

## **I d c**

How species move within and across habitat edges is an outstanding and unresolved issue facing ecologists and conservation biologists (Murcia 1995; Harrison and Bruna 1999). Forest edges apparently offer a particular challenge to myrmecochorous (ant-dispersed) plants. Ant-dispersed plants can be rare along “hard” edges (i.e., those that separate forests from other habitats such as clearcuts or old fields) (Jules 2000), and their distribution suggests that population centers may even move away from those edges over the course of successional time (Matlack 1994a). Ant-dispersed plants also disperse slowly across “soft” edges, those that separate old growth forest from adjacent secondary forest within a contiguous stand, relative to wind-dispersed, ingested, and adhesive seeds (Matlack 1994b; Brunet and Von Oheimb 1998; McLachlan and Bazely 2001). One explanation for this apparently constrained distribution is that pollination and seed survival can be decreased along forest edges (Jules and Rathcke 1999). It would be surprising, however, if such effects were limited to ant-dispersed plants. An alternative, non-conflicting, hypothesis is that the interactions between plants and ants change at and across forest edges. Ant community composition can change along these edges (Majer et al. 1997; Carvalho and Vasconcelos 1999), and patches with high edge-to-interior ratios or disturbance-induced edges are highly susceptible to exotic ant invasion (Majer 1985, 1994; Majer et al. 1997; Suarez et al. 1998; Holway et al. 2002). These changes in ant community composition could act to the detriment of ant-dispersed plants.

Many ants collect myrmecochorous seeds to ingest the elaiosome, an attached lipid-rich food-body. Potential benefits to the seed include the colonization of new patches (Pudlo et al.



Data analyses

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The effects of forest edges and ant invasions on the mean number of seeds dispersed from each depot were evaluated with general linear models that included habitat type (forest interior versus edge), invasion status (uninvaded versus invaded), and a habitat  $\times$  invasion

where collection occurred were compared (Table 3). Dispersal of seeds within a single depot to multiple nests, however, was observed more frequently at unin- vaded than invaded depots (34 versus 16% of depots with more than one dispersal event, respectively;  $\chi^2=32.2$ ,  $df =1$ ,  $P <0.0001$ ). Seed collection rates at all depots differed among the five forests (Table 3) due to greater incidence of visitation at depots at the Helfmeyer Homestead relative to the other four forests. The five forests were indistinguish- able when collection rates were compared only at depots where at least one dispersal event occurred (mean  $\pm$  SE =4.3 $\pm$ 0.2 seeds collected; Table 3).

### Seed dispersal distance

Mean seed dispersal distances were influenced by invasion status but not habitat type or forest (Table 3). Mean dispersal distance was greater in unin- vaded than invaded habitats (grand mean  $\pm$  SE =100.8 $\pm$ 11.4 versus 39.4  $\pm$ 6.9 cm;  $t =4.61$ ,  $df =207$ ,  $P <0.0001$ ), as were the

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collection rates were not affected by either variable. These distances and destinations are likely to be useful indicators of the fate of those individual seeds over longer time periods, as (i) most seeds were dispersed, (ii) secondary dispersal was rarely observed, (iii) seed collection rates are greatest within hours of dehiscence or seed presentation and are negligible thereafter (Smith et al. [1989](#))

nests. Seeds at invaded depots were also more likely to be dispersed to a single ant nest, perhaps leading to a more clumped distribution of related seeds. As a result, seeds in invaded habitats are less likely to experience any of the colonization, escape, or directed dispersal benefits ascribed to dispersal by ants (see above). The ant's social organization and small size provide two explanations for its deficiencies as a disperser. In invaded habitats, *S. invicta* nests are found at high densities per unit area and colonies aggressively defend their territories against other ant species, both common characteristics among invasive ants (Holway et al. 2002). These same characteristics are predicted to decrease mean seed dispersal distances and shorten the dispersal curve tail (Andersen 1988). Furthermore, *S. invicta* was among the smallest of ants observed dispersing seeds in this study (Table 2). Many researchers have used body size to contrast ant species. Although the unit of measure can differ among studies (body length: Beattie et al. 1979; Pudlo et al. 1980; Carney et al. 2003; head width: Kaspari 1996; Garrido et al. 2002), they generally concluded that small ants collect and carry seeds with difficulty.

The presence of forest edges had no effect on how far seeds were dispersed, although it had a strong effect on where those seeds arrived. Seeds at non-invaded forest edges were seven times more likely to be dispersed towards the forest interior as towards the matrix (and/or edge). In comparisons limited to seeds dispersed greater than 10 cm, I found that the average seed in uninvaded edge habitats was dispersed almost 70 cm away from the forest edge. This biased dispersal offers a new explanation for the decrease in myrmecochorous plant recruitment noticed by other researchers along intervals from forest interiors to edges (e.g., Matlack 1994a; Jules 2000). Intriguingly, this biased dispersal may simultaneously increase the likelihood that propagules arrive in the forest interiors, where some perform better (Jules and Rathcke 1999, but see Marino et al. 1997), while decreasing the likelihood that propagules emigrate from and between forests. This is the first demonstration of edge-sensitive dispersal in ant-dispersed plants, although this phenomenon been noted in bird- and bat-dispersed plants (Thomas et al. 1988; Gorchov et al. 1993; Ingle 2003).

The finding that seed dispersal direction is unbiased in invaded edges but biased towards the interior in non-invaded edges offers the only indication of a habitat  $\times$  invasion interaction. This evidence is tentative, however, as the sample size of dispersal events suitable for analysis (>10 cm) was lowest in invaded sites, and the argument solely rests upon the absence of a statistically significant edge effect in these sites.

This study demonstrates three points. First, plant immigration and emigration may play important roles in determining the distributions of ant-dispersed plants. To

