Seed fate and distribution of ant-dispersed plant species in Australia

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Certificate

The work described in this thesis is original and has not been submitted, in any form for a higher degree at any other university or institution.

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Abstract

Plant species adapted for ant dispersal occur in many different types of habitats, but are most common in sclerophyll vegetation (which occurs on infertile soils) in Australia and South Africa. The investigations presented in this thesis were centred around the potential selective forces imposed by ant behaviour on seeds adapted for ant dispersal in sclerophyll vegetation around Sydney, Australia. Two complementary questions were posed: 1) How does variation in behaviour between ant species affect the fate of elaiosome-bearing seeds? and 2) Can differences in the behaviour of ant species on infertile compared to fertile soils provide an explanation for the fact that plant species adapted for ant dispersal are much more common on infertile than fertile soils, in Australia?

Ant behaviour may affect the fate of seeds in a number of different ways including predation, dispersal distance and burial depth. Some of the ways in which a plant may respond over evolutionary time to ant predation and the chance of burial were assessed. The factors examined were seed release by the plant (specifically the quantity and duration of seed release), the composition of the ant diet (in terms of the ratio of insects to seeds) and the presence of larvae within the ant colony. The rationale behind these two last factors were that they both vary seasonally, therefore, a plant has the evolutionary potential to adjust its seed release to periods when seed predation is less likely to occur.

Seed predation assays were performed on laboratory colonies of *Rhytidoponera metallica,* which were kept in artificial nests. *R. metallica* is a common seed-removing species in sclerophyll vegetation. These nests enabled both the number of seeds eaten and the number of seeds remaining buried within the nest to be unambiguously determined. To examine how seed quantity may affect both the chance of seed predation and seed burial, four species were used, namely *Bauera rubioides, Boronia pinnata, Dillwynia juniperina and Poranthera ericifolia.* The quantity of seeds which entered the nest did not affect either the level of seed predation or the incidence of seed burial for *B. pinnata, D. juniperina and P. ericifolia,* however, for *B. rubioides* the number of seeds eaten increased with the quantity of seeds. Variation in the duration over which seeds entered the nest was assessed for *D. juniperina and P. ericifolia,* and was found to have no effect on the level of either seed predation or seed burial.

The effect of dietary composition for *R. metallica*, was investigated by varying the ratio of insects:seeds in the diet and was found to have no effect on the level of either seed predation or seed burial. Similarly, the presence/absence of larvae in the colony did not affect the level of seed predation or the chance of seed burial.

A common view (Morton 1985, Andersen 1988, Davidson and Morton 1988, Hughes and Westoby 1992a and b) has been that seed predation by ants may be an important selective force in Australia. The results from the set of experiments described above were contrary to this view and so an explanation was sought. The mechanical properties of a range of species adapted for ant dispersal were assessed in terms of defence strategies against seed predators. Seed strength was measured using two techniques, a Universal Force Tester and pressure applied with forceps. Most species tested produce relatively strong seeds, though a significant minority had relatively soft seeds. Laboratory seed predation assays revealed that the strength of the seed appeared to be related to the level of seed predation in that strong seeds were rarely eaten by *R. metallica* and *Pheidole* sp. 4. In contrast, species with relatively soft seeds experienced much higher levels of seed predation, up to 100%.

In Australia plant species which are adapted for ant dispersal are common in vegetation which occurs on infertile soils and relatively rare in vegetation which occurs on more fertile soils. In an attempt to explain this pattern the seed-removing ant assemblages on the two soil types were assessed in terms of their behaviour towards elaiosome-bearing seeds. Observations of seed removals indicated that there was a greater diversity of seed-removing ant species on infertile (22 spp.) than on fertile soils (11 spp.). On fertile soils one species, *Pheidole* sp. 4, was responsible for most removals, whilst on infertile soils several species were important seed removers (*Anonychomyrma "biconvexa"*, *Pheidole* sp. 4, *Rhytidoponera metallica* and *R. victoriae*).

The hypothesis that these differences in the ant assemblages result in a higher probability of seed predation for species adapted for ant dispersal on infertile compared to fertile soils was tested. Seed predation assays were performed on the major seed-removing species on infertile and fertile soils, both in the field and in the laboratory. The results of these assays indicated that there was not a clear difference in predation pressure between the two soil types, thus this hypothesis was tentatively rejected.

Another hypothesis was tested, which stated that the different seed-removing ant assemblages result in greater dispersal distances for elaiosome-bearing seeds on infertile compared to fertile soils. Measurements of dispersal distances, obtained through observations of seed removals, indicated that elaiosome-bearing seeds were likely to travel, on average, five times further on infertile than on fertile soils. The mean (± s.d.) dispersal distance on infertile soils was 1.29 m (± 1.28 m) compared to 0.27 m (± 0.17m) on fertile soils. The mean (± s.d.) canopy diameter of a range of species adapted for ant dispersal was 0.65 m (± 0.65 m), therefore, the average dispersal distance achieved on fertile soils would not be sufficient to disperse a seed a minimum of one canopy diameter, whereas the dispersal distances on infertile soils would achieve this.

In light of the findings from this study, each of the proposed benefits for seeds adapted for ant dispersal is reviewed, as well as the factors influencing the distribution of ant-dispersed species, both in Australia and worldwide. The proposed benefits of dispersal by ants include placement of seeds in nutrient-enriched microsites, escape from predators, competitors or fire, and dispersal for distance. The conclusion from this review was that there is not a single universal benefit conveyed to seeds adapted for ant dispersal, but rather, the importance of each of these benefits depends on the habitat under consideration.

Several hypotheses, which attempt to explain the distribution of species adapted for ant dispersal, on infertile and fertile soils in Australia, have been tested and the evidence for each is assessed. These hypotheses deal with differences between infertile and fertile soils and involve nutrient-enriched microsites, cost of elaiosomes versus fruit, removal rates of vertebrate and ant-dispersed seeds, seed predation by small mammals and ants, seed sizes, growth forms and dispersal distances. The available evidence indicates that most of these explanations are unlikely to be adequate, except those dealing with differences in growth forms and dispersal distances between infertile and fertile soils.

Finally, a set of hypotheses is formulated, based on plant, ant and habitat traits, which when considered together, highlight possible factors affecting the worldwide distribution of species adapted for ant dispersal. The purpose of this set of hypotheses is to provide a framework for future experimental and comparative studies.

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