6.1 Introduction

The historical emphasis on the ecological and evolutionary importance of antagonistic interactions such as competition, predation, and parasitism is increasingly informed by a recognition of facilitative and mutualistic interactions where one or both participants receive a net benefit (Bertness and Callaway 1994; Bruno et al. 2003; Grosholz 2005; Stachowicz 2001). Interactions between ants and their partners provide some of the best examples of the reciprocally beneficial interactions (Bronstein 1998) and, in particular, the mutualisms that play critical roles in structuring community composition and functioning (e.g. Christian 2001; Kaplan and Eubanks 2005; Mooney 2007; O'Dowd et al. 2003; Poulsen and Currie 2006; Wimp and Whitham 2001). Interactions between ants and their partners date to 45–60 Mya (Poulsen and Currie 2006; Stadler and Dixon 2005) and are critical to understanding the evolution and ecological success of ants as a taxon. The rewards provided by mutualists can increase the survival and reproduction of ants and colonies, provide the fuel that allows ants to collect new resources and engage in aggressive behaviours (Davidson 1998), and encourage colonies to reallocate resources towards particular responsibilities and/or locations. Here, we describe the currencies and dynamics of these mutualistic interactions, and highlight recent developments in our understanding of ants' participation in mutualisms.

The complexity and breadth of this topic warrant two caveats. First, the dynamics of particular ant mutualisms have been the focus of substantive reviews (e.g. refer to plant protection in Bronstein 1998, Heil and McKey 2003; insect tending in Pierce et al. 2002, Stadler and Dixon 2005, Way 1963; seed dispersal in Giladi 2006; ant–plant symbioses in Davidson and McKey 1993; Heil and McKey 2003; and ant–fungi–bacteria in Poulsen and Currie 2006) and are featured in several books (e.g. Beattie 1985; Huxley 1991; Rico-Gray and Oliveira 2007; Stadler and Dixon 2008). We encourage readers to seek out these more in-depth works. Second, the mutualisms we describe often include currencies based on antagonistic interactions and/or access to food. Competition, predation, and parasitism of (and by) ants are treated in other chapters (see Chapters 5, 12, 9, 10, and 11, respectively, and Box 6.1), and aspects of ant diet and shelter are the focus of Chapter 7. In many cases, dissecting mutualistic interactions requires an understanding of those currencies.

We begin by describing mutualisms on the basis of the resources and services being traded. We focus on trophobiotic interactions (Section 6.2), wherein ants receive access to food resources in exchange for services provided to the reward producer (whether plant or insect; bacterial endosymbionts are discussed in Chapter 7), interactions where ants receive nutritive profit while dispersing plant propagules (seeds and pollen) (Section 6.3), and the tripartite mutualism among ants, fungal cultivars, and bacteria, in which food, protection, and dispersal are the currencies (Section 6.4). In each case, we identify instances in which these interactions can have consequences for the larger biotic communities and identify characteristics of ants that make them particularly well suited for participation in the interaction. We then take a synthetic approach to explore elements of context

Successful transmission to a terminal host is one of the biggest challenges in a parasite's life cycle. Consequently, parasites have evolved a variety of mechanisms to change the behaviour and appearance of intermediate hosts to facil-

dependency in these interactions (Section 6.5), and put this variation in the context of macroevolutionary variation (Section 6.6). Finally, we highlight the utility of these interactions for addressing questions fundamental to the field of ecology (Section 6.7) and conclude (Section 6.8) by identifying promising areas of future research.

6.2 Ants providing protection for food

Trophobiotic interactions involve the consumption of a food reward, often in return for protection from

water, carbohydrates are the dominant constituents of hemipteran honeydew. However, sugar type, nutrients, and plant secondary compounds all influence the attractiveness and presumably nutritive value of honeydew for ants (Blüthgen et al. 2004b; see Figure 6.1 and Chapter 7). Because direct measures of ant fitness are rare (but see Helms and Vinson 2008), we can only infer that honeydew attractiveness is indicative of nutritive value and value to the colony.

Because ants are effective and abundant predators of many arthropods, ant–hemipteran mutualisms have been defined as a 'keystone interaction' (Styrsky and Eubanks 2007) where variation in the strength or occurrence of the interaction has far-reaching consequences for the community in which it is embedded (see Bishop and Bristow 2001; Kaplan and Eubanks 2005; O'Dowd et al. 2003; Wimp and Whitham 2001). With respect to herbivores, hemipteran-tending ants increase mutualist abundance while often preying upon untended herbivores (e.g. Bishop and Bristow 2001; Mooney 2007). Key questions for the ecology of ant–hemipteran mutualisms have been whether the net effect of tending ants is to increase or de-

somewhat specialized as hemipteran predators, including ladybird beetle larvae and adults (Coleoptera: Coccinellidae), syrphid fly larvae (Diptera: Syrphidae), lacewing larvae (Neuroptera: Chrysopidae), and parasitoid wasps (Hymenoptera: Braconidae), although ants can also provide protection against more generalist predators such as spiders (Cushman and Whitham 1989; Del-Claro and Oliveira 2000). Other benefits can include reduced fouling from honeydew accumulation (Bach 1991), reduced competition from other herbivorous insects (Smith et al. 2008), and allowing aphids to divert resources away from predator avoidance or parental care, and towards feeding, growth, and reproduction (Abbot et al. 2008; Bristow 1983; Flatt and Weisser 2000). Such non-protective benefits are rarely studied, and their frequency or importance compared to protection from predators is not well understood.

It would seem that the entire benefit of tending hemipterans for ants is nutritional. Aside from

hemipterans (Gaume et al. 1998; Palmer et al. 2008)

produces modest rewards to, nonetheless, engage ants in a beneficial manner (see Figure 6.1). For example, foraging costs are reduced if the prospective ant partners are capable of establishing satellite nests at the base of plants with EFNs or hemipteran aggregations, or if the plant itself is the domicile of the colony. Because trophobiosis invariably involves the collection of sugary and/or nutrient-rich liquid, key adaptations include the capacity for trophallactic exchange of liquid food among members of the colony (Fiedler 2006) and morphological changes to the ant's proventriculus and gaster, which enable them to carry large amounts of sugary fluids (honeydew and nectar) and regulate the digestion of these fluids (Davidson

et al. 1994). As a result of the nutritive value and chemical signalling component of the elaiosome and a durable seed coat, ants that might otherwise act as seed consumers are perhaps converted into elaiosome consumers, and hence, seed dispersers (Rico-Gray and Oliveira 2007). Interestingly, plants may also co-opt the attention of carnivorous ants; the most avid collectors of elaiosome-bearing seeds rarely include plant material in other aspects of their diet (Hughes et al. 1994). Myrmecochorous species are found in >80 plant families, and the morphological features associated with myrme-cochory have evolved at least 20 times in the mono-cots (Dunn et al. 2007a). This estimate may be conservative, as some seeds that rely on ants for dispersal lack food rewards. For example, the dia-spores of some 'ant garden' plants use odorants,

limit these indirect costs by including ant-deterring compounds in their flowers (e.g. Ness 2006; Will-mer and Stone 1997a).

6.3 Ants provide dispersal for food

6.3.1

Myrmecochory is the dispersal of ant-adapted seeds by ants. Over 90% of the >3,000 ant-dispersed plant species are found in the South African fynbos and in areas of Australia dominated by sclerophyllous plants (Berg 1975; Bond and Slingsby 1983). Most of the remaining identified ant-dispersed species are spring ephemerals in the temperate deciduous for-ests of northern Europe, Japan, and North America; myrmecochores account for 40% of the herbaceous species and 60% of emergent stems in portions of temperate deciduous forests of the eastern United States (Beattie and Culver 1981; Handel 1981).

Myrmecochorous seeds have an attached, lipid-rich food reward, called an elaiosome, which at-tracts ant foragers (Figure 6.5). Because the elaio-some's fatty acid composition is similar to that of insect prey (Hughes et al. 1994), the diaspore (seed + reward) is attractive to omnivorous foragers. Ants may preferentially collect seeds with larger elaiosomes or more favorable elaiosome-to-seed ratios (Mark and Oleson 1996), and some elaio-somes also include compounds that elicit collection behaviors by workers (e.g. 1,2-diolein in Hughes
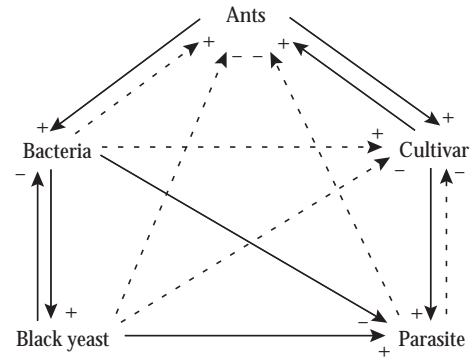
a

Figure 6.7

b

Figure 6.6 Atta are among the most conspicuous ants in the Neotropics and their colonies can number millions of workers in multiple subcastes. (a) An Atta cephalotes worker carries its harvest back to the nest to feed the colony's fungal cultivar. (b) Atta cephalotes workers tend the colony's fungal garden. (Photos: Alex Wild)

inedible plant material into lipid and carbohydrate-rich gonglydia, making the monophagous ants 'ecologically polyphagous' (Rico-Gray and Oliveira 2007). As a result, the ant–fungal composite feeds on a great diversity of widely distributed plants that would otherwise be inaccessible to the fungi and/or inedible to the ants.

Fungus-cultivating ants have an elaborate set of behaviours and traits that facilitate fungal cultivation. The selection of an appropriate substrate is key to fungal growth. Leaf-cutting ants avoid harvesting from plants with incompatible chemistry, possibly via feedback from the fungus (North et al. 1997). Attines further promote the growth of their fungal cultivars by pruning, redistributing fungus-pro-

duced proteolytic enzymes around the fungal garden, and maintaining the garden chamber at the appropriate temperature and humidity (Poulsen and Currie 2006). The ants employ behavioural and chemical means to protect their fungal gardens from other microbes. The use of a platform by founding Atta queens reduces the risk of infection by microbes in the soil (Fernández-Marín et al. 2007). Weeding and grooming by workers also reduce contamination by non-mutualist microbes (Currie and Stuart 1991). Metapleural gland secretions provide effective general antibiotics and defend the fungal cultivars from an array of microbes (Poulsen et al. 2002; see Box 9.1).

The weeding and grooming behaviours and metapleural gland secretions are not effective against specialized fungal parasites in the genus Escovopsis. Thus the ants and their fungi depend on another mutualist, actinomycete bacteria (Figure 6.7). These actinomycetes, in the genus Pseuodonocardia, are reared in specialized, elaborate crypts present in genus-specific locations on the cuticles of attines (Currie et al. 1999, 2006). The bacteria produce antibiotics that selectively inhibit the growth of Escovopsis (Currie et al. 1999) and are associated with all attine ants that have been examined (Currie et al.

2006). In Acromyrmex, the bacteria are most abundant on major workers that are most active at the bottom of the fungal garden where Escovopsis is

depends on the availability of other sources of honeydew and nectar (Cushman and Addicott 1989). There is also evidence that host plants can mediate not only the strength of ant benefits to aphids, but also the direction of ant effects (Mooney and Agrawal 2008). Variation in phloem sap quantity or quality may be responsible for mediating these ant–aphid interactions (see also Figure 6.1).

Context-dependency might be particularly prevalent in interactions where ants primarily provide benefit by conferring protection. Most ant visitors (or at least visits) may not benefit the myrmecophile because: (a) the workers do not protect the partner (i.e. when ants are timid or ineffectual against ant-adapted herbivores) or (b) the partner's need for protection does not coincide with interactions with particular ant species or populations (e.g. EFNs: Schemske 1980; hemipterans: Cushman and Whitham 1989; myrmecochores: Fedriani et al. 2004). Perhaps as a result of selection pressures to increase the likelihood that ants can provide appropriate services when that service is required, the spatiotemporal distribution of reward production is correlated with the plant's vulnerability to natural enemies. For example, EFNs are often located in areas where the consequences of herbivory could be severe (e.g. young leaves, at the base of reproductive units; Horvitz and Schemske 1990; Oliveira et al. 1999; Schemske 1980). Likewise, myrmecochores drop seeds during the day, when foraging by granivorous rodents is lessened and the likelihood of seeds being collected by ants is greatest (Cuatle et al

collecting fungal substrates and maintaining suitable fungal growing conditions in return for edible mycelia differ from those of aggressive defense and ingesting sugary secretions (Oliver et al. 2008).

Among facultative associations, there is evidence that the adaptations favouring myrmecophily are evolutionarily labile (i.e. can be acquired and/or lost at the species level of resolution). Hemipteran traits associated with ant tending include modification of honeydew chemical composition, aggregated feeding, longer proboscis length (Bristow 1991, Shingleton et al. 2005), and loss of defensive structures and predator avoidance behaviours (Stadler and Dixon 2005). A complete understanding of hemipteran adaptations to ant-tending is still forthcoming; some of the observed associations between traits and ant-tending are known from single hemipteran lineages, while associations among taxonomically disparate species do not distinguish between evolutionary convergence (as is presumed) and common ancestry. Nevertheless, that myrmecophily is not constrained to any single lineage suggests multiple origins and high lability for mutualism with ants. Consequently, many untended hemipteran species may be only a few evolutionary or ecological steps away from such mutualisms, and adaptations may be subtle. Among ants, adaptations that are correlated with, and perhaps favour, trophobiosis include a modified proventriculus, polygyny, and polydomy (Oliver et al. 2008).

Ant–myrmecochore interactions were not included in the aforementioned phylogenetic analyses. In so far as elaiosomes are dead insect analogues, their collection and utilization by ants may require little specialization or trade-offs with other mutualisms. Further, the repeated independent origins of myrmecochory (Dunn et al. 2007a) and diversity of elaiosome shapes, weights, histological origins, caloric and nutritional content, and manner of diaspore presentation in that guild imply great generalization by the plants. Nonetheless, the existing field observations demonstrate that two ant genera collect a majority of the myrmecochorous seeds in sclerophyllous Australia (Rhytidoponera spp., Figure 6.5; Gove et al. 2007) and temperate North America (Aphaenogaster rudis complex). Whether this consti-

6. .2

include odorants that elicit collection behaviours by workers (e.g. Hughes et al. 1994), and in some cases an elaiosome reward is entirely absent (e.g. Youngsteadt et al. 2008). In some respects, these interactions may function more as 'behavioural usurpation' than a reciprocal exchange of resources. Ecologists have yet to ask whether diaspores will be collected when these compounds are experimentally disassociated with the seed, although we know that other non-rewarding substances impregnated with the volatiles will be collected by workers (e.g. Hughes et al. 1994).

The outcome that benefits the myrmecophile may be a product of strategies that best suit the ant. In such a case, the concept of 'cheating' becomes meaningless. For example, if an ant colony is capable of the vigorous defence of a resource against real or perceived competitors, be they rival colonies, herbivores, or carnivores, it will do so. If it cannot, the opportunity to harvest that resource may well be usurped by a more aggressive colony that provides even greater protection to the reward (plant or insect). On a different vein, Ness et al. (2009)

and benefits of the multiguild relationships await discovery.

6. .5\

Experimental studies have begun to explore the importance of variation in abiotic resources on the evolution and functioning of ant mutualisms. In so far as these resources are limiting, they can alter the incentives for particular interactions. For example, carbon-rich resources such as extrafloral nectar and ant domatia should be less costly for plants to produce where carbon is in excess (Folgarait and Davidson 1994). Perhaps as a result, EFN-bearing plants are common in sunlight-rich habitats such as rainforest canopies (Blüthgen et al. 2000), forest edges (Bentley 1976), and deserts (Pemberton 1988). The influence of resource limitation (or surplus) is also detectable at smaller spatio-temporal scales. Nitrogen fertilization of host plants can increase tending rates of some trophobionts (e.g. lycaenids: Billick et al. 2005, but see Morales and Beal 2006 re. membracids), and alter plant investment in indirect defences (Folgarait and Davidson 1995). Ant mutualisms can also reorganize abiotic resources. The construction, maintenance, and feeding of ant colonies and nests often concentrate resources, expose buried nutrients, and alter moisture retention rates (Moutinho et al. 2003), perhaps to the benefit of their partners (Davidson and Morton 1981; Giladi 2006; Wagner 1997). Remarkably, there is also evidence that tending by ants can alter the nitrogen content of tended hemipterans and their host plants (Kay et al. 2004, but see Abbot et al. 2008). The generality of these documented patterns, and how such modifications will influence the incentives for ant mutualisms, is largely unknown. To make matters more complex (and worthy of attention), the availability of nitrogen and CO_2 continues to increase at scales ranging from individual plants to the biosphere as a result of anthropogenic influences.

6. .6 , , , |

Ant mutualisms are unevenly distributed across habitats. Perhaps problematically, the settings for the research that underpins our understanding of these interactions rarely occur in proportion to the density or diversity of these interactions. How might our understanding of these interactions change if we studied them in the settings where they most often occur? Most studies of myrmecochory (and all that quantify benefit to the ants) focus on temperate deciduous myrmecochores; what do the costs and benefits described in this nutrient-, moisture-, and granivore-rich biome tell us about the >90% of myrmecochores that reside in dissimilar biomes in Australia and South Africa? Might our sense of the costs, benefits, and selection pressures on ant-tended insects and plants differ if we studied them in communities such as tropical rainforest canopies or some deserts where tending by ants is the modal interaction? The characteristics of ants, prospective natural enemies, and competition for services may be sufficiently different in these settings to profoundly alter those interactions. We recognize that particular systems offer advantages for studying particular ecological and/or evolutionary phenomena. However, we propose that the wealth of studies that comprise the current literature and inform reviews, meta-analyses, and our gestalt sense of how interactions function may describe the range and modal version of the interactions only in so far as those studies occur in comparable environments. Our understanding of those interactions will change as we better place our questions in the context of the larger environment.

6.9 Summary

Ants are perhaps the most common and dominant animal mutualists in terrestrial environments. As a result, better understanding the dynamics of these interactions should be a priority for those who hope to understand the taxon, their role in communities, and mutualism as a widespread interspecific interaction. These mutualisms include interactions with ant-loving plants, insects, fungi, and bacteria, with the ants typically receiving food and/or shelter, and their partners receiving food, protection, and/or propagule dispersal. Context dependency, wherein the magnitude of costs and benefits incurred as a result of participation in the interactions varies with the ecological setting may be particularly prevalent

in interactions involving protection by ants. Adapta-