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Forest edges and fire ants alter the seed shadow of an ant-dispersed plant

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Abstract Exotic species invade fragmented, edge-rich habitats readily, yet the distinct impacts of habitat edges and invaders on native biota are rarely distinguished. Both appear detrimental to ant-dispersed plants such as bloodroot, *Sanguinaria canadensis*. Working in northeastern Georgia (USA), an area characterized by a rich ant-dispersed flora, fragmented forests, and invasions by the red imported fire ant, *Solenopsis invicta* , I monitored the interactions between ants and *S. canadensis* seeds in uninvaded forest interiors, uninvaded forest edges, invaded forest interiors, and invaded forest edges. I observed 95% of the seed dispersal events that occurred within the 60-min observation intervals. Seed collection rates were similar among all four (habitat × invasion) groups. The presence of invasive ants had a strong effect on seed dispersal distance: *S. invicta* collected most seeds in invaded sites, but was a poorer disperser than four of five native ant taxa. Habitat type (interior versus edge) had no effect on seed dispersal distance, but it had a strong effect on seed dispersal direction. Dispersal towards the edge was disproportionately rare in uninvaded forest edges, and ants in those habitats moved the average dispersed seed approximately 70 cm away from that edge. Dispersal direction was also skewed away from the edge in uninvaded forest interiors and invaded forest edges, albeit non-significantly. This biased dispersal may help explain the rarity of myrmecochorous plants in younger forests and edges, and their poor ability to disperse between fragments. This is the first demonstration that forest edges and *S. invicta* invasion influence seed dispersal destination and distance, respectively. These forces act independently.

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Introduction

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. 1980; Andersen 1988), escape from predators (Heithaus 1981; Bond and Slingsby 1984;

Gibson 1993; Christian 2001) and/or related plants, and directed dispersal to safe, nutrient-rich microsites such as ant nests (Beattie and Culver 1981; Bond and Slingsby 1984). These benefits are quite variable in space or time. For example, the invasive Argentine ant, *Linepithema humile* , invades fragmented, edge-rich habitats readily (Suarez et al. 1998). Myrmecochorous plants in habitats invaded by this ant are less abundant, rarely escape the parental canopy, have a clumped distribution, and suffer from high seed predation rates relative to plants in uninvaded sites (Bond and Slingsby 1984; Christian 2001; Carney et al. 2003). Even in the absence of ant invasions, edge and interior habitats can differ in the rates that seeds are collected by native ants that presumably benefit those seeds (Majer 1985; Jules and Rathcke 1999), and by rodents that presumably act as seed predators (Jules and Rathcke 1999). Whether other features of dispersal, including the configuration of seed shadows and seed destinations, differ among these same habitats is unknown.

Because habitat disturbance and the presence of invaders can act simultaneously while having different effects, placing each in the context of the other is most informative (Butz Huryn 1997; Suarez et al. 1998; Hobbs 2001; Holway et al. 2002). This field study evaluated the independent effects of forest edges and invasion by the red imported fire ant *Solenopsis invicta* Buren on seed dispersal of *Sanguinaria canadensis* L. (Papaveraceae), a myrmecochorous herb commonly known as bloodroot. I studied the effects of forest edges and *S. invicta* invasion on: (i) rates of seed collection by ants; (ii) the distances that ants dispersed seeds; and (iii) the direction in which seeds were dispersed, relative to the forest edge.

Materials and methods

Study organisms

Sanguinaria canadensis L. (Papaveraceae) is a perennial herb common in deciduous forests throughout eastern North America, a region that includes a rich myrmecochorous flora (~30% of herbaceous species; Beattie and Culver 1981; Gaddy 1986). Plants flower in the spring and seeds dehisce from fruits approximately 30–40 days later (Schemske 1978). The populations included in this study flowered in March. I collected seeds in April, and observed ant-seed interactions in June and July 2002 using seeds frozen for the intermediate month. Ants readily collected these thawed seeds. Seeds are large (mean mass ± SD =13.7±1.6 mg, n =26), with 10–30 seeds per fruit (Schemske 1978; Pudlo et al. 1980; Heithaus 1981). Seeds fall passively to the ground beneath parent plants with elaiosomes attached. Subsequent collection by ants, including species observed in the present study, benefits the seeds by distributing them within the habitat (Pudlo et al. 1980) and decreasing the likelihood of predation by small mammals (Heithaus 1981). *Sanguinaria canadensis* is sensitive to habitat alteration. Pudlo et al. (1980) found that seeds are dispersed shorter distances and that plants are more aggregated in disturbed forests, and Pearson et al. (1998) found that percent cover and the density of emergent stems are reduced in small forest stands relative to larger stands. Although *S. canadensis* is most commonly found in the shaded understory of large, deciduous forests, transplant experiments by Marino et al. (1997) demonstrate that it can grow vigorously in light-rich habitats such as the open fields that typically border forest edges and separate forest fragments in the eastern United States.

Solenopsis invicta, a South American ant, arrived in the southeastern United States in the early 1900s. Its invasion has been linked with declines in native ant species richness within southeastern USA (Porter and Savignano 1990; Gotelli and Arnett 2000; Holway et al. 2002). The interactions between *S. invicta* and myrmecochorous seeds have been addressed in one previous study. Zettler et al. (2000) used a combination of lawn and laboratory experiments to demonstrate that *S. invicta* does collect myrmecochorous seeds, and judged that it can inflict damage on the seeds of several myrmecochores, including *S. canadensis*, *Viola* , *Iris* , and *Trillium* spp., sufficient to impair germination.

Sites and methods

Five mesic deciduous forests >70 years old were selected in Clarke and Oglethorpe counties in Georgia, USA (33°52′N, 83°15′W): Whitehall Experimental Forest, Horseshoe Bend Experimental Forest, the State Botanical Gardens of Georgia, Memorial Park, and the Helfmeyer Homestead. Each forest included myrmecochorous flora (e.g., *S. canadensis* , *Viola* spp, *Trillium* spp.), a portion of the forest invaded by *S. invicta*, and at least one disturbed, linear edge characterized by weedy secondary growth and high access to light relative to the forest interiors. These edges were produced by electrical power lines, dirt roads, large tree falls, and stream floodplains. *Solenopsis invicta* arrived in Clarke and Oglethorpe counties in the mid-1970s, although the exact time of invasion for these individual forests is not known.

Seed depots were used as the unit of replication in this study. Depots consisted of five seeds placed on a 5×5 cm white card that facilitated observing ants. Each depot was observed for an hour, or until all seeds were dispersed. For each dispersal event, I recorded ant identity, dispersal distance (displacement distance from depot to nest, or until seed-carrying ants were lost from sight), and dispersal direction (towards edge, parallel to edge, or towards interior, encompassing 90, 180, and 90° sections of a circle centered at the depot, respectively). Because preliminary observation indicated that ant activity decreased into the afternoon, all observations were performed between 800 and 1300 hours. No fewer than 12 depots were observed in each forest (mean =14.4). Each depot was separated by >20 m, a distance that exceeded the farthest foraging distance observed for the ants in this study (see below). Ant foragers and ant colonies thus perceive depots as independent, even though other depots are present, allowing depots to be treated as independent replicates (e.g., Kaspari 1996).

I used the trunks of canopy dominants to demarcate the transition from the forest to the adjoining matrix. Depots designated as “edge” were <10 m interior of these trunks. “Interior” depots were >30 m from these edges, a point where in other North American temperate deciduous forests, microenvironment [e.g., temperature, shrub cover, litter moisture, litter depth, humidity, rainfall (Matlack 1993), soil moisture and canopy cover (Jules 2000)] is indistinguishable from that further inward. Canopy dominants are a useful point to define edges, as they indicate the point of edge creation (Murcia 1995).

To classify the invasion status of each microsite (depot), a 1 g piece of processed meat was placed on the depot subsequent to the seed trials. Baits were inspected 90 min later, and depots with *S. invicta* at the baits were classified as invaded. This duration should be sufficient to classify depots regarding invasion, as Porter and Savignano (1990) found that *S. invicta* typically discovered meat baits within 1 min and recruited >10 workers to baits within 10 min in invaded habitats. Each forest included depots in the uninvaded interior, uninvaded edge, and invaded edges. Perhaps because invasions are disproportionately common along edges, invaded depots in forest interiors were only found in four of the five forests.

Data analyses

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 × invasion interaction term as class variables. Separate models were examined for (1) all depots and (2) the subset of depots from which dispersal occurred, as dispersal could occur more frequently at *S. invicta* -dominated depots simply as a result of the sampling design (i.e., invaded depots have ants present, by definition). Depots were used as independent replicates, and the five forests were included as statistical blocks.

The effects of forest edges and ant invasions on seed dispersal distances were evaluated in three ways. First, I used a general linear model of the form described above to compare mean dispersal distances among depots using all five seeds. Second, I used an identical model to compare mean dispersal distances using only the subset of dispersed seeds at a depot as the dependent variable. Distances were log-transformed for both analyses. Third, because the use of mean dispersal distances within a depot obscures rare long distance-dispersal events that may be important to plants, I contrasted the distribution of dispersal distances (i.e., the “dispersal curve”) observed within the four (habitat × invasion status) groups. Here, individual dispersal events are used as replicates, although pseudoreplication within depots precluded a formal analysis.

The frequency of dispersal towards the forest interior versus the edge/matrix was compared with Wilcoxon paired-sample tests. Paired frequencies were compared within individual depots. Separate tests were performed for non-invaded forest interiors, non-invaded edges, and invaded edges. I also asked whether the average collected seed arrived at destinations closer to or further from the forest edge, relative to their original position in the seed depot. Dispersal towards the forest interior was designated as a positive value, dispersal towards the edge as a negative value, and dispersal parallel to the edge as a zero, because such dispersal does not change the seed’s position relative to the edge. Two-sided *t* -tests addressed whether the mean dispersal distance of collected seeds at a depot differed from zero, that is, whether the seed cohort was dispersed significantly towards or away from the forest interior. Only seeds dispersed >10 cm were included in both these analyses, as dispersal direction for shorter distances largely reflected microhabitat characteristics (e.g., workers circumventing logs). Dispersal direction was not evaluated in invaded forest interiors, due to the lack of dispersal >10 cm (see below).

All analyses were performed with SAS statistical software version 6.12.

Results

Seventy-two depots were observed over the course of this study ($n_{\text{uninvaded interior}}=25$; $n_{\text{uninvaded edge}}=25$, $n_{\text{invaded edge}}=18$; $n_{\text{invaded interior}}=4$). Most *S. invicta* -dominated depots (77%) were located in forest edges. Two hundred and twenty nine of 360 seeds (64%) were removed during the 1-h observation periods, and 218 of these dispersal events (95%) were directly observed. Only 3% of the dispersed seeds were dropped by one ant species and secondarily dispersed by another species. Spiders interrupted 2% of the dispersal events by ambushing the ants, but the spiders were never observed handling or collecting the seeds.

Seed-dispersing ants included *Aphaenogaster* spp. (*A. texana carolinensis*, *A. flemingi*, and *A. fulva*), *Formica schaufussi*, *F. subsericea*, *Camponotus castaneus*, *Crematogaster ashmeadi* and *S. invicta*. All except *S. invicta* are native to the southeastern United States. Observations for the *Aphaenogaster* species were pooled, as the ants are very difficult to distinguish in the field. The species composition of the seed-collecting ant community differed among invaded and uninvaded habitats, but not among forest interiors and edges (Table 1). The two smallest ants, *S. invicta* and *C. ashmeadi*, typically pulled seeds just under adjacent leaves, whereas the larger species generally dispersed seeds greater distances (see body length, Table 2) and deposited them in their nests. Soil excavations underneath half of the invaded depots revealed that 63% of *Solenopsis* -dispersed seeds remained within 10 cm of the depot 2 h later, and that the elaiosomes were removed from 63% of these seeds.

Seed collection

Seeds were collected from 75% of the depots. Neither habitat configuration (interior versus edge) nor ant invasion significantly influenced the number of seeds collected, regardless of whether all depots or only those

Table 1 Frequency of seed collection by different ant taxa among sites that differ in invasion status and habitat configuration (forest interior versus edge). Five seeds were observed for 1 h at each depot

Ant taxa	Uninvaded interior	Uninvaded edge	Invaded interior	Invaded edge
Aphaenogaster spp.	57	43	1	18
Camponotus castaneus	0	4	0	4
Crematogaster ashmeadi	3	1	0	1
Formica schaufussi	0	6	0	0
Formica subsericea	7	10	0	2
Solenopsis invicta	4	0	15	40
Number of depots observed	25	25	4	18

Table 2 Seed dispersal distances of *Sanguinaria canadensis*, a myrmecochorous plant, by different ant taxa in deciduous forests in Georgia, USA. Dispersal to individual ant nests was used as the unit of replication, rather than individual dispersal events

Ant species	No. of nests	Mean dispersal distance (cm) (± SD)	Body length (mm) (± SD)
Aphaenogaster spp.	42	64.0±35.6	4.74±0.49 (*n* =19)
Camponotus castaneus	2	58.0±4.2	8.9±1.3 (*n* =9)
Crematogaster ashmeadi	5	5.4±5.3	3.1
Formica schaufussi	2	547±66.4	6.16±0.9 (*n* =7)
Formica subsericea	10	257.2±181.4	8.9

where collection occurred were compared (Table 3). Dispersal of seeds within a single depot to multiple nests, however, was observed more frequently at uninvaded than invaded depots (34 versus 16% of depots with more than one dispersal event, respectively; χ^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 indistinguishable when collection rates were compared only at depots where at least one dispersal event occurred (mean ± SE =4.3±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 uninvaded than invaded habitats (grand mean ± SE =100.8±11.4 versus 39.4 ±6.9 cm; *t* =4.61, *df* =207, *P* <0.0001), as were the maximum dispersal distances (Fig. 1). The frequency distribution of dispersal distances also differed among the four habitat × invasion groups (Fig. 1). *Solenopsis invicta* dispersed 68% of the seeds at invaded depots, and were responsible for all but one of the <10 cm dispersal events so frequent at those depots (Fig. 1a, b). Long-distance dispersal events were also rarer in invaded habitats, relative to non-invaded forest interiors and edges (Fig. 1c, d).

Seed dispersal direction

Seeds at uninvaded forest edge depots were dispersed towards the forest interior more frequently than towards the edge / matrix (T^e=19, *n* =19, *P* <0.005). For the purpose of illustration, a null hypothesis for random dispersal would predict that seeds should be dispersed by ants towards edges and/or the matrix, parallel to edges, and towards the interior in a 1:2:1 ratio. The ratio for dispersal directions in the uninvaded forest edges was 1:6.5:7.8 (*n* =61), indicating that dispersal towards the forest interior was more common than dispersal across the edge or along it. Mean seed dispersal distance was also skewed toward the forest interior at uninvaded edge depots (*t* =2.44, *v* =15, *P* <0.05); the average collected seed moved 68.6±28.1 cm closer to the forest interior. In contrast, seeds were dispersed towards and away from the edge / matrix at equal frequencies in uninvaded forest interiors (T^e=44.5, *n* =14, *P* >0.5) and invaded edges (T^i =20, *n* =9, *P* >0.5). Mean seed dispersal distances were skewed toward the forest interior in these two groups (mean±SE: uninvaded interior =20.1±21.6 cm; invaded edge =47.0±55.2 cm), although neither difference was statistically significant (*t* =0.93, *v* =17, *P* >0.3 and *t* =0.85, *v* =7, *P* >0.3, respectively).

Discussion

Results of this study indicate that ant invasions and forest edges have strong and independent effects on the seed dispersal process. Neither seed collection rates nor the seed dispersal curves suggest a habitat by invasion interaction. Below, I focus on how edges and ant invasion affect seed dispersal distances and destinations, as seed

Table 3 General linear models evaluating the effects of habitat type (forest interior vs edge) and *Solenopsis invicta*invasion on the seed dispersal of *Sanguinaria canadensis*, a myrmecochorous herb. Depots were arrayed within five partially disturbed and invaded forests in northeastern Georgia, USA, and each depot is treated as an independent replicate

Dependent variable	Independent variable	*F* statistic	*P*
Seed removal at all depots	Forest	3.23	0.017
	Habitat	0.01	0.933
	Invasion status	2.49	0.119
	Habitat × Invasion status	0.1	0.748
Seed removal at depots with dispersal	Forest	1.34	0.269
	Habitat	0.21	0.651
	Invasion status	0.06	0.814
	Habitat × Invasion status	0.34	0.564
Mean dispersal distance at depots with dispersal (all seeds)	Forest	0.55	0.702
	Habitat	1.58	0.215
	Invasion status	5.15	0.028
	Habitat × Invasion status	0	0.988
Mean dispersal distance at depots with dispersal (removed seeds only)	Forest	0.38	0.821
	Habitat	1.7	0.199
	Invasion status	5.46	0.024
	Habitat × Invasion status	0	0.956

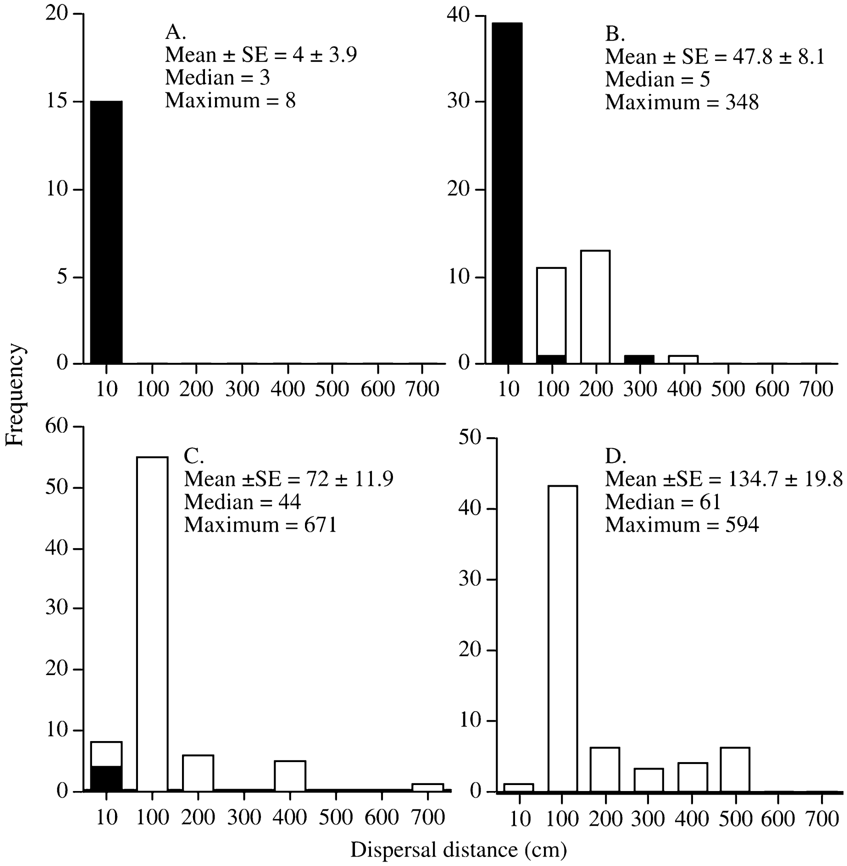

Fig. 1A–D Dispersal curves of *Sanguinaria canadensis*, an ant-dispersed plant, in sites that differ in ant community composition and habitat configuration (forest interior versus edge). **A** *Solenopsis invicta*-invaded forest interiors. **B** *S. invicta*-invaded forest edges. **C** Non-invaded forest interiors. **D** Non-invaded forest edges. Dispersal by native ants and *S. invicta* is shown in *white* and *shaded columns*, respectively. Dispersal <10 cm is insufficient to escape the maternal canopy of a typical *S. canadensis* plant

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; Quilichini and Debussche 2000), and (iv) subsequent dispersal by ants is unlikely after the elaiosomes have been consumed or removed from seeds (Gibson 1993; Garrido et al. 2002; Carney et al. 2003).

Both mean dispersal distance and the shape of the dispersal curve were influenced by the presence of invasive ants but not by forest edges, perhaps because the community composition of the seed-collecting ant guild differs as a result of the former but not the latter (Table 1). Is the difference in seed dispersal distance among invaded and uninvaded habitats significant to the plant? The mean radius of *S. canadensis* clones is approximately 10 cm (Pudlo et al. 1980), and the median dispersal distance fell short of this distance at invaded depots (Fig. 1). As a result, a majority of the germinating seedlings in invaded habitats would fail even to escape the maternal canopy, perhaps leading to intensified competition with that maternal plant. Although a 60 cm difference in dispersal distance among invaded and non-invaded habitats may seem rather minor (means =39.4 and 100.8 cm, respectively), even short dispersal distances can be significant to small myrmecochorous plants. For example, Kjellsson (1991) found that the life expectancy and fecundity of myrmecochorous seedlings within 50 cm of their parent plant was less than one-fifth those observed for seedlings dispersed 51–215 cm away from adult plants. Boyd (2001) reported that seedlings growing outside the parental plant's canopy edge were less likely to die from competition and herbivory than were those failing to escape the parental canopy. Other researchers have noted that *S. canadensis* plants are more aggregated at sites with short seed dispersal distances (Pudlo et al. 1980). Seed dispersal far beyond the parent canopy may accrue additional benefits if the recipient sites are suitable but unoccupied due to dispersal limitation (Ehrlen and Eriksson 2000). This benefit appears particularly important to ant-dispersed herbs, as many species, including *S. canadensis*, colonize new sites by establishing isolated individuals rather than by expanding along a wave front (Matlack 1994a; Brunet and Von Oheimb 1998). Long-distance seed dispersal events were rarer from invaded depots compared to non-invaded depots, and seeds in invaded sites are expected to colonize distant sites less frequently as a result.

Sanguinaria canadensis may suffer in invaded habitats because *S. invicta*, the most common seed collector, is a poorer disperser than most native ants found in the same forests. This study demonstrates that *S. invicta* disperses seeds shorter distances, and that these same seeds are frequently robbed of their elaisomes and unlikely to arrive at high-nutrient and/or well-defended sites such as ant 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 × 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 the extent that ants fail to disperse seeds across forest edges, the plants remain confined to the interiors of remnant forests. Second, seed collection should not be equated with successful dispersal. Field studies focusing on edge effects (Majer 1985; Jules and Rathcke 1999) or ant invasion (Quilichini and Debussche 2000; Christian 2001; Zettler et al. 2001; Carney et al. 2003) have used the act of seed collection as a surrogate measure of a functioning ant-plant mutualism. Here, seed collection rates in the four habitat × invasion groups were indistinguishable, but actual dispersal of those seeds differed markedly. Third, the detrimental effects of invasive ants on myrmecochorous plants are not limited to a well-studied ant species such as *L. humile,* or a single biome, such as the South African fynbos. The effect of *S. invicta* on the dispersal of temperate deciduous forest herbs demonstrated in this field study, combined with this ant's role as a seed predator demonstrated by the laboratory feeding trials by Zettler et al. (2001), suggest that invasive ants act to the detriment of ant-dispersed plants in two of the three world centers for myrmecochorous plant diversity.

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