

Seed dispersal mutualisms with ants and patterns of plant diversity in Western Australia.

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ABSTRACT

Ant dispersal is among the most common seed dispersal modes in Western Australia. We examine the history of Western Australia and in turn the potential causes of the preponderance of ant dispersal. We then consider the potential evolutionary and ecological consequences of the evolution of ant dispersal in Western Australia, focusing on the potential role of ants in maintaining or engendering patterns of Western Australian plant diversity.

The Western Australian environment

Two hundred million year ago, the major landmasses of the world formed a contiguous supercontinent known as Pangaea. Following the mid-Jurassic, Pangaea split into northern and southern blocks, known as Laurasia and Gondwana respectively. The latter linked Australia, Africa, India and South America, through direct connection, and also via Antarctica. This north-south split resulted in separate evolutionary pathways in the world's modern biota (e.g., Hopper *et al.* 1996). Australia continued to be part of Gondwana until the Cenozoic, during which its links with Antarctica were finally broken; it became a true island approximately 30 million years ago. As well as having been isolated from the rest of the world for a long time, Western Australia contains the oldest known fragments of the Earth's crust (4,300 million years old) and is dominated by two large blocks, the Pilbara Block to the north, and the Yilgarn Block in the southwest. These areas have remained

unglaciated and above sea level for 200 million years, providing unique opportunities for persistence of relictual taxa and, in the case of certain lineages, considerable speciation.

Other characteristics to note are the low nutrient levels of many Western Australian soils, a consequence of leaching that has occurred over millions of years. Lack of glaciation, erosion and the nature of the tectonic activity have also produced a subdued landscape, with few mountainous regions. Further, rainfall is high and centred around winter (Mediterranean climate) in the southwest tip of the State, progressively dropping off to a dry Desert climate in a north-easterly direction. Conversely, rainfall is extremely high and centred around summer in the far north (Dry, hot, tropical climate), but it also declines in a southerly direction towards the desert regions. All of the preceding characteristics, plus the more recent arrival of organisms from the Indo-Malay region to the north, have led to existence of three major Botanical Provinces (Fig. 1), the South-West Province with its heavily Gondwanan-derived biota, the Northern Province with its tropical-derived biota, and the central Eremaean Province whose biota has evolved to cope with the arid conditions of much of central Australia. Finally, as a result of the sclerophyllous nature of the vegetation in the south, the extensive grasslands in the north, and the generally dry climate, the entire region is extremely vulnerable to fire. The frequency and intensity of these fires is such that they have played a key, and maybe even primary, role in the evolution of the Australian biota (Gill 1975).

Within the South-West Province, the Northern sandplains and those around Esperance (see Fig. 1) support a massive diversity of plant species and higher taxa. These areas consist of undulating dunes, rarely more than 5 m tall, which support a species-rich heathland vegetation (Fig. 2). Despite only contributing to 10 % of the area of this Province, this vegetation represents over 4,000 (roughly 50 %) of the Province's plant species (Lamont 2005). Plant families which reach their peak richness in sandplain country include the woody Myrtaceae, especially *Melaleuca*, the Proteaceae, especially *Grevillea*, *Banksia*, and *Hakea*, the legumes, especially *Daviesia* and *Acacia*, and the Ericaceae, especially *Leucopogon* (Lamont *et al.* 1984). This exceptional species richness is also reflected at the fine scale; at one site on the Northern Sandplain, Griffin *et al.* (1990) found that quadrats in the same vegetation type exhibit a 40 % reduction in plant species similarity over a distance of 0.5 km.

The vegetation (and perhaps fauna) of the South-West Province is so diverse that it is considered to be one of the World's biodiversity hotspots (Myers *et al.* 2000).

The Western Australian ant fauna

The flora of Western Australia is diverse, even in comparison to tropical floras. In contrast, the ant fauna is phylogenetically unique (with several very basal ant taxa), but not exceptionally diverse. A study of the ants of south western Australia (B.E. Heterick pers. comm.) has yielded 475 species of ants and is considered unlikely to produce many additional species. For comparison, Longino and Colwell (1997) estimate that nearly 500 species of ants will be collected from one site, La Selva Biological Station, in the Costa Rican rain forest and Wilson (1987) collected 43 species of ants from a single species of tree in Peru. Comparisons between La Selva Biological Station (a mere 500 hectares) and south western Australia are similar at higher taxonomic levels. For example, 13 of 21 extant ant subfamilies are represented on the continent, and most of them occur in Western Australia (Shattuck 1999), whereas 14 subfamilies can be found at La Selva Biological Station (J. Longino, <http://www.evergreen.edu/ants/Genera.html>, Longino and Colwell 1997). The similarity in ant species and subfamily diversity between La Selva Biological Station and south western Australia is very different to the matching comparisons for plants. For example, the flora of La Selva Biological Station contains 145 families of plants and 1936 species of plants (<http://www.ots.ac.cr/local/forula>, Version August, 2005). South western Australia contains, in contrast, approximately 7380 plant species (Hopper and Gioia 2004), more than three times the number found at La Selva Biological Station. Thus, at least by one of the simple measures considered above, south western Australia does not stand out as a biodiversity hot spot for ants (and perhaps for other insect taxa) nearly to the extent that it does for plants.

Within Western Australia, patterns in the composition and diversity of ant species remain poorly resolved. The diversity of canopy ants decreases as one goes from the tropical fauna in the north to the more Gondwanan fauna further south (Majer *et al.* 2001). Similar patterns may exist at the generic level for the terrestrial fauna (Shattuck 1999). The latitudinal gradient in ant species richness is relatively weak and even as far south as Eneabba, in the sand plains of the south west one can

find almost 100 species (Bisevac and Majer 1999). Overall, the decline in generic richness as one passes south may be offset by an increase in species per genus at the southern latitudes, such that in contrast to other continents ant diversity is reasonably high (50-100 species per hectare) across large geographic areas.

Ant-seed interactions in Australia

In most regions, many plant species depend on animals for transport of their seeds. Though we know of no global survey of the predominance of different dispersal modes, dispersal of seeds by vertebrates (mostly bats, birds, small and large mammals) is undoubtedly the most common form of zoochory (dispersal by animals). However, in a few regions of the world, for reasons that remain unclear, plant species and lineages have evolved seed morphologies that encourage dispersal of their diaspores (dispersal unit) by ants. Based on a global database on myrmecochory that we have compiled, we find that myrmecochory occurs in four main bioregions or habitats: temperate forest understories, tropical forest canopies and the Mediterranean vegetation of the Fynbos of South Africa and south western Australia. In the monocots, for example, ant dispersal has evolved no fewer than 17 times. Of those events, seven represent lineages found predominately in temperate forest understories (e.g., *Trillium* spp.), two represent lineages from tropical forest canopies (e.g., *Globba* spp.), and two represent lineages from tropical forest understories (e.g., *Calathea* spp.) No fewer than five, and more likely 18, events (the indeterminacy due to lack of phylogenetic data for many of the endemic Australian plant genera) represent the evolution of ant dispersal in Mediterranean habitats, including primarily the South African Fynbos and south western Australia (R.R. Dunn *et al.* in prep.). Ant dispersal is much more common, at least in terms of numbers of lineages, in the dicots than in the monocots, such that the total number of independent origins of elaiosomes is likely to be in the order of 80 (R.R. Dunn *et al.* in prep.).

In terms of a variety of measures, Australia appears to contribute disproportionately to the global numbers of ant dispersed plant lineages. The frequency with which ant-dispersal has evolved in those lineages found in Australia can also be seen by simply examining the list of plant families in which ant-dispersal occurs in Australia (Table 1). Ant dispersal is found in no fewer than 37 plant families and 134 genera in Australia (Table 1) and has evolved multiple times in

several of those families (e.g. Proteaceae). This represents 5 % of all plant genera in Australia and 14 % of all families. Further, given that roughly 80 plant families worldwide include species dispersed by ants (Beattie 1985), Australia contains almost half of all those families with ant dispersed species! Preliminary analyses indicate that in most plant families, in Australia and elsewhere, elaiosomes evolved relatively recently (last 40 million years). Fabaceae could be an interesting exception to this general pattern in that at least some phylogenetic reconstructions suggest that ant dispersal could be the ancestral trait for much older clades.

In Australia, vertebrates can and do disperse seeds. For example, we have documented dispersal of many species of plants by emus in Western Australia (Cancela *et al.*, in review). However, the most common form of zoochory, is dispersal by ants, as evinced both in regional surveys (Berg 1975, our unpublished data) and local studies (Jurado *et al.* 1991). For example, Lamont and co-workers sampled four plots each containing 10000 plants in each of four plant communities in the Eneabba Plains in Western Australia. Their plots revealed only 5% of species adapted for endozoochorous dispersal, but 36% of species had adaptations for dispersal by ants (Cancela *et al.* in review, B. B. Lamont *et al.* unpublished).

The removal of seeds, or diaspores, by ants conforms to three categories: *nest decoration* - removal and incorporation of the diaspore into the nest structure (Majer 1982); *granivory* - removal of the diaspore and subsequent consumption of the embryo; and *myrmecochory* - dispersal of the diaspore while leaving the embryo intact. Granivory is detrimental, nest decoration is not widespread, but myrmecochory is particularly prevalent in Australia. In this last category, seeds possess an elaiosome, often an oil- or fat-bearing body, which is attractive to ants (Fig. 3a). After the diaspore is transported (Fig.3b), the ants eat the elaiosome and discard the seed (Fig. 3c). The resulting seedlings often grow in a concentrated patch on, or around ant nests (Fig, 3d). This may benefit the seed by a) dispersing it (Andersen 1988a, Whitney 2002), b) isolating it from seed predators (O'Dowd and Gill 1986, Auld and Denham 1999, Christian 2001, Manzaneda *et al.* 2005), c) enhancing longevity via seed storage (Slingsby and Bond 1981), d) protecting it from wildfires while exposing it to germination-inducing temperatures (Auld 1986), e) placing it in a nutrient enriched environment (Davidson and Morton 1981, Beattie and Culver 1983), or f) a combination of these (Andersen 1990, Majer 1990).

Ants' relationships with seeds can be further divided into four categories, granivory, seed parasitism, seed dispersal and ambivalence. While a given species might under different circumstances fall into each of these categories, broadly speaking those species that effectively disperse seeds are rarely seed parasites, granivores or ambivalent toward seeds. Known granivores include members of the genera *Melophorus*, *Meranoplus*, *Monomorium*, and *Pheidole*. Species of the genera *Rhytidoponera*, *Camponotus*, and *Iridomyrmex* on the other hand tend to disperse seeds (e.g., Majer 1982, studies in Table 2). Just as for other ecosystems (Ness *et al.* 2004), those species most often recorded as seed dispersers tend to be large-bodied, as is the case for all of the genera mentioned above as seed dispersers; where smaller-bodied species are attracted to seeds, they typically are seed parasites, eating the elaiosomes without moving the seed (Auld and Denham 1999). In any given ant community, most ant species fall into the final category of ambivalence. In our main field site in the Eneabba sandplains, although nearly 100 species of ants have been recorded, only a dozen or so species have actually been observed interacting with seeds.

Species of *Rhytidoponera* are perhaps the most important dispersers of seeds in Western Australia and more generally in Australia. *Rhytidoponera* species are reported as taking seeds in ecosystems ranging from monsoonal savannas in the north to Jarrah (*Eucalyptus marginata*) forests in the southwest (Table 2). In 27 of 34 cases in which ant dispersal has been studied, *Rhytidoponera* has taken the majority of seeds presented. Our own observations confirm the general pattern that species of *Rhytidoponera* (primarily *R. inornata*, *R. metallica* group and *R. violacea*) are the most, or among the most, important species in much of the Country. Despite the important role of *Rhytidoponera* species in the dispersal of seeds, these ant species do not appear to have any particular adaptations for dispersal of seeds. That is to say, the morphology, phenology and other aspects of the life history of *Rhytidoponera* species, where studied, do not appear (at least to date) to have evolved in concert with the evolution of elaiosomes on seeds. Moreover, *Rhytidoponera* are among the most generalist Western Australian ants, both in their habitat preferences (Bisevac and Majer 1999, May and Heterick 2000), and in their diet (Briese and Macauley, Sochacki 1978, Searle 1978), which contains a mix of elaiosomes, seed and insects.

Why is myrmecochory so predominant in Australia?

While it has become increasingly clear since the 1970s (Berg 1975) that ant dispersal is exceedingly common in Australia (e.g., R. R. Dunn *et al.*, unpublished), it has not become clear why that should be the case. Below, we review each of the main hypotheses for its preponderance in Australia and the predictions they make. We consider three groups of hypotheses, though we acknowledge that different versions of these hypotheses make slightly different predictions.

Dispersal distance and lack of vertebrate dispersers of seeds

Firstly, ants may assume the role of seed dispersal that, in other regions of the world, is carried out by other organisms. Even though ants typically disperse seeds only short distances, those distances may be great enough to avoid parent-offspring competition and pathogens associated with parents (Higashi *et al.* 1989, Boyd 2001, Whitney 2002). Vertebrate dispersers, it has been speculated, might be lacking in Western Australia and other habitats where ant dispersal is common. For ant dispersal to simply be making up for the lack of other vectors, several predictions would have to be supported. First, vertebrate dispersers would have to be rarer in Western Australia than in comparable ecosystems elsewhere. This prediction has not been well tested, but at its face value seems unsupported. Emus, for example, are common across much of Australia (Grice *et al.* 1985) and have been shown to disperse many species of seeds (Cancela *et al.* in review). An alternative version of this hypothesis posits that ant dispersal is common not because vertebrates are rare, but because the rewards necessary for vertebrate dispersal are costly because of the low nutrient content of Australian soils (Westoby *et al.* 1991). Aspects of the latter hypothesis seem tenable (for example, the nutrient content of a given bird dispersed seeds tends to be greater than that of a given ant dispersed seed).

Soil storage

Secondly, Australian conditions might expose seeds to higher rates of mortality on the soil surface or in the superficial soil layers than they would experience elsewhere. There are three reasons why this might be so. First, conditions on soil surfaces in Australia are often hotter, drier, and generally harsher than in many

ecosystems, thus providing a threat of desiccation to the seed. Second, most Australian ecosystems are fire-adapted, so seeds must survive the fire itself to germinate. Third, because of the frequency of fire in most of Australia (frequent enough to lead to fire adaptations, but infrequent enough to lead most plants to germinate only following fires and not in the intervening years), seeds must not only survive hostile conditions on the soil surface, they must do so for many years. In addition, like in many sites, predation of seeds on the soil surface might be greater than in the soil. The role of predation is unlikely to be unique to Australia (that is there is no reason to believe densities of predator are particularly great in those regions where ant dispersal is common), but predation may also select for seed storage and burial (Heithaus 1981, Higashi *et al.* 1989, Smith *et al.* 1989, Ohkawara and Higashi 1994, Ohkawara *et al.* 1996). The combination of these factors may lead to a strong selective advantage for means of soil storage other than on the soil surface (Auld 1986, Bradstock and Auld 1995, Majer 1982, Pieterse and Cairns 1986). If this soil storage hypothesis is right, then we expect ant dispersal to be common in the same regions where canopy seed storage through serotiny is common. Just as predicted, the same regions in which the frequency of ant dispersal peaks (A. D. Gove *et al.* in review) are those in which serotiny is most pronounced (Lamont and Connell 1996, Cowling *et al.* 2005).

Site effects and soil quality

Finally, ant dispersed seeds may find more favourable microsites for germination and later growth than exist around the parent plant (Beattie and Culver 1982, Beattie and Culver 1983, Beattie 1985, Hanzawa *et al.* 1988). Beattie (1985), in his review of the literature on ant dispersal, concludes that the site effect hypothesis is the best supported at the global scale. There may be a direct fitness advantage to the concentration of seeds in or near ant nests, where soil might be enriched by excreta and refuse. This might confer advantages to germinating seeds in the nutrient-poor soils that are so characteristic of certain Australian landscapes (Andersen 1988b), although see (Bond *et al.* 1990, Westoby *et al.* 1991). Directed dispersal of seeds to nutrient rich microsites has long been suggested to be important. In some regions, both in Australia and more generally, ant nests appear to be enriched relative to surrounding areas in limiting nutrients (Beattie and Culver 1982). However, this does

not always appear to be true (Rice and Westoby 1986, Westoby *et al.* 1991). One key factor determining whether or not ant nests are nutrient enriched may be nest longevity. In species where ants construct new nests frequently and hence where refuse has a limited time to build up (Hughes 1991), nests are typically not enriched with nutrients relative to the surrounding soils. In contrast, those Australian species with longer lived nests such as *Rhytidoponera mayri* and the meat ant group of the genus *Iridomyrmex* (Lobry de Bruyn 1993), may tend to have more nutrient enriched nests relative to surrounding soils. Unknown is what factors govern the relocation frequency of ant nests at a large scale, and the commonness of species that relocate their nest entrances.

Conclusions as to the causes of myrmecochory

The truth with regard to the selective pressures acting on the evolution of ant-dispersal is ultimately multivariate. Where nutrient levels in ant nests are elevated relative to the surrounding soils, ant dispersed seeds may have an increased probability of germination and seedling growth. Where fires are frequent and germination only occurs following fires, ant nests may provide some protection from those fires, while storing seeds between fire events. Finally, where parasites and pathogens are abundant near parent plants and dispersal for distance is advantageous, ants provide some dispersal for distance. The key is not, as some authors have attempted, to prove, which of these factors does not play a role (they each have been shown to act, at least in some circumstances), the key is to understand which factor is likely to have played the greatest role when elaiosomes evolved, but is absent from those regions where elaiosomes are absent or rare.

Ultimately, we suspect the most believable answers to the question will result from a combination of large-scale spatial analyses of the correlations between the diversity of ant dispersed species and variables associated with each of the hypotheses (e.g., fire frequency, soil quality and the abundance and/or diversity of vertebrates) and local experiments testing the fitness of buried and unburied seeds.

Has the predominance of myrmecochory in Western Australia enhanced the diversity of plants?

The main focus in the study of myrmecochory has been the question of why myrmecochory exists and what the advantages of myrmecochory are. However, by result of the short distances ants typically disperse seeds, myrmecochory might also be expected to have important consequences for plant species at scales larger than those relevant to fitness as well as on plant communities. There are several scales at which ant-mediated dispersal might affect patterns of diversity: local within-patch patterns of diversity in ecological time, meta-community patterns of diversity in ecological time and landscape patterns of diversity and distribution in both ecological and evolutionary time. We consider each scale in turn.

Local scale

At the **local scale**, short distance dispersal by ants might create dispersal limitations which would prevent ecological dominance by competitively superior species. Were this to be the case, we would predict that at local scales that ant-dispersed species would be more spatially clumped than other species. For seedlings, ant dispersed species are almost by definition clumped spatially (Fig. 3d), with seeds most dense around the nests of ants. However, if clumped distributions of ant dispersed species are to have ecological significance for patterns of diversity, they have to persist as the plants mature. Such persistence is unlikely if the effects of other factors (predation, pathogens, competition) are density dependent, which is likely the case. We regard the local effects of ant dispersal on plant diversity as a possibility, but analyses remain lacking.

Metacommunity scale

The field of metacommunity ecology has recently emerged as a community level framework for considering the same kinds of explicitly spatial questions addressed in metapopulation analyses. Regardless of the particular metacommunity framework adopted (e.g., Chase *et al.* 2006), dispersal is thought to play a primary role. In metacommunities where dispersal is poor, individual communities are predicted to have low diversity, but the species turnover among communities is predicted to be great. In contrast, where dispersal is extensive, individual communities are expected to be diverse, but the turnover among communities is

expected to be low. In other words, poor dispersal equates to high beta diversity (Chase *et al.* 2006). To our knowledge, the beta diversity of communities differing in mean dispersal distances has not been well compared, with the possible exception of comparisons among microcosm treatments (e.g., Cadotte and Fukami 2005), where the predictions of metacommunity models with regard to beta diversity tend to be supported. However, if any plant communities might be expected to show evidence of the patterns predicted by metacommunity dynamics, we think they will be communities like those in Western Australia where ant dispersal predominates.

Regional ecological scale

Several studies (Lennon *et al.* 1997, Holt and Keitt 2000) have suggested that in the absence of other intervening factors, species with shorter average dispersal distances can be predicted to have smaller geographic ranges. In most scenarios, small ranges are predicted as a consequence of the inability of short distance dispersal to maintain gene flow to peripheral populations. Alternatively, in a non-equilibrium scenario, clades with shorter average dispersal distances might have smaller ranges, simply because of the frequent fragmentation of ranges due to speciation. Several analyses to date support the hypothesis that range size is correlated with dispersal mode. In both Australia and the South African Fynbos, ant-dispersed species appear to have more restricted ranges than do other species (Rebelo 1991, Oakwood *et al.* 1993, Cowling *et al.* 1994, Hughes *et al.* 1994). However, our more recent analyses suggest that when compared to the effects of the size of the bioregion in which a species finds itself (ie. species in large bioregions tend to have large ranges), the role of dispersal role is relatively minimal (A. D. Gove *et al.* in review).

Evolutionary time scale

It has long been hypothesized that if organisms evolve seed dispersal strategies which lead to short average dispersal distances, they might be more likely to be isolated by barriers, and hence to speciate (Mayr 1963, De Santis and Regalia 1978, Erriksson and Bremer 1991, Tiffney and Manchester 2001). So long as a given dispersal mode leads to long-distance dispersal frequently enough to occasionally surmount environmental barriers, and pollen dispersal distances are not positively

correlated with seed dispersal distances, speciation is predicted to occur with greater frequency where average seed dispersal distances are short (Wisheu *et al.* 2000). Empirical studies on the role of different dispersal vectors, particularly with regard to plant speciation, have proven inconclusive. While several studies have found no difference between the speciation rates of animal and wind dispersed taxa (Herrera 1989, Fleming 1991, Ricklefs and Renner 1994), three other studies (Eriksson and Bremer 1991, Smith 2001, Tiffney and Manchester 2001) found that biotic dispersal facilitates diversification, at least for woody plants. More recently, Bolmgren and Eriksson (2005) demonstrated that the influence of dispersers on speciation rate could be dependent upon life form – they found that fleshy fruit were associated with higher speciation rates in woody plants, but the opposite was true in herbaceous groups. Much of the discrepancy among studies in terms of whether animal dispersal is found to facilitate speciation may also be due to the breadth of the category “animal dispersal” (Smith, 2001). Animal dispersed plants vary from species dispersed tens of kilometers by Hornbills (Holbrook *et al.* 2002) to species dispersed no more than a few meters by ants (Gomez and Espadaler 1998). Some animal vectors are more effective than wind at accomplishing distance dispersal, and some are much less effective (e.g., Cain *et al.* 1998). Hence, bulk comparisons between wind and animal dispersed plant species are almost certain to find varied results, depending upon which animals are considered to be the vectors.

One way to better understand whether dispersal mode affects speciation rate is by focusing on the extreme dispersal modes, where dispersal distances are either very short or very long. If dispersal-vector has an effect on speciation patterns anywhere, it should be for ant-dispersed plant clades, where average dispersal distances are often just a few meters (Gomez and Espadaler 1998). If ant-dispersed clades do not speciate more rapidly than other clades, particularly those with wind dispersal, it would be unlikely to find differences due to more subtle differences in dispersal vector or distance. Where they have been compared, dispersal distances of ant-dispersed species are much shorter than those of plants with other dispersal modes (Bond *et al.* 1991). Bond *et al.* (1991), for example, found dispersal distances for an ant-dispersed species in the Fynbos were less than half that of a confamilial wind-dispersed species. So long as ant-dispersed species occasionally cross barriers, as they apparently do (Auld and Denham 1999, Vellend *et al.* 2003), their short dispersal distances mean that their gene flow across barriers via seeds will almost inevitably be less than that of

wind or vertebrate dispersed species. It is enticing to link the high diversity of plants in south western Australia to the preponderance of ant dispersal there, but it would be premature to do so without analyses explicitly comparing the speciation and extinction rates of plant species dispersed by ants and other means.

Extinction rates

In addition to their potentially positive effects on diversity, dispersal of seeds by ants might also be expected to affect extinction rates. Two mechanisms by which dispersal mode might influence extinction rates are possible. These mechanisms differ in the direction of their effects. First, if ant dispersed species tend to have small ranges, patchy distributions, and an inability to migrate with environmental change, ant dispersed species might be more likely to go extinct than are other species. Such an effect may not have been strong historically (since climate shifts in Western Australia have been minimal over the last 20 million years), but may be great given the combination of habitat loss and climate change that has already occurred in Western Australia and is predicted for the next 50 years. On the other hand, the fact that ants bury seeds in their nests, often at great depths (Fig 4), means that ants may disperse seeds through time. Such dispersal through time for seeds buried in shallow depths may occur from one fire to the next, thereby protecting seeds in the intervals but allowing them to germinate following fires. Dispersal of seeds through time for seeds buried more deeply than 5 or 10 centimeters may play out over much longer time intervals, including across severe fires or other similar disturbances, such as mining events. In fact, because many ant-dispersed species, such as some *Acacia*, are likely to be capable of living many hundreds of years in the soil, ant dispersal may be much more effective at dispersal through time than through space. This dispersal through time may work as a kind of bet-hedging by increasing the likelihood that even where recruitment is poor for other reasons (poor dispersal through space, disturbance, etc.) dispersal through time may rescue populations.

Caveat disperser

A key to all of the effects of ant dispersal on plant diversity (with the possible effect of dispersal through time on extinction rates) is the idea that dispersal distances

of seeds by ants are short. Field based studies of seed dispersal by ants almost universally find that ant dispersed seeds are carried short distances (typically a few metres (Gómez and Espadaler 1998)). In the few comparisons that have been done among dispersal modes, ant-dispersed species are dispersed much shorter distances than are species dispersed by other means (e.g., Cain *et al.* 1998). Finally, studies of gene flow in ant dispersed species tend to show limited evidence of local gene flow (suggesting poor seed dispersal; (Kalisz *et al.* 2001)). In contrast, however, several pieces of information point to a more limited role for ant dispersal in governing patterns of gene flow at large scales. First, several studies have revealed that ‘non standard’ modes of dispersal, particularly those with higher than average dispersal distances, are an integral component of the dispersal kernels of many species often considered to be primarily ant dispersed (Vellend *et al.* 2003). For example, emigration models indicate that such non-standard dispersal events can account for observed rates of migration of North American ant dispersed species in the Pleistocene (Vellend *et al.* 2006). Further, migration rates of ant-dispersed understory herbs in North America (inferred from pollen data) suggest that they have migrated faster than would be predicted were their seeds only carried by ants. However, the results of large-scale dispersal models and pollen data need to be verified with other sources of data. What are needed are comparisons of the gene flow patterns of plant species differing in dispersal modes at the landscape scale. We know of no such analyses. However, recent phylogeographic analyses of patterns of gene flow and range expansion in North American trees (McLachlan *et al.* 2005) indicate that even tree species known to be dispersed by wind, may have dispersed far more slowly than previously thought based on emigration models and pollen data. Thus the jury is still out with regard to the role of ant dispersal in large-scale patterns of gene flow, speciation and extinction, but hopefully not for long.

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References

- Andersen, A. N. 1988a.** Dispersal distance as a benefit of myrmecochory. *Oecologia* **75**:507-511.
- Andersen, A. N. 1988b.** Soil of the nest-mound of the seed-dispersing ant, *Aphaenogaster longiceps*, enhances seedling growth. *Aust. J. Ecol.* **13**:469-471.
- Andersen, A. N. 1990.** Seed harvesting ant pests in Australia. Pages 34-39 in R. K. Vander Meer, K. Jaffe, and A. Cedeno, editors. *Applied myrmecology: a world perspective*. Westview Press, Boulder.
- Andersen, A. N., and D. H. Ashton. 1985.** Rates of seed removal by ants at heath and woodland sites in southeastern Australia. *Aust. J. Ecol.* **10**:381-390.
- Andersen, A. N., and S. C. Morrison. 1998.** Myrmecochory in Australia's seasonal tropics: effects of disturbance on distance dispersal. *Aust. J. Ecol.* **23**:483-491.
- Auld, T. D. 1986.** Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: dispersal and the dynamics of the soil seed-bank. *Aust. J. Ecol.* **11**:235-254.
- Auld, T. D., and A. J. Denham. 1999.** The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecol.* **144**:201-213.
- Beattie, A. J. 1985.** *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, New York.
- Beattie, A., and D. C. Culver. 1982.** Inhumation: how ants and other invertebrates help seeds. *Nature* **297**:627.
- Beattie, A. J., and D. C. Culver. 1983.** The nest chemistry of two seed-dispersing ant species: Effect of nest chemistry on survivorship of seeds. *Oecologia* **56**:99-103.
- Berg, R. Y. 1975.** Myrmecochorous plants in Australia and their dispersal by ants. *Aust. J. Bot.* **23**:475-508.
- Bisevac, L., and J. D. Majer. 1999.** Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia. *Restor. Ecol.* **7**:117-126.
- Bolmgren, K. & Eriksson, O. 2005.** Fleshy fruits - origins, niche shifts, and diversification. *Oikos*, **109**: 255-272.
- Bond, W. J., D. Le Roux, and R. Erntzen. 1990.** Fire intensity and regeneration of myrmecochorous Proteaceae. *S. Afr. J. Bot. S. Afr. Tydskr. Plantkd.* **56**:326-330.
- Bond, W. J., R. Yeaton, and W. D. Stock. 1991.** Myrmecochory in Cape Fynbos. Pages 448-462 in C. R. Huxley and D. F. Cutler, editors. *Ant-plant interactions*. Oxford University Press, Oxford. xviii + 601 p.
- Boyd, R. S. 2001.** Ecological benefits of myrmecochory for the endangered chaparral shrub *Fremontodendron decumbens* (Sterculiaceae). *Am. J. Bot.* **88**:234-241.
- Bradstock, R.A. & Auld, T.D. 1995.** Soil temperatures during experimental bushfires in relation to fire intensity: Consequences for legume germination and fire management in South-Eastern Australia. *J. Appl. Ecol.* **32**: 76-84.
- Briese, D. T., and B. J. Macauley. 1981.** Food collection within an ant community in semi-arid Australia, with special reference to seed harvesters. *Aust. J. Ecol.* **6**:1-19.

- Cadotte, M. W. and Fukami, T. 2005.** Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecol. Lett.* **8**: 548-557.
- Cain, M. L., H. Damman, and A. Muir. 1998.** Seed dispersal and the Holocene migration of woodland herbs. *Ecol. Monogr.* **68**:325-347.
- Cancela, M.C., R. R. Dunn, E. van Etten and B. Lamont. (in review)** Long-distance dispersal of “ant-dispersed” seeds by Emus in Western Australia. *Ecography*.
- Chase, J. M., N. Mouquet, D. Tilman, P. Amarasekare, R. Holt, M. Holyoak, J. Shurin, M. Leibold. 2006.** Towards a really unified theory of biodiversity. In M. Holyoak, M. Leibold, and R. Holt (eds). *Meta-communities*. University of Chicago press.
- Christian, C. 2001.** Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413**:635-639.
- Clifford, H.T. & Monteith, G.B. 1989.** A three phase seed dispersal mechanism in Australian Quinine Bush (*Petalostigma pubescens* Domin). *Biotropica*, **21**: 284-286.
- Cowling, R. M., F. Ojeda, B. B. Lamont, P. W. Rundel, and R. Lechmere-Oertel. 2005.** Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecol. Biogeogr.* **14**:509-519.
- Cowling, R. M., S. M. Pierce, W. D. Stock, and M. Cocks. 1994.** Why are there so many myrmecochorous species in the Cape fynbos? Pages 159-168 in M. Arianoutsou and R. H. Groves, editors. *Plant animal interactions in Mediterranean type ecosystems*. Kluwer Academic Publishers, Dordrecht.
- Davidson, D. W., and S. R. Morton. 1981.** Myrmecochory in some Chenopodiaceae of the Australian arid zone. *Oecologia* **50**:357-366.
- De Santis, L., and J. A. V. S. d. Regalia. 1978.** Hormigas recolectoras de polen en colmenas. *Cien. Abejas* **3(12)**:42-46.
- Drake, W. E. 1981.** Ant-seed interaction in dry sclerophyll forest on North Stradbroke Island, Queensland. *Aust. J. Bot.* **29**:293-309.
- Erriksson, O., and B. Bremer. 1991.** Fruit characteristics, life forms, and species richness in the plant family Rubiaceae. *Am. Nat.* **138**:751-761.
- Fleming, T. H. 1991.** Fruiting plant-frugivore mutualism: The evolutionary theater and the ecological play. in P. W. Price, T. M. Lewinsohn, G.W. Fernandes, and W. W. Benson, editors. *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions*. J. Wiley & Sons, New York.
- Gill, A. M. 1975.** Fire and the Australian flora: a review. *Australian Forestry* **38**: 4-25.
- Gomez, C., and X. Espadaler. 1998.** Myrmecochorous dispersal distances: a world survey. *J. Biogeogr.* **25**:573-580.
- Gove, A. D., Dunn, R.R. and Majer, J.D. (in review).** Biogeographic gradients in seed dispersal
- Grice, D., Caughley, G., & Short, J. 1985.** Density and distribution of emus. *Aust. Wildl. Res.* **12**: 69-73.
- Griffin, E. A., Hopper, S. D. & Hopkins, A. J. M. 1990.** Flora. Pages 39-69 in A. A. Burbidge et al. eds. *Nature conservation, landscape and recreational values of the Lesueur area*. Environmental protection Authority, Perth.
- Hanzawa, F. M., A. J. Beattie, and D. C. Culver. 1988.** Directed dispersal: demographic analysis of an ant-seed mutualism. *Am. Nat.* **131**:1-13.

- Heithaus, E. R. 1981.** Seed predation by rodents on three ant-dispersed plants. *Ecology* **62**:136-145.
- Herrera, C. M. 1989.** Seed dispersal by animals: a role in angiosperm diversification? *Am. Nat.* **133**.
- Higashi, S., S. Tsuyuzaki, M. Ohara, and F. Ito. 1989.** Adaptive Advantages of Ant-Dispersed Seeds in the Myrmecochorous Plant *Trillium tschonoskii* (Liliaceae). *Oikos* **54**:389-394.
- Holbrook, K. M., T. B. Smith, and B. D. Hardesty. 2002.** Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* **25**:745-749.
- Holt, R. D., and T. H. Keitt. 2000.** Alternative causes for range limits: a metapopulation perspective. *Ecol. Lett.* **3**:41-47.
- Hopper S. D., Harvey, M. S., Chappill, J. A., Main, A. R. & York Main, B. 1996.** The Western Australian biota as Gondwanan heritage – a review. Pages 1-46 *in*: ed. S. D. Hopper et al. eds. *Gondwana heritage: Past, present and future of Western Australian biota*. Surrey Beatty & Sons, Chipping Norton.
- Hopper, S. D., and P. Gioia. 2004.** The Southwest Australian Floristic Region: Evolution and conservation of a global hot spot of biodiversity. *Ann. Rev. Ecol. Evol. S.* **35**:623-650.
- Hughes, L. 1991.** The relocation of ant nest entrances: potential consequences for ant-dispersed seeds. *Aust. J. Ecol.* **16**:207-214.
- Hughes, L., M. Dunlop, K. French, M. R. Leishman, B. Rice, L. Rodgerson, and M. Westoby. 1994.** Predicting dispersal spectra - a minimal set of hypotheses based on plant attributes. *J. Ecol.* **82**:933-950.
- Hughes, L., and M. Westoby. 1990.** Removal rates of seeds adapted for dispersal by ants. *Ecology* **71**:138-148.
- Hughes, L., and M. Westoby. 1992.** Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* **73**:1285-1299.
- Jurado, E., M. Westoby, and D. Nelson. 1991.** Diaspore weight, dispersal, growth form and perenniality of central Australian plants. *J. Ecol.* **79**:811-830.
- Kalisz, S., J. D. Nason, F. M. Hanzawa, and S. J. Tonsor. 2001.** Spatial population genetic structure in *Trillium grandiflorum*: The roles of dispersal, mating, history, and selection. *Evolution* **55**:1560-1568.
- Lamont, B.B. 2005.** Sandplain country of southwestern Australia. *in* Proceedings of the Seminar Program and AJ Swaby Address from the 23rd Biennial Conference and Seminar of the Association of Societies for Growing Australian Native Plants.
- Lamont, B. B., Hopkins, A. J. M. and Hnatiuk, R. J. 1984.** The flora – composition, diversity and origins. Pages 27-50 *in* J. S. Pate and J. S. Beard eds *Kwongan: plant life of the sandplain*. University of Western Australia Press, Nedlands.
- Lamont, B. B., and S. W. Connell. 1996.** Biogeography of *Banksia* in southwestern Australia. *J. Biogeogr.* **23**:295-309.
- Lennon, J. J., J. R. G. Turner, and D. Connell. 1997.** A metapopulation model of species boundaries. *Oikos* **78**:486-502.
- Lobry de Bruyn, L. A. 1993.** Ant composition and activity in naturally-vegetated and farmland environments on contrasting soils at Kellerberrin, Western Australia. *Soil Biol. Biochem.* **25**:1043-1056.

- Longino, J. T., and R. K. Colwell. 1997.** Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecol. Appl.* **7**:1263-1277.
- Majer, J. D. 1980.** The influence of ants on broadcast and naturally spread seeds in rehabilitated bauxite mined areas. *Reclamation Review*, **3**, 3-9.
- Majer, J. D. 1982.** Ant-plant interactions in the Darling botanical district of Western Australia. Pages 45-61 *in* R. C. Buckley, editor. *Ant-plant interactions in Australia*. Dr. W. Junk, The Hague.
- Majer, J. D. 1983.** The influence of ants on seeding operations in northern Australian mined areas. *Reclam. Reveg. Res.*, **2**: 299-313.
- Majer, J. D. 1990.** The role of ants in Australian land reclamation seeding operations. Pages 544-554 *in* R. K. Vander Meer, K. Jaffe, and A. Cedeno, editors. *Applied myrmecology: a world perspective*. Westview Press, Boulder.
- Majer, J. D., R. L. Kitching, B. E. Heterick, K. Hurley, and K. E. C. Brennan. 2001.** North-south patterns within arboreal ant assemblages from rain forests in eastern Australia. *Biotropica* **33**:643-661.
- Majer, J. D., and B. B. Lamont. 1985.** Removal of seed of *Grevillea pteridifolia* (Proteaceae) by ants. *Aust. J. Bot.* **33**:611-618.
- Manzaneda, A. J., J. M. Fedriani, and P. J. Rey. 2005.** Adaptive advantages of myrmecochory: the predator-avoidance hypothesis tested over a wide geographic range. *Ecography* **28**:583-592.
- May, J. E., and B. E. Heterick. 2000.** Effects of the coastal brown ant, *Pheidole megacephala* (Fabricius), on the ant fauna of the Perth metropolitan region, Western Australia. *Pacific Conservation Biology* **6**:81-85.
- Mayr, E. 1963.** *Animal species and evolution*. Harvard University Press, Cambridge, MA.
- McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005.** Molecular indicators of tree migration capacity under rapid climate change. *Ecology* **86**:2088-2098.
- Morton, S. R. 1979.** Diversity of desert-dwelling mammals: a comparison of Australia and North America. *J. Mammal.* **60**, 253-264
- Myers, N., Mittermeier, R.A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. 2000.** Biodiversity hotspots for conservation priorities. *Nature* **403**: 853-858.
- Ness, J. H., J. L. Bronstein, A. N. Andersen, and J. N. Holland. 2004.** Ant body size predicts dispersal distance of ant-adapted seeds: Implications of small-ant invasions. *Ecology* **85**:1244-1250.
- O'Dowd, D., and A. M. Gill. 1986.** Seed dispersal syndromes in Australian *Acacia*. Pages 87-121 *in* D. Murray, editor. *Seed dispersal*. Academic Press, Sydney, Orlando. 322 p.
- Oakwood, M., E. Jurado, M. Leishman, and M. Westoby. 1993.** Geographic ranges of plant species in relation to dispersal morphology, growth form and diaspore weight. *J. Biogeogr.* **20**:563-572.
- Ohkawara, K., and S. Higashi. 1994.** Relative importance of ballistic and ant dispersal in two diplochorous *Viola* species (Violaceae). *Oecologia* **100**:135-140.
- Ohkawara, K., S. Higashi, and M. Ohara. 1996.** Effects of ants, ground beetles and the seed-fall patterns on myrmecochory of *Erythronium japonicum* Decne. (Liliaceae). *Oecologia* **106**:500-506.
- Pieterse, P.J. & Cairns, A.L.P. 1986.** The effect of fire on an *Acacia longifolia* seed bank in the south-western cape. *S. Afr. J. Bot.* **52**: 233-236.

- Rebelo, A. G. 1991.** The preservation of the Cape flora. Status, causes of rarity, ideals and priorities. Dissertation. University of Capetown, Capetown, South Africa.
- Rice, B., and M. Westoby. 1986.** Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. *Ecology* **67**:1270-1274.
- Ricklefs, R. E., and S. S. Renner. 1994.** Species richness within families of flowering plants. *Evolution* **48**:1619-1636.
- Rodgerson, L. 1998.** Mechanical defense in seeds adapted for ant dispersal. *Ecology* **79**:1669-1677.
- Schatral, A., S. G. Kailis, and J. E. D. Fox. 1994.** Seed dispersal of *Hibbertia hypericoides* (Dilleniaceae) by ants. *J. Roy. Soc. West. Aust.* **77**:81-85.
- Searle, P.A. 1978** The ecology of the seed feeding ant *Rhytidoponera violacea*, Curtin University of Technology, Perth, Western Australia.
- Shattuck, S. O. 1999.** Australian ants: their biology and identification. CSIRO, Collingwood, Vic.
- Slingsby, P., and W. Bond. 1981.** Ants--friends of the Fynbos. *Veld Flora* **67**:39-45.
- Smith, B. H., P. D. Forman, and A. E. Boyd. 1989.** Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. *Ecology* **70**:1649-1656.
- Smith, J. F. 2001.** High species diversity in fleshy-fruited tropical understory plants. *Am. Nat.* **157**:646-653.
- Sochacki, S.J. 1978** The ecology of the seed feeding ant, *Rhytidoponera inornata*, Curtin University of Technology, Perth, Western Australia.
- Tiffney, B. H., and S. R. Manchester. 2001.** The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere tertiary. *Int. J. Plant Sci.* **162**:S3-S17.
- Vellend, M., T. M. Knight, and J. M. Drake. 2006.** Antagonistic effects of seed dispersal and herbivory on plant migration. *Ecol. Lett.* **9**:316-323.
- Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003.** Dispersal of Trillium seeds by deer: Implications for long-distance migration of forest herbs. *Ecology* **84**:1067-1072.
- Westoby, M., K. French, L. Hughes, B. Rice, and L. Rodgerson. 1991.** Why do more plant species use ants for dispersal on infertile compared with fertile soils. *Aust. J. Ecol.* **16**:445-455.
- Westoby, M., B. Rice, and J. Howell. 1990.** Seed size and plant growth form as factors in dispersal spectra. *Ecology* **71**:1307-1315.
- Whitney, K. D. 2002.** Dispersal for distance? *Acacia ligulata* seeds and meat ants *Iridomyrmex viridiaeneus*. *Aust. Ecol.* **27**:589-595.
- Wilson, E. O. 1987.** The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica* **19**:245-251.
- Wisheu, I. C., M. L. Rosenzweig, L. Olsvig-Whittaker, and A. Shmida. 2000.** What makes nutrient-poor mediterranean heathlands so rich in plant diversity? *Evol. Ecol. Res.* **2**:935-955.

Figure 1. *Phytogeographic regions of Western Australia (from Beard 1990).*

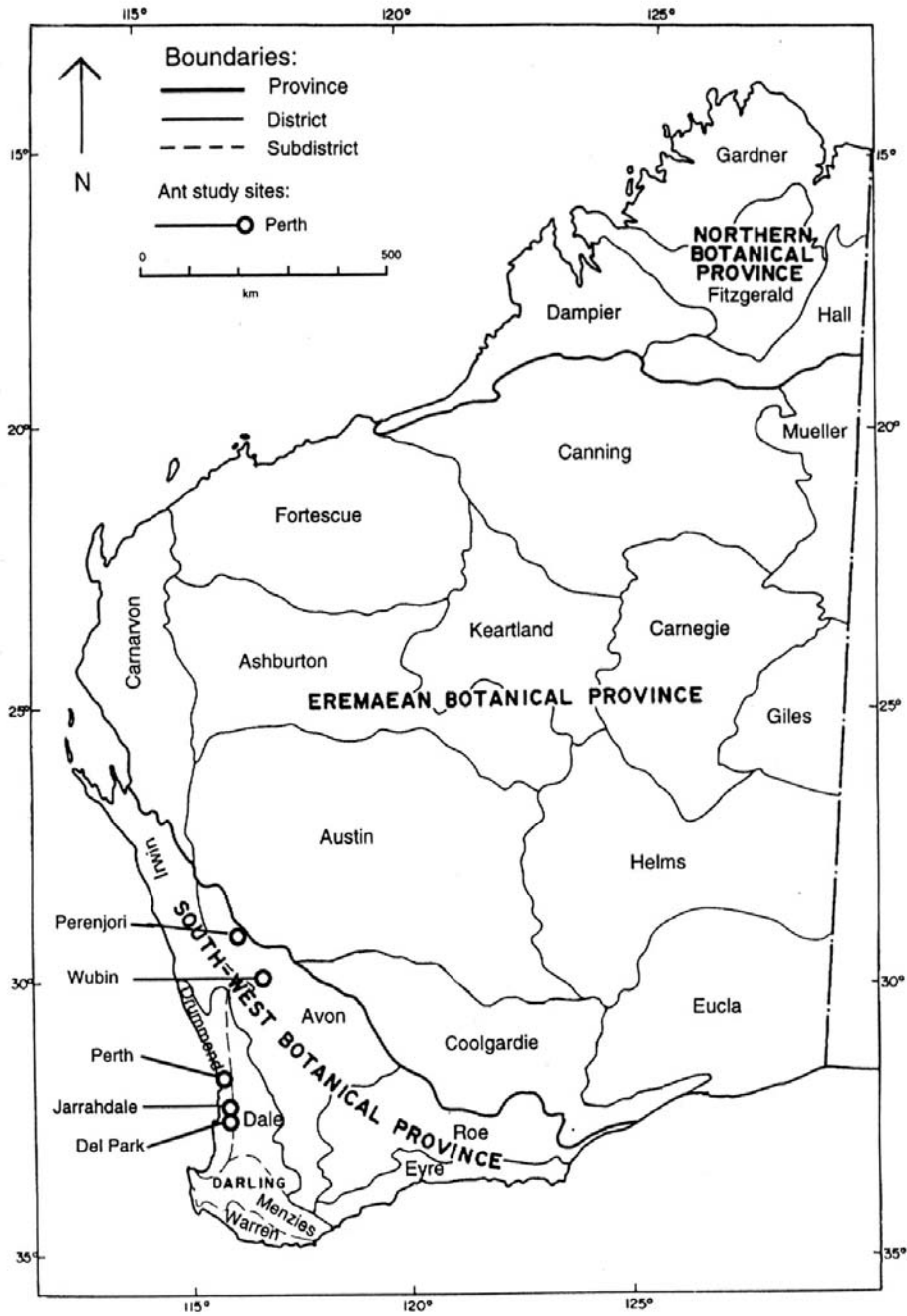


Figure 2. General view of species-rich heathland (kwongan) at Eneabba, Western Australia. The crests and troughs of the dunes, plus the lateritic uplands, account for some of the plant diversity, but alone cannot explain the massive richness of plants that exists in this region.



Figure 3. Seeds of *Acacia longifolia*, *Daviesia divaricata*, *Daviesia flexuosa* and *Dodonia viscosa* (in clockwise order, starting from top left) showing the elaiosome in white (a); *Melophorus wheeleri* carrying a legume seed by the elaiosome. (b); dump of myrmecochorous legume seeds around nest entrance of *Melophorus wheeleri*. (c); and seedlings of *Acacia sp.* germinating on old ant nest following a forest fire (d).



Figure 4. Mean burial depth of seed found in excavated *Rhytidoponera violacea* nests (n=6), in sclerophyll heathland near Eneabba, Western Australia.

