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SHORT COMMUNICATION

Dispersal of *Schinus fasciculatus* seeds by the leaf-cutting ant *Acromyrmex striatus* in a shrubland of the dry Chaco, Argentina

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Ants are important agents of seed dispersal and they can play a fundamental role in the establishment and survival of plants (Beattie 1985). Leaf-cutting or fungus-growing ants (Myrmicinae: Attini) are dominant elements of the ant fauna throughout the neotropics. They collect different types of vegetative and reproductive plant material that serve as substrate for underground fungus gardens, which are the only food source for their larvae (Stradling 1991).

Recent field studies (Kaspari 1996, Leal & Oliveira 1998, Roberts & Heithaus 1986) have shown that leaf-cutting ants may remove significant quantities of seeds and fruits from the ground in neotropical forests. Therefore, they may have an important role as seed dispersers of higher plants. Moreover, through the removal of fleshy tissue of diaspores, they may also reduce fungal attack on ripe fruits that fall on the ground in neotropical forests, and therefore facilitate seed germination of vertebrate-dispersed seeds (Oliveira *et al.* 1995). On the other hand, abandoned nests of leaf-cutting ants may become important foci of plant recruitment, as has been mentioned for neotropical pastures (Jonkman 1978), savannas (Farji Brenner & Silva 1995, 1996) and rain forests (Garretson *et al.* 1998). In the Chaco dry forests of Argentina, leaf-cutting ants (*Acromyrmex* and *Atta*) are particularly abundant and one of their most important herbivores (Bucher 1982). Despite the fact that leaf-cutting ants are perhaps the most likely animals to interact with plant diaspores on the forest floor, they have been overlooked as frugivorous seed dispersers. Observational and experimental evidence are provided on the role of the leaf-cutting ant *Acromyrmex striatus* Roger (Fomicidae: Attini) as dispersal agent of *Schinus fasciculatus* Johnst. (Anacardiaceae), a fleshy-fruited shrub from the dry Chaco forest of Argentina.

Schinus fasciculatus is a pioneer shrub (1.5–3 m in height) common in disturbed areas of the Chaco. Ripe fruits of *S. fasciculatus* occur from late August to December, peaking in October–November, just at the time when other fruits are less abundant in the area. The fruit is a small (4–5 mm in diameter) spherical drupe, with one seed covered by a coriaceous endocarp. The exocarp is thin, chartaceous purple, shiny, and separated from the thin resinous mesocarp at maturity (Barkley 1944). The fruit characteristics (colour, size, persistence on the plant) suggest a bird-dispersal syndrome (*sensu* Howe 1986). Droppings of several bird species captured in the forests in Copo National Park (province of Santiago del Estero, Argentina) contained seeds of *S. fasciculatus* apparently intact (Cazziani 1996).

Acromyrmex striatus is a very common ant in the Chaco, particularly abundant in denuded areas of shrublands or disturbed forests. This ant species is active throughout September to May. It harvests leaves, flowers, fruits and seeds for fungus culture (Bucher & Montenegro 1974, Farji Brenner & Protomastro 1992). Refuse such as plant fibre, seeds, ant faeces, dead ants, debris and soil particles (from gallery excavation) are dumped on the soil surface nearby, covering an area of 0.4–1.0 m^2.

Field work was conducted in a private ranch 6 km from Frías city (28°38′S, 08′W; elevation 330 m), province of Santiago del Estero, Argentina. The local climate is semi-arid, strongly seasonal, with a cool/dry (April–October) and a warm/rainy (November–March) season. Mean annual temperature is about 22 °C. Mean annual rainfall is 600 mm (Bianchi & Yañez 1992). The local vegetation is the typical semi-arid Chaco forest, included in the

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Occidental District of the Chaco phytogeographic province (Cabrera 1994). The study site has been strongly disturbed by logging and livestock grazing, resulting in an open shrubland. *Schinus fasciculatus*, together with *Condalia microphylla* Cavan. (Rhamnaceae) and *Celtis pallida* Torrey (Ulmaceae), are the predominant shrub species.

The study was conducted from 1995 to 1999. The activity of 10 *A. striatus* colonies that were carrying fruits to their nests was recorded each year during the peak fruiting period of *S. fasciculatus* (September–November). The distance between 20 different fruiting shrubs and the ant refuse piles of ten different colonies was measured. Direct observations of seeds germinating in the ants' refuse dump provided qualitative evidence of the viability of seeds after being handled by the ants.

To compare the abundance of viable seeds in the soil of both the ant refuse-pile soil and the surrounding area (3–8 m from the refuse site), 10 soil samples from each type of soil were taken and the number of seedlings recruited in the samples was counted. Each sample consisted of 500 g of soil from 0–6 cm depth extracted with a soil auger. Samples were placed in plastic pots inside a well-lit room. They were watered regularly, and checked for seedling emergence every 3 d over 2 mo. Emerging seedlings were immediately removed to reduce competition on the remaining ungerminated seeds.

The number of young plants of *S. fasciculatus* established in (seven) ant refuse piles and (32) surrounding sites within a 0.80-m^2 quadrat was recorded. Only the plants < 60 cm in height were considered, assuming that they were younger than the ant colonies. The quadrat samples at surrounding sites were located under the crown of reproductive individuals of *S. fasciculatus*, *Condalia microphylla* and *Prosopis nigra* (Fabaceae), since the ant refuse piles were associated with the same species.

To investigate the effects of ant handling and refuse-site soil conditions on seed germination, two laboratory experiments were conducted under controlled conditions of temperature (32 °C). In the first test, germination percentage of seeds (n = 600) from 10 ant refuse piles (seeds completely clean of pulp) were compared with seeds from 10 different shrubs (manually extracted from their fruits) which germinated in ant refuse-pile soil as substrate. Previously, all the seeds of *S. fasciculatus* present in the refuse soil were removed with a sieve. In the second test, germination percentage of seeds (n = 600) taken from 10 ant refuse piles on both ant refuse-pile soil and soil of surrounding areas were compared. Seeds showing marks of attack by beetles were discarded. In each treatment 10 groups of 60 seeds were placed in separate plastic boxes (20 × 30 cm). Seeds were buried 3 mm into the substrate, watered regularly and checked for germination every 3 d until 2 wk after the last germinated seed was recorded (2 mo). Germination was defined as the emergence of any seedling part from the seeds. Data were analysed by non-parametric Mann–Whitney U test (Fowler *et al.* 2000) because of departures from normality.

Ants collected mostly fallen fruits from the soil around the plant, and rarely picked fruits from the plant. Ripe *S. fasciculatus* fruits were clearly preferred. Only occasionally ants collected green, immature fruits. On most occasions workers carried individual fruits. In a few cases we observed ants carrying short shoots supporting groups of 2–8 fruits. Ant workers took the whole fruit within the nest, where the fruit pulp attached to the seeds was removed. The inedible seed was abandoned unharmed (after 1–6 d) on the refuse pile, 1–3 m away from the nests. Mean distance of seed dispersal from the parent plant to the refuse pile was 6.5 m (SD = 6.3 m, range = 2–25 m, sample size = 20).

Acromyrmex striatus nest density in the study area fell in the range 8–15 nests ha^{-1}. Although the exact age of the ant colonies studied is unknown, there was certainty that they were at least 5 y old.

Seeds of *S. fasciculatus* in ant-refuse soils germinated in all trays (n = 10), indicating that they were viable. The average of germinated seeds per tray was 22.6 (SD = 4.9, range = 14–31), totalling 226 seeds in the 10 trays. No germination was recorded in soil samples (n = 10) taken from surrounding sites. At the end of the experiment the soil from the surrounding site was sieved and only six seeds were found, but their viability was not tested.

The seven ant refuse piles supported seedlings of *S. fasciculatus*. There was an average of 3.9 (SD = 2.8) seedlings per ant refuse pile (range = 1–8, total number = 27). Only 47% of the surrounding sites (n = 15) had seedlings. The average number of seedlings per surrounding site was 1.2 (SD = 1.7, range = 0–7, total number = 38). The number of seedlings in the ant refuse piles was significantly higher compared with the surrounding sites (U = 45.5, P < 0.01).

No statistically significant difference was found between the germination rate of seeds taken directly from fruits (42%) and those collected from the ant refuse piles (45%). However, the seeds planted in the surrounding-site soil showed a higher germination percentage (59%) when compared with those located in soil of ant refuse piles (U = 4, P < 0.01).

The field data obtained and the laboratory evidence show that *A. striatus* carries away undamaged seeds from the parental plant, suggesting that ants act as legitimate seed dispersers. Ants do not disperse seeds to a long distance, however, because they tend to forage from fruiting plants close to their nests. Shorter distances have been frequently reported for cases of ant dispersal (Andersen 1998, Horvitz & Beattie 1980, Hughes & Westoby 1992).

Although seed density in the surrounding soil was not measured, the data obtained on abundance of viable seeds and seedling density suggest that as a consequence of ant seed dispersal, the ant refuse piles accumulate a higher number of seeds than the surrounding areas. At least at a small spatial scale, ants could be responsible for altering the density of the soil seed bank, increasing its patchiness.

Studies on several neotropical ecosystems show that the nests of the leaf-cutting ants show improved soil physical and chemical conditions (increased fertility and water-retention capacity, reduced temperature variation) for plant growth (Alvarado *et al*. 1981, Farji Brenner & Silva 1995, E. H. Bucher, unpubl. data). Our field data indicate that ant refuse piles support more seedlings than surrounding sites, being therefore important recruitment foci for *S. fasciculatus*. Survival of seedlings in ant refuse piles is the remaining issue. Although various adult plants of *S. fasciculatus* were present in the ant refuse piles, it was not clear whether they were recruited before or after the establishment of ant colonies. Long-term studies would be necessary to answer these questions.

In extremely dry and warm habitats, water loss by soil transpiration is a common cause of stress and mortality of plants (Cook 1979). The highly degraded soils of the semi-arid Chaco (500–600 mm annual rainfall) are markedly limiting in organic matter (Abril & Bucher 1998), and consequently their moisture-retention capacity is reduced. It is thus conceivable that ant refuse piles may provide relatively long-term nutrient supplement and humidity, playing a key role in the establishment and probably in the survival of the seedlings of *S. fasciculatus*.

Escape from seed predation has been suggested as an important selective advantage of seed dispersal by ants (Beattie 1985). There are no quantitative data on predation of *S. fasciculatus* seeds by invertebrates, but it was observed that seeds of *S. fasciculatus* were intensely parasitized on the standing plant and appeared uninfected on the ant refuse pile. It is reasonable to suggest that in the ant refuse pile the seeds have low probability (vulnerability) to be detected by predators since they remain covered by debris deposited by the ants.

There are few reports on the effect of attine ants on seed germination (Dalling & Wirth 1998, Leal & Oliveira 1998, Oliveira *et al*. 1995). Increases in seed germination related to some plant species have been reported (Leal & Oliveira 1998, Oliveira *et al*. 1995). In other cases no positive effect has been founded (Leal & Oliveira 1998). On the other hand, Dalling & Wirth (1998) reported that germination of seeds handled by *Atta colombica* was significantly lower than control seeds (pulp removed). In this study, seeds of *S. fasciculatus* from ant refuse piles tend to germinate slightly faster than controls, but differences between treatments were not significant. This suggests that seed treatment by ants does not cause scarification on the seed coat.

Germination and plant growth may be enhanced by the characteristics of the ant-nest environment (Culver & Beattie 1978, Danin & Yom-Tov 1990). No information was found about the effect of ant refuse-pile soil on germination success. Nevertheless, the present results indicate that seeds of *S. fasciculatus* germinated more successfully in soils of surrounding sites than in ant refuse piles. It is possible that chemical substances in the refuse pile inhibited or delayed germination. An alternative explanation is that pathogens (such as bacteria, and mainly fungi) may have reduced the seed viability.

The interaction reported in this study is an example of non-specialized mutualism, as suggested by the following: (1) *S. fasciculatus* does not seem to be adapted for dispersal by ants. For instance, seeds lack an oil-rich food reward (often termed elaiosome) to attract ants, and plants do not have mature fruit exposure at ground level or ballistic discharge of seeds such as the true myrmecochorus plants (Beattie 1985); (2) leaf-cutting ants are opportunistic and generalized feeders (Bucher & Montenegro 1974, Farji Brenner & Protomastro 1992). Although the frugivorous birds of the Chaco (Cazziani 1986) are perhaps the main seed dispersers of *S. fasciculatus*, the present data suggest that in areas strongly denuded, the colonies of *A. striatus* could be playing at least a minor role in the dispersal and survival of this shrub.

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