula, Tapinoma nigerrimum, Tetramorium semilaeve</td>
<td>Euphorbia characias (Euphorbiaceae)</td>
</tr>
<tr>
<td>Oliveras et al. (2007)</td>
<td>seeds removed</td>
<td>Messor bouvieri</td>
<td>Calicotome spinosa (Papilionaceae), Porala bituminosa (Papilionaceae), Spartium junceum (Papilionaceae)</td>
</tr>
<tr>
<td>Quilichini &amp; Debussche (2000)</td>
<td>seeds removed</td>
<td>Aphaenogaster spinosa, Tapinoma nigerrimum, Tetramorium semilaeve</td>
<td>Anthus crispa (Boraginaceae)</td>
</tr>
<tr>
<td>Rowles &amp; O’Dowd (2009)</td>
<td>seeds removed</td>
<td>Pheidole sp., Rhytidoponera victoriae</td>
<td>Acacia sophorae (Mimosaceae), Acacia retinodes (Mimosaceae)</td>
</tr>
<tr>
<td>Witt et al. (2004)</td>
<td>seeds removed</td>
<td>Anoplolepis custodiiens, Anoplolepis stingroveri, Ocyymyrmex cilliei, Pheidole capensis, Tetramorium quadrispinosum</td>
<td>Agathosma ovata (Rutaceae), Leucospermum cordifolium (Proteaceae), Paranomus reflexus (Proteaceae), Phyllica pubescens (Rhamnaceae), Podalyria calyptrate (Fabaceae), Polygala myrtfolia (Polygalaceae)</td>
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