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Seed re-dispersal of four myrmecochorous plants by a keystone ant in central China

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Abstract Seed re-dispersal following initial harvesting by ants may have important implications for the distribution and fate of myrmecochorous seeds. However, the probability of seed re-dispersed by ants and the effect it may have on subsequent survival appear variable, the functional role of diaspore, disperser and seed predator to the fate of discarded seeds remain unclear. To clarify the ecology, we compared the consequences of seed re-dispersal by a keystone seed-dispersing ant (*Myrmica ruginodis* Nylander) for four sympatric myrmecochorous plants common to the temperate deciduous forests in Qinling Mountains, central China. Plants varied in the probability of re-dispersal and in elaiosome condition. Ants preferred seeds with residual elaiosomes, while rodents only consumed the two larger-seeded species, regardless of the elaiosome presence. The scattered distribution of discarded seeds increased the probability of ant re-harvesting and, to some extent, reduced rodent predation. Thus, difference in the probability of seed re-dispersal and its subsequent effect on seed fate in relation to ants and rodents was attributed primarily to the elaiosome condition, seed size and seed spatial pattern. The results imply that seed re-dispersal could affect the fitness of plants and ultimately influence the plant abundance and distribution pattern. This highlights the necessity to incorporate re-dispersal into myrmecochory to advance

our understanding of the benefits of myrmecochory to plants.

Keywords Myrmecochory · Re-dispersal · Ant behavior · Seed survival · Rodents

Introduction

Myrmecochory (seed dispersal by ants) has been documented in over 11,000 plant species residing in at least 77 families (Lengyel et al. 2010). The seeds of such plants attract dispersers by offering lipid-rich elaiosome baits (Serrander 1906; Beattie 1985; Giladi 2006; Rico-Gray and Oliveira 2007). These plants are found in a wide range of ecosystems (Giladi 2006; Rico-Gray and Oliveira 2007; Lengyel et al. 2010) and are well represented in temperate forest communities, where they may constitute 30–50% of the understory (Handel et al. 1981; Gorb and Gorb 2003). These plants can benefit from interactions with ants in several ways, including directed dispersal, distance dispersal, fire avoidance and seed predator avoidance (Giladi 2006).

In the deciduous forests of central China, myrmecochory benefits appear restricted to dispersal distance, which limits seedling crowding and promotes avoidance of rodent seed predators (Heithaus 1981; Manzaneda et al. 2005; Giladi 2006). However, ant dispersers do not always bury seeds in the nest; rather, they may discard them in nest middens, or at sites some distance from nest entrances (Davidson and Morton 1981; Beattie 1985), creating spatial dispersion of seeds. This process, defined by the term “seed re-dispersal” is thought to represent an additional phase of myrmecochory (Gorb and Gorb 2003; Canner et al. 2012; Beaumont et al. 2013; Warren and Giladi 2014; Connell et al. 2016). While seeds re-dispersed from nests may further increase dispersal distances away from the parent plant and reduce sib competition (Canner et al. 2012), it may also re-expose seeds to predators like rodents and insects (Hughes and Westoby 1992; Lôbo et al. 2011; Tanaka et al. 2015). Furthermore, discarded seeds often have the elaiosome only partially removed (Servigne and

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Detrain 2010; Beaumont et al. 2013), as there is much interspecific variation in elaiosome location and tissue origin (Sernander 1906; Gorb and Gorb 2003). Thus, the likelihood of elaiosome removal by ants may be variable and may affect subsequent attraction to rodents.

The purpose of this study is to investigate the probability of seed re-dispersed by ants and the effect it may have on subsequent survival. We focus on four myrmecochorous plants common to the temperate deciduous forests of central China. Specifically, we address these questions: (1) does the proportion of seeds discarded differ among plant species? (2) Does elaiosome condition affect post-relocation fate? (3) Does re-dispersal pattern affect subsequent harvesting?

Materials and methods

Study site

The study was conducted in the Zibai Mountain National Forest Park (33°40'N, 106°49'E) on the south slope of the Qinling Mountains, Shaanxi Province, China. The Qinling range at the subtropical/warm-temperate transition (11.5°C mean annual temperature, 886.3 mm mean annual rainfall) and is dominated by Chinese filbert (*Corylus chinensis* Franch.), Wutai mountain oak (*Quercus wutaishanica* Mayr), Chinese cork oak (*Q. variabilis* Bl.) and a diverse understory. Three sites 600–900 m apart were selected, and one study plot (40 × 45 m) was established within each site. The study was undertaken during the natural seed dispersal period of the plants (May–July, 2016).

Study organisms

Within the understory assemblage were four plant species that are typically ant-dispersed: *Corydalis pseudoincisa* C. Y. Wu, *Luzula plumosa* E. Mey., *Epimedium pubescens* Maxim., and *Helleborus thibetanus* Franch. The seeds of these plant species differ significantly in size, weight and ESMR (elaiosome: seed mass ratio), with *L. plumosa* and *H. thibetanus* displaying the highest and lowest ESMR, respectively (Table S1; Fig. 1).

Previous observations showed that ants were the only organisms dispersing seeds at the study sites and that the red ant *Myrmica ruginodis* Nylander (Formicidae: Myrmicinae) dominated seed removal of these plants (Zhu et al. unpublished data). This ant is a well-known dispersal vector for many myrmecochorous plants, and it often subsequently discards seeds outside nests (Beattie 1983; Kjellsson 1985). According to our observations and interviews with local residents, at least nine rodent species are present in the study area (Table S2).

Effect of plant species

We installed plastic cylinders (10 cm diameter, 15 cm height) around the entrances of 28 nests at two study

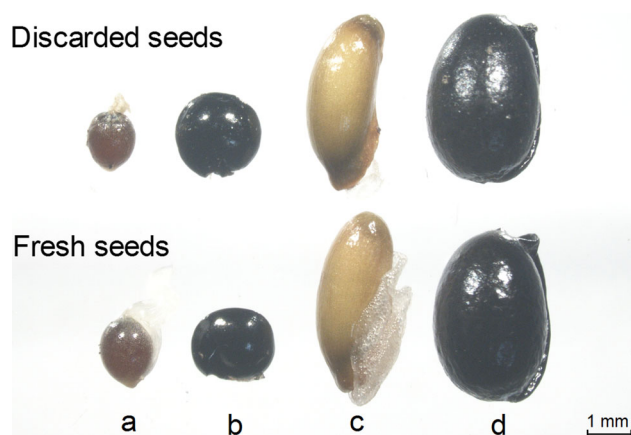


Fig. 1 Discarded and fresh seeds. **a** *Luzula plumosa*, **b** *Corydalis pseudoincisa*, **c** *Epimedium pubescens*, **d** *Helleborus thibetanus*

sites (inter-colony distance > 5 m) so that discarded seeds could be located. We placed fine sand around the base of each cylinder to prevent ants from tunneling out and applied Tangle-Trap gel to the inner and outer surfaces so that seeds were not available to other ants (see Beaumont et al. 2013). We supplied each colony with one house cricket [*Acheta domesticus* (L.)] once weekly. At each entrance, we placed ten seeds from a single species and observed until all seeds were taken into the nest. We checked for discarded seeds daily until all were accounted for or until none were discarded for three consecutive days. We scored the elaiosome condition of subsequently discarded seeds as: (1) *Intact*—elaiosome complete; (2) *Handled*—elaiosome partially removed; (3) *Detached*—elaiosome completely removed. Discarded seeds were refrigerated for several days prior to reuse in subsequent experiments. The experiment was replicated for each of the four species.

Effect of elaiosome condition

The three seed items above were used in the following experiments. Twelve 1-m² quadrats were randomly established (inter-quadrat distance > 5 m). Each quadrat included three seed depots 1 m apart. For each depot, ten seeds of one item were placed on a white card (5 × 5 cm). All experiments were conducted during peak foraging periods (0800–1100, 1400–1800 h; Zhu, pers. obs.). Observations lasted 1 h, at which point the number of seeds removed from each depot was recorded. The experiments were conducted for all plant species over non-consecutive sunny days with similar weather conditions for a total of 144 trials.

In addition, we assembled nine foraging platforms 10 m apart in a 3 × 3 grid at each of three sites. Each platform was randomly assigned to one of nine treatments [access (ant exclusion, rodent exclusion, full-access) × condition (fresh, handled, detached)]. (1) *Ant exclusion*—Tangle-Trap gel applied to surface rim of

platform; (2) *Rodent exclusion*—platform covered by 15-cm cubic wire cage with 1.5-cm mesh; (3) *Full-access*—seed platform unobstructed. Each trial was conducted with seeds of only one species at a time. Experiments were assembled by 0800 h; after 48 rain-free hours, the number of seeds remaining was recorded.

Effect of re-dispersal pattern

We used *E. pubescens* seeds to evaluate the effect of re-dispersal pattern on seed removal. We located another eight colonies and offered 30 seeds to each colony. For each trial, the distance and the seed position were recorded. Trials started before 0900 h and continued for 10 h. Finally, by using the exclusion methods described above, we placed 20 *E. pubescens* seeds on the ground in three patterns for 24 h: (1) in a mass; (2) evenly distributed in a 20 × 20 cm area; (3) evenly distributed in a 40 × 40 cm area. Ten replicates were conducted.

Statistical analyses

We examined the assumptions of normality for all data, whenever necessary, data were transformed prior to analysis. If the data was not normally distributed even after transformations, non-parametric analyses were used. The number of seeds discarded outside the nest was compared among plant species using one-way ANOVA tests followed by post hoc Duncan tests. The number of discarded seeds with and without elaiosome was compared by paired t-tests. The proportion of seeds removal (arcsine square-root transformed) among different seed conditions for each plant species in different treatments was also compared using one-way ANOVA/Duncan tests. Kruskal–Wallis test was used to examine the effects of scattering on seed removal by ants and rodents. SPSS v20 (IBM, Inc.) was used for all statistical analyses, and the significant difference was set at $P < 0.05$.

Results

Effect of plant species

The number of seeds discarded outside the nest differed among species ($F_{3, 111} = 110.19$, $P < 0.001$; Fig. 2), with the proportion of *C. pseudoincisa* seeds discarded being significantly greater than that of other species. Of these discarded seeds, more than 90% seeds were discarded for each plant species within the first day.

Effect of elaiosome condition

Among discarded seeds, *H. thibetanus* seeds were more likely to retain residual elaiosome tissue (64.0%;

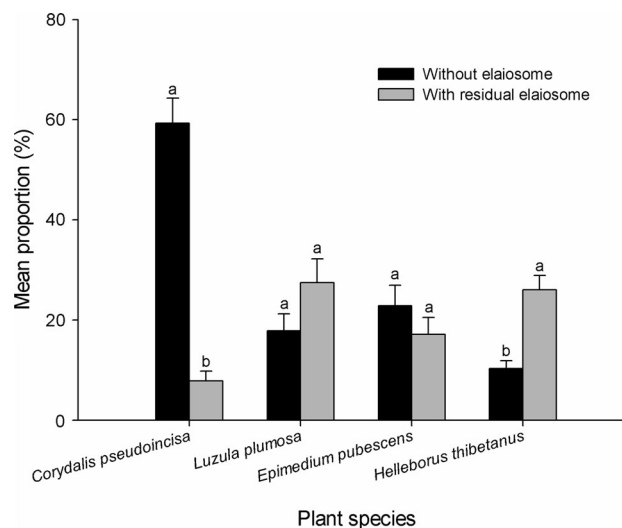


Fig. 2 Mean proportion of seeds (\pm SE) carried out of nests. Different Roman letters on each bar denotes significant differences between seeds with elaiosome detached and seeds with elaiosome partially remaining

$t = -5.37$, $df = 27$, $P < 0.01$; Fig. 2), while *C. pseudoincisa* elaiosomes were more likely to be completely removed (88.3%; $t = 9.82$, $df = 27$, $P < 0.01$; Fig. 2). The proportion of seeds with and without elaiosomes was similar for the remaining two species (Fig. 2).

M. ruginodis was responsible for the majority (64.1%) of dispersal events (Table 1). In rodent exclusion treatments, removal of seeds by ants varied significantly among seed conditions for all plant species (Table S3; Fig. 3). In the ant exclusion treatments, removal of seeds by rodents was not affected by seed condition (Table S3; Fig. 3). In the full access treatments, removal of seeds varied significantly among seed conditions for both *C. pseudoincisa* and *L. plumosa* (Table S3; Fig. 3).

Effect of re-dispersal pattern

Ninety-five *E. pubescens* seeds (39.58%) were carried out of the nests during the observation period. They were deposited 26.75 ± 2.00 cm from nest entrances (range 5–110 cm; Fig. 4). Mean discarded distances varied among colonies (range 15.21–39.61 cm; Fig. 5). Ants preferred scattered seeds to clumped ($df = 2$, $H = 7.50$, $P = 0.024$; Table 2), while rodents showed no significant pattern preference ($df = 2$, $H = 2.618$, $P = 0.27$; Table 2).

Discussion

Probability of seed re-dispersal by *Myrmica ruginodis*

We found that *M. ruginodis* frequently discarded plant seeds outside the nest. Previous studies have also re-

Table 1 Number of seed removal by ants with three seed condition

| | Number of removed seeds | | | | | | | | | | | |
|--------------------------|-------------------------------|----|---|-----------------------|----|----|----------------------------|----|----|------------------------------|---|---|
| | <i>Corydalis pseudoincisa</i> | | | <i>Luzula plumosa</i> | | | <i>Epimedium pubescens</i> | | | <i>Helleborus thibetanus</i> | | |
| | F | H | D | F | R | D | F | R | D | F | R | D |
| <i>Myrmica ruginodis</i> | 44 | 3 | 3 | 41 | 22 | 7 | 48 | 45 | 9 | 15 | 5 | 1 |
| <i>Paratrechina</i> sp1. | 21 | 4 | 1 | 8 | 7 | 4 | 20 | 7 | 2 | — | — | — |
| <i>Paratrechina</i> sp2. | 10 | 2 | — | 2 | 2 | — | 7 | 3 | — | — | 1 | — |
| <i>Tetramorium</i> sp. | 18 | 6 | — | 12 | 3 | — | 3 | — | 1 | — | 1 | — |
| <i>Temnothorax</i> sp. | 1 | — | — | — | — | — | — | 1 | — | — | — | — |
| Total | 94 | 15 | 4 | 63 | 34 | 11 | 78 | 56 | 12 | 15 | 7 | 1 |

F fresh seeds, H handled seeds, D detached seeds

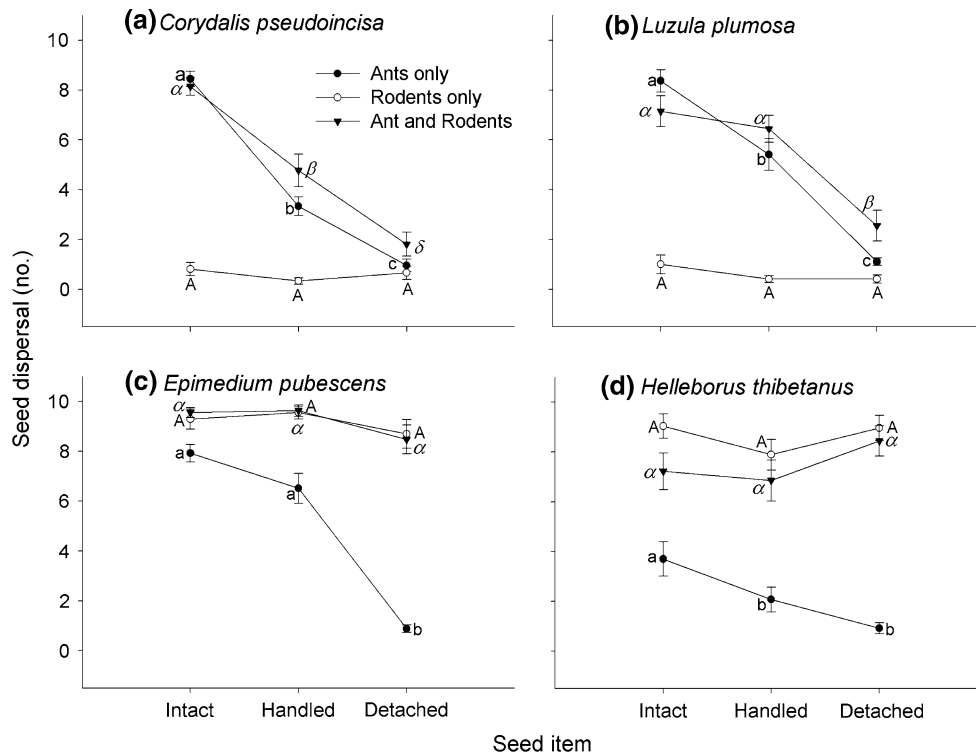


Fig. 3 Mean number of removed seeds (\pm SE) by ants and rodents with three seed condition. Different Roman lower letters, Roman capital letters and Greek letters denotes significant differences among seeds with different elaiosome conditions by ants only, rodents only and both, respectively

ported seed re-dispersal of other myrmecochorous plants in *Myrmica* spp. and found that the dynamic of re-dispersed seeds appears inconsistent (Beattie 1983; Kjellsson 1985; Prior et al. 2014). For example, Prior et al. (2014) stated that *M. rubra* relocated the majority of seeds within 24 h, while Kjellsson (1985) found that only 16% of *Carex pilulifera* seeds were carried out within 24 h. In our study, re-dispersal indeed mainly occurred within the first day, but the likelihood of re-dispersal varied among plant species. Re-dispersal frequency may vary with seed size (Gómez et al. 2005), as small seeds require less colony energy to transport. We

found that *M. ruginodis* can quickly grasp and move seeds of both *C. pseudoincisa* and *L. plumosa*, both of which have small seeds. The longer retention of *L. plumosa* seeds may be due to the difficulty in removing the elaiosome which is attached tightly to seed. In short, re-dispersal by ants, for whatever ultimate reason, can facilitate seed deposition outside nests, and seed characteristics affect this process.

We found that elaiosomes were not always totally consumed by ants while in the nest, and there was difference in elaiosome condition of discarded seeds among plant species. Except for *C. pseudoincisa*, other species

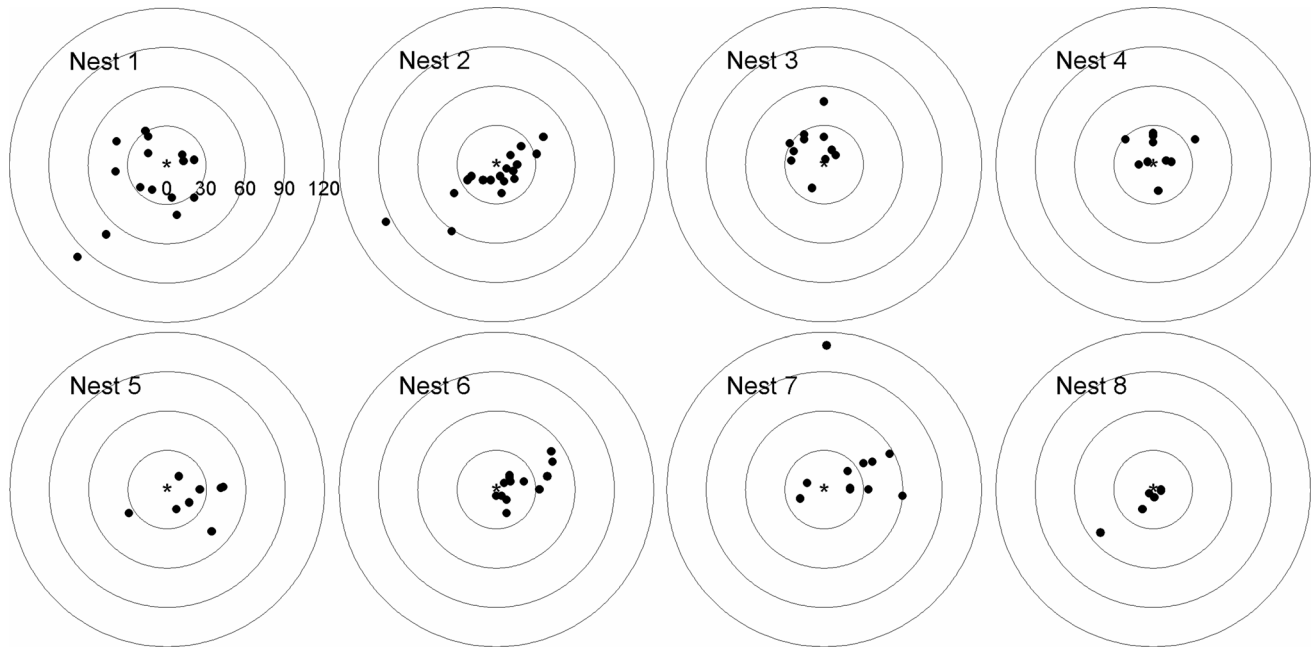


Fig. 4 Location and distance (cm) of individual seeds of *Epimedii pubescens* (dark circles) found in relation to eight nests (asterisk)

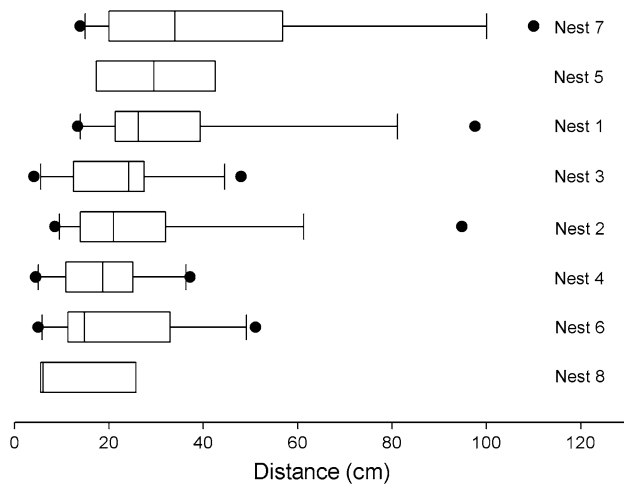


Fig. 5 Box-plots for individual nest re-dispersal distances

frequently had residual elaiosome tissue attached to discarded seeds. The ability to completely utilize the elaiosome probably depends on a variety of factors (Servigne and Detrain 2008, 2010), including elaiosome toughness (Beaumont et al. 2013) and nutrient distribution (Bresinsky 1963). Moreover, the tightness of elaiosome-seed connection is expected to be associated with the primary mode of seed dispersal. The elaiosome was often easily removed for species that released their

seeds ballistically than species in which seeds released by gravity (Nakanishi 1994). Of the four study species, only *C. pseudoincisa* primarily releases their seeds ballistically, and we found that their elaiosomes were likely to be completely removed. This suggested that the magnitude of elaiosome-seed connection may also be a possible factor influencing the utilization of elaiosome.

Kjellsson (1985) reported that the discarded distances of *C. pilulifera* seeds by *M. ruginodis* were between 0 and 140 cm. In this study, *M. ruginodis* discarded the seeds over distances of 5–110 cm with an average of 26.75 cm. However, some studies reported different discarded distances by other ant species. For example, *Formica cinerea* often deposited seeds near nest entrances (Gorb and Gorb 2000), *Aphaenogaster rudis* discarded *Asarum canadense* seeds about 51.5 cm from the nests (Canner et al. 2012) and *Iridomyrmex viridiaeneus* discarded *Acacia ligulata* seeds up to 250 cm from the nests (Whitney 2002). This suggested that the discarded distance of seeds appears to be dependent on ant species.

The influence of the elaiosome condition, seed size and seed spatial pattern in relation to ants and rodents on seed fate

Many studies have shown that seed size and/or elaiosome presence influences seed selection in rodents (Smith

Table 2 Mean number of removed *Epimedii pubescens* seeds (\pm SE) by ants and rodents within different seed patterns

| | In a mass | Within 20 \times 20 cm | Within 40 \times 40 cm |
|---------|------------------------|--------------------------|--------------------------|
| Ants | 17.0 \pm 1.2 (85.0%) | 19.5 \pm 0.3 (97.5%) | 19.4 \pm 0.3 (97%) |
| Rodents | 18.0 \pm 2.0 (90.0%) | 17.1 \pm 1.5 (85.5%) | 15.7 \pm 1.4 (78.5%) |

et al. 1989; Auld and Denham 1999; Ferreira et al. 2011). In general, bigger seeds increase profitability by offering greater energy per unit handling time (Herrera et al. 1994), and prior removal of the elaiosome can alter this balance (Heithaus 1981; Auld and Denham 1999). In this study, only the two large-seeded species (*E. pubescens* and *H. tibetanus*) suffered heavy rodent predation, and this was unaffected by elaiosome presence. Hanzawa et al. (1985) found that *Corydalis aurea* elaiosomes were actually avoided by rodents. Thus, there appears to be considerable variation in the response of rodents to seeds.

Seed distribution likely influences retrieval (Ohkawara and Higashi 1994; Gorb and Gorb 2000; Giladi 2006). Re-dispersal of seeds by ants generates a subsequent spatial pattern with different implications (Davidson and Morton 1981; Lôbo et al. 2011; Canner et al. 2012). In this study, *M. ruginodis* discarded seeds in a scattered pattern, increasing the probability of ant re-harvesting and, reducing the probability of rodent predation. Thus, relocation behavior may facilitate the success of seed dispersal.

Potential benefits of seed re-dispersal for myrmecochorous plants

Natural fires are rare in our study area (Cochrane 2003), and Giladi's (2006) meta-analysis showed that the directed dispersal hypothesis was rarely supported in temperate forests. Therefore, we are left to consider the contributions of predator avoidance and distance dispersal to the ecological significance of myrmecochory in our system. The predator avoidance hypothesis argues that rapid removal and burial of seeds can reduce encounters (Heithaus 1981; Manzaneda et al. 2005; Giladi 2006). This means that any re-dispersed seeds are exposed to predation risk again. Indeed, our findings showed that rodent predation on discarded seeds were present, while the scattered pattern reduced the probability of discovery.

The distance dispersal hypothesis proposes that seed dispersal can reduce parent-offspring conflict and sib competition (Andersen 1988; Giladi 2006). Although ant dispersal may move seeds a seemingly short distance, it is sufficient to remove seeds from beneath the parent canopy (Giladi 2006). In the process of seed re-dispersal, ants may further increase the dispersal distance from the parent plants (Gorb and Gorb 2003; Bas et al. 2009; Canner et al. 2012) and decrease seed density in and around nests (Giladi 2004).

In conclusion, re-dispersal of seeds out of nests by ants has been increasingly recognized, yet factors influencing the ecology of re-dispersal are relatively little addressed. The results of this study highlight the elaiosome condition, seed size and seed spatial pattern and their interaction with ants and rodents are major determinants of the fate of discarded seed and that have

more general implications for the plant abundance and distribution pattern.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

Statement of human and animal right All applicable international and/or national guidelines for the care and use of animals were followed.

References

- Andersen AN (1988) Nest mound soil of the seed dispersing ant *Aphaenogaster longiceps* enhances seedling growth. *Aust J Ecol* 13:469–471. doi:10.1111/j.1442-9993.1988.tb00995.x
- Auld TD, Denham AJ (1999) The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecol* 144:201–213. doi:10.1023/A:1009817132378
- Bas JM, Oliveras J, Gómez C (2009) Myrmecochory and short-term seed fate in *Rhamnus alaternus*: ant species and seed characteristics. *Acta Oecol* 35:380–384. doi:10.1016/j.actao.2009.02.003
- Beattie AJ (1983) Distribution of ant-dispersed plants. In: Kubitzki K (ed) *Dispersal and distribution*. Parey, Hamburg, pp 249–267
- Beattie AJ (1985) *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, Cambridge
- Beaumont KP, Mackay DA, Whalen MA (2013) Multiphase myrmecochory: the roles of different ant species and effects of fire. *Oecologia* 172:791–803. doi:10.1007/s00442-012-2534-2
- Bresinsky A (1963) Bau, entwicklungsgeschichte und inhaltsstoffeder elaiosomen. *Bibl Bot* 126:1–54
- Canner JE, Dunn RR, Giladi I, Gross K (2012) Redispersal of seeds by a keystone ant augments the spread of common wildflowers. *Acta Oecol* 40:31–39. doi:10.1016/j.actao.2012.02.004
- Cochrane MA (2003) Fire science for rainforests. *Nature* 421:913–919. doi:10.1038/nature01437
- Connell RK, Pfennigwerth AA, Classen AT, Kwit C (2016) Incorporating redispersal microsites into myrmecochory in eastern North American forests. *Ecosphere* 7:e01456. doi:10.1002/ecs2.1456
- Davidson DW, Morton SR (1981) Myrmecochory in some plants (*F. chenopodiaceae*) of the Australian arid zone. *Oecologia* 50:357–366. doi:10.1007/BF00344976
- Ferreira AV, Bruna EM, Vasconcelos HL (2011) Seed predators limit plant recruitment in Neotropical savannas. *Oikos* 120:1013–1022. doi:10.1111/j.1600-0706.2010.19052.x
- Giladi I (2004) *The role of habitat-specific demography, habitat-specific dispersal, and the evolution of dispersal distances in determining current and future distributions of the ant dispersed forest herb, Hexastylis arifolia*. Dissertation, University of Georgia
- Giladi I (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112:481–492. doi:10.1111/j.0030-1299.2006.14258.x

- Gómez C, Espadaler X, Bas JM (2005) Ant behaviour and seed morphology: a missing link of myrmecochory. *Oecologia* 146:244–246. doi:[10.1007/s00442-005-0200-7](https://doi.org/10.1007/s00442-005-0200-7)
- Gorb E, Gorb S (2000) Effects of seed aggregation on the removal rates of elaiosome-bearing *Chelidonium majus* and *Viola odourata* seeds carried by *Formica polyctena* ants. *Ecol Res* 15:187–192. doi:[10.1046/j.1440-1703.2000.00338.x](https://doi.org/10.1046/j.1440-1703.2000.00338.x)
- Gorb E, Gorb S (2003) Seed dispersal by ants in a deciduous forest ecosystem. Kluwer, Dordrecht
- Handel SN, Fisch SB, Schatz GE (1981) Ants disperse a majority of herbs in a mesic forest community in New York State. *Bull Torrey Bot Club* 108:430–437. doi:[10.2307/2484443](https://doi.org/10.2307/2484443)
- Hanzawa FM, Beattie AJ, Holmes A (1985) Dual function of the elaiosome of *Corydalis aurea* (Fumariaceae): attraction of dispersal agents and repulsion of *Peromyscus maniculatus*, a seed predator. *Am J Bot* 72:1707–1711. doi:[10.2307/2443727](https://doi.org/10.2307/2443727)
- Heithaus ER (1981) Seed predation by rodents on three ant-dispersed plants. *Ecology* 62:136–145. doi:[10.2307/1936677](https://doi.org/10.2307/1936677)
- Herrera CM, Jordano P, Lopez-Soria L, Amat JA (1994) Recruitment of a mast-fruited, bird-dispersed tree: birding frugivore activity and seedling establishment. *Ecol Monogr* 64:315–344. doi:[10.2307/2937165](https://doi.org/10.2307/2937165)
- Hughes L, Westoby M (1992) Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. *Ecology* 73:1300–1312. doi:[10.2307/1940677](https://doi.org/10.2307/1940677)
- Kjellsson G (1985) Seed fate in a population of *Carex pilulifera* L. I. Seed dispersal and ant-seed mutualism. *Oecologia* 67:416–423. doi:[10.1007/BF00384949](https://doi.org/10.1007/BF00384949)
- Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR (2010) Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. *Perspect Plant Ecol* 12:43–55. doi:[10.1016/j.ppees.2009.08.001](https://doi.org/10.1016/j.ppees.2009.08.001)
- Lôbo D, Tabarelli M, Leal IR (2011) Relocation of *Croton sonderianus* (Euphorbiaceae) seeds by *Pheidole fallax* Mayr (Formicidae): a case of post-dispersal seed protection by ants? *Neotrop Entomol* 40:440–444. doi:[10.1590/S1519-566X2011000400005](https://doi.org/10.1590/S1519-566X2011000400005)
- Manzaneda AJ, Fedriani JM, Rey PJ (2005) Adaptive advantages of myrmecochory: the predator avoidance-hypothesis tested over a wide geographic range. *Ecography* 28:583–592. doi:[10.1111/j.2005.0906-7590.04309.x](https://doi.org/10.1111/j.2005.0906-7590.04309.x)
- Nakanishi H (1994) Myrmecochorous adaptations of *Corydalis* species (Papaveraceae) in southern Japan. *Ecol Res* 9:1–8. doi:[10.1007/BF02347236](https://doi.org/10.1007/BF02347236)
- Ohkawara K, Higashi S (1994) Relative importance of ballistic and ant dispersal in two diplochorous *Viola* species (Violaceae). *Oecologia* 100:135–140. doi:[10.1007/BF00317140](https://doi.org/10.1007/BF00317140)
- Prior KM, Saxena K, Frederickson ME (2014) Seed handling behaviours of native and invasive seed-dispersing ants differentially influence seedling emergence in an introduced plant. *Ecol Entomol* 39:66–74. doi:[10.1111/een.12068](https://doi.org/10.1111/een.12068)
- Rico-Gray V, Oliveira PS (2007) The ecology and evolution of ant-plant interactions. University of Chicago Press, Chicago
- Sernander R (1906) Entwurf einer Monographie der europäischen Myrmekochoren. *K Sven Vetensk Akad Handl* 41:1–407
- Servigne P, Detrain C (2008) Ant-seed interactions: combined effects of ant and plant species on seed removal patterns. *Insect Soc* 55:220–230. doi:[10.1007/s00040-008-0991-8](https://doi.org/10.1007/s00040-008-0991-8)
- Servigne P, Detrain C (2010) Opening myrmecochory's black box: what happens inside the ant nest? *Ecol Res* 25:663–672. doi:[10.1007/s11284-010-0700-8](https://doi.org/10.1007/s11284-010-0700-8)
- Smith BH, Forman PD, Boyd AE (1989) Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. *Ecology* 70:1649–1656. doi:[10.2307/1938099](https://doi.org/10.2307/1938099)
- Tanaka K, Ogata K, Mukai H, Yamawo A, Tokuda M (2015) Adaptive advantage of myrmecochory in the ant-dispersed herb *Lamium amplexicaule* (Lamiaceae): predation avoidance through the deterrence of post-dispersal seed predators. *PLoS ONE* 10:e0133677. doi:[10.1371/journal.pone.0133677](https://doi.org/10.1371/journal.pone.0133677)
- Warren RJ, Giladi I (2014) Ant-mediated seed dispersal: a few ant species (Hymenoptera: Formicidae) benefit many plants. *Myrmecol News* 20:129–140
- Whitney KD (2002) Dispersal for distance? *Acacia ligulata* seeds and meat ants *Iridomyrmex viridiaeneus*. *Austral Ecol* 27:589–595. doi:[10.1046/j.1442-9993.2002.01216.x](https://doi.org/10.1046/j.1442-9993.2002.01216.x)