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Host-plant stickiness disrupts novel ant–mealybug association

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Abstract Ants commonly engage in facultative mutualisms with honeydew-excreting homopterans such as mealybugs and other scale insects. Attendant ants obtain a high-energy carbohydrate of predictable availability, while the homopteran trophobiont gains protection from natural enemies and potential benefits of sanitation (honeydew removal), maintenance of host-plant quality, and transport. In a California, USA, arboretum, we observed large numbers of dead and dying Argentine ants (*Linepithema humile*) that had become entrapped on viscid flower buds and flowers of South African species of *Erica* as they attempted to tend a South African mealybug (*Delottococcus confusus*). Mealybugs on viscid ericas were found on clusters of small buds before they had become sticky (and later in other areas that minimized exposure to stickiness). As buds developed, they became viscid, enclosing mealybugs within sticky flower parts and precluding further attendance by ants. Ants, however, were able to tend mealybugs without disruption on nonsticky ericas. Counts ($n = 118$) of haphazardly chosen stems of sticky ericas showed that significantly more dead ants were present on mealybug-infested stems. We suggest that evolutionary histories help explain the disparate outcomes for ants and mealybugs on sticky ericas. The Argentine ant lacks an evolutionary history with sticky ericas, whereas the native South African mealybug presumably shares an evolutionary relationship with species of *Erica* in South Africa's Cape Floristic Region. We propose that the mealybug's behavior and waxy coating are adaptations for circumventing plant stickiness. Our observations might represent the first documentation of plant stickiness disrupting an ant–homopteran association.

Keywords Argentine ant · Mealybug · *Delottococcus confusus* · Waxy secretions · *Erica* · Sticky plants · Ant–homopteran association · Tritrophic interactions

Introduction

The Argentine ant (*Linepithema humile*) is globally widespread and invasive in its introduced range. It forms facultative mutualisms with phloem-feeding, honeydew-excreting homopterans such as aphids, scale insects, and treehoppers (Newell and Barber 1913; Way 1963; Buckley 1987; Ness and Bronstein 2004; Styrsky and Eubanks 2006). Given the propensity for Argentine ants to engage in mutualisms with homopterans, we did not consider it unusual to find *L. humile* on mealybug-infested heaths (*Erica* spp.) in a California, USA, arboretum. Unexpected, however, was our observation of ants dying en masse, entrapped in exudates of sticky species of *Erica*. We observed ant and mealybug behavior on sticky and nonsticky ericas throughout plant development to try to explain the apparently maladaptive behavior of Argentine ants, as well as the mealybug's ability to circumvent host-plant stickiness.

We present observations on a system comprising adventive taxa: the Argentine ant, an immigrant South African mealybug, and South African plants of the diverse genus *Erica*. We suggest explanations for the disparate

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outcomes for ants and mealybugs on sticky ericas and note previous literature references to ants trapped in sticky plant secretions.

Methods

Study site and system

University of California Santa Cruz (UCSC) arboretum

Our study area, the UCSC Arboretum, consists of 40 ha near the southern edge of campus. Santa Cruz, on the northern edge of Monterey Bay, has a Mediterranean climate: cool, rainy winters and warm to hot, dry summers. Annual rainfall on the UCSC campus ranges from 76 to 114 cm, with January the wettest month ($\overline{X} = 17$ cm) and July the driest ($\overline{X} = 0.1$ cm). January also is the coolest month ($\overline{X} = 8.8$ °C), with August the warmest ($\overline{X} = 17.7$ °C) (Haff et al. 2008). A South African garden (36°58.92′N 122°03.67′W; elevation ca. 120 m) in the south-central area of the arboretum includes an extensive *Erica* collection that we used for periodic observations during daylight (1000–1600 h). Diverse soil types characterize the arboretum. Ericas thrive in the South African Garden's nutrient-poor soils (Peterson 2008; UCSC 2013), which resemble the infertile sandy soils of their native Cape Region in South Africa (Cowling et al. 1996; Goldblatt and Manning 2002).

Cape heaths (*Erica* spp.; Ericales: Ericaceae)

The genus *Erica* has undergone spectacular radiation in South Africa's Cape Floristic Region (CFR). About 680 of ca. 840 species in the genus are found in the CFR (Pirie et al. 2011), with endemicity more than 95 % (Goldblatt and Manning 2002). The biome known locally as fynbos (Afrikaans: "fine bush") is fire-prone heathland characterized by evergreen, sclerophyllous shrubs with linear or needlelike leaves (Oliver et al. 1983; Goldblatt and Manning 2002; Linder 2003). Fynbos occupies much of the CFR, includes most of the region's endemic plants, and is analogous to Californian chaparral except that plant diversity in fynbos is greater, soils are more nutrient deficient, and water stress is not as intense (Keeley 1992; Goldblatt and Manning 2002).

Ericas exhibit great diversity in flower color and shape. Corollas are sympetalous, often tubular, and sometimes color polymorphic (Rebelo and Siegfried 1985; Rebelo et al. 1985; Schumann et al. 1992; Goldblatt and Manning 2002). Flower diversity in *Erica* is linked with insect pollinator richness and diversity of pollinator strategies (Rebelo and Siegfried 1985; Rebelo et al. 1985; Goldblatt and Manning 2002). Ericas are pollinated mainly by insects (80 %), including flies with long proboscises (Nemestrinidae, Tabanidae) (Goldblatt and Manning 2000). Except for an apparently rodent-pollinated species (Turner et al. 2011), the remaining species are pollinated by birds (15 %) or wind (5 %) (Rebelo et al. 1985; Pirie et al. 2011). Southwestern Cape ericas rarely are self-fertile (autogamous) (Rebelo et al. 1985).

Flowers can be dry or viscid (Schumann et al. 1992). Certain species of *Erica*, including sticky ericas in the UCSC Arboretum, have large sessile glands on the sepals (marginal or on the inner surface) that produce exudates in the bud stage, resulting in a sticky corolla (Oliver 2000). Corollas of other species are sticky due to exudates from glandular trichomes on the calyx (Schumann et al. 1992; Oliver 2000). Sticky ericas generally produce fewer ovules than nonsticky conspecifics, but the physiological costs of producing exudates might be offset by ecological benefits such as deterring potential nectar-robbing ants and other insects, aiding in seed dispersal (Schumann et al. 1992), and restricting water loss during summer (Vlok and Schutte-Vlok 2003).

Identification of the ericas in our study system was hampered by the establishment of seedlings, probable hybridization, and inaccurate identifications from visitors repositioning plant labels and tags. The red and green-flowered sticky species we observed, and a green-flowered variant, might be *E. unicolor* (possibly also *E. discolor* var. *hebecalyx*). *Erica baueri* and *E. cruenta* were common nonviscid species that served as mealybug hosts. In all cases, we recorded whether focal plants were sticky or not.

Ant (*Linepithema humile*; Hymenoptera: Formicidae)

The Argentine ant is native to major waterways of the Paraná River drainage in northern Argentina and nearby portions of Brazil, Paraguay, and Uruguay (Wild 2004; Wetterer et al. 2009). First collected in South Africa near Cape Town in 1893 (Lounsbury 1909; Wetterer et al. 2009), *L. humile* now is established in Cape fynbos, mainly in disturbed sites (Bond and Slingsby 1984; Donnelly and Giliomee 1985; De Kock and Giliomee 1989) but also in natural environments, where it has disrupted seed mutualisms (De Kock and Giliomee 1989; Witt et al. 2004; Mothapo and Wossler 2011) and displaced floral arthropods (Lach 2008). Although the rate of spread has not been rapid (Richardson et al. 1992) and relatively few protected areas in the Western Cape are infested (Vorster 2011), the ant continues to spread, invading forests via waterways, and threatens Cape biodiversity (Pryke and Samways 2008).

Detected in southern California in 1905 (Smith 1936), *L. humile* soon was recorded from Santa Cruz (Newell and Barber 1913) and is established on the UCSC campus (Haff 2008).

Mealybug (*Delottococcus confusus*; Coccoidea: Pseudococcidae)

The genus is restricted to southern parts of the Afrotropical Region, with at least five species endemic to South Africa. *Delottococcus confusus* apparently is endemic to the Cape Region, where it is found on Proteaceae (*Leucadendron* and *Protea* spp.) and species of several other families (Millar 2002; Miller and Giliomee 2011). This mealybug is intercepted in California by plant regulatory personnel and since 2003 has been collected from proteoid hosts in several California nurseries (Watson 2007; Miller and Giliomee 2011). Females feed and oviposit on the undersides of leaves (Miller and Giliomee 2011), but on ericas, whose leaves are needlelike, they were found on reproductive structures. We did not find the mealybug on proteaceous plants in the arboretum, including *Leucadendron argenteum*, a known host (Miller and Giliomee 2011). Voucher specimens of *D. confusus* from the UCSC arboretum have been deposited in the National Museum of Natural History (USNM), Coccoidea Collection, Beltsville, MD, USA.

Ant–mealybug associations on ericas

On our first trip to the arboretum (April 5, 2011), we were intrigued by the sheer numbers of entrapped ants on sticky ericas. On subsequent visits (July 27, 2011, April 27 and September 25, 2012, March 11–12, 2013, and January 22, 2014), we observed the behavior of Argentine ants as they walked over plant surfaces, interacted with mealybugs on sticky ericas, and became entrapped. We examined flower buds in different developmental stages to determine when they become sticky. Our observations focused on viscid ericas, but we also examined species with nonviscid flowers for mealybugs and attendant Argentine ants. The ant–mealybug interactions on nonsticky ericas in the arboretum probably represent a mutualism, although it is not known if both partners benefit from the association.

We observed the position of mealybugs, both colonies and solitary individuals, on viscid and nonviscid ericas in the arboretum. In addition, stereomicroscopy (Wild M5 Stereomicroscope) was used to observe how mealybugs walked on sticky surfaces. In the field and with stereomicroscopy, we followed the progress of individuals that appeared to be entrapped on sticky corollas to determine whether they could extricate themselves.

Dead ants on mealybug-infested versus uninfested stems

On April 27, 2012, we counted all dead ants on haphazardly selected stems ($n = 118$) of sticky species of *Erica*. We also recorded the presence or absence of mealybugs on each stem. To determine whether ants were stuck more often on mealybug-infested stems, we used least squares analysis of variance comparing abundance of dead ants on stems with and without mealybugs. The analysis was performed using JMP (version 10, SAS Institute Inc., Cary, NC, 1989–2013).

Other arthropods on sticky ericas

We examined sticky ericas for other arthropods, both live and stuck on flower buds and corollas (Fig. 4), and recorded the species that could be identified in the field (e.g., the lady beetle *Coccinella septempunctata*). We collected adults of certain other insects for identification by specialists; voucher specimens are deposited in the University of Georgia Collection of Arthropods, Athens, GA, USA. The identity of a common flower-associated thrips (Thysanoptera) and larvae of an uncommon microlepidopteran was not obtained. Harvestmen stuck in exudates were not collected and were recorded as “Opiliones.” Flowers of viscid and nonviscid species of *Erica* were observed for the presence of potential pollinating

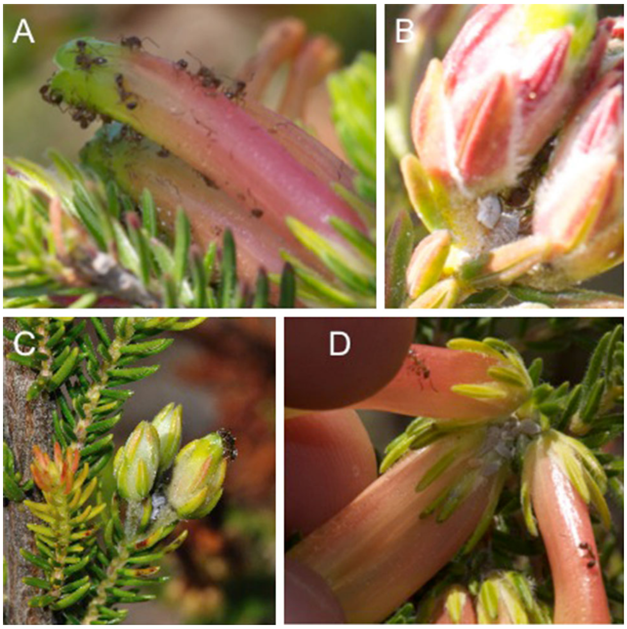

Fig. 1 **a** Ants stuck to mature *Erica* flower cluster infested with mealybugs, **b** ants tending mealybugs during early flower bud development, before buds become sticky, **c** and **d** mealybugs clustered between groups of sticky buds, and dead ants stuck to buds

insects; the presence of honey bees (*Apis mellifera*) was recorded, and an unknown bumblebee species was collected for identification.

Results

Ant–mealybug associations on ericas

On our first visit to the arboretum (April 2011), we observed large numbers of Argentine ants trapped on sticky ericas (Fig. 1a). *Linepithema humile* was the only ant species found on viscid and nonviscid ericas. On additional visits, we found an Argentine ant nest in a length of old redwood fencing that delimits erica beds in the South African Garden. A mealybug, later identified as the South African *D. confusus*, had colonized flower buds of different sizes. Newly initiated buds of viscid ericas lacked stickiness, but as they enlarged, they became coated with exudates. Ant–attended mealybugs were visible at the bases of small, nonviscid flower buds (Fig. 1b); with bud development, mealybugs became enclosed within viscid, multipedicelled clusters of larger buds (Figs. 1c, d). Flower buds apparently grow around the mealybug colonies. The position of mealybugs inside clusters of larger buds prevented ants from tending them without contacting sticky exudates.

Ants became entrapped as they walked onto the larger, sticky buds and probed mealybugs with their antennae (Fig. 2). Ants also attempted to remove trapped conspecifics, which often resulted in their own entrapment. Intact ants, as well as scattered antennae, heads, legs, and abdomens were stuck to buds and corollas (Figs. 1, 2).

In contrast to unsuccessful attempts by Argentine ants to engage in potential mutualisms with mealybugs on sticky ericas, ants were able to tend mealybug colonies on nonviscid ericas. Dead ants were not found on nonviscid, mealybug-infested species of *Erica.*

Fig. 2 Ants tend to walk across petals and become entrapped while searching for mealybugs or attempting to remove entrapped conspecifics

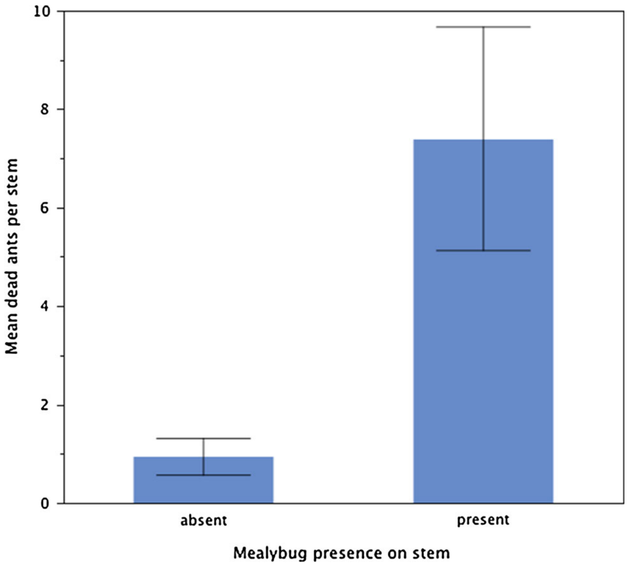

Fig. 3 Average dead ants counted on stems with and without mealybugs. Error *bars* denote standard error. Least *squares* model; $df = 1$; $F = 9.54$; $p = .0025$; 65 plants without mealybugs and 53 with mealybugs

On sticky ericas, one or two mealybugs typically occupied a pubescent, nonviscid area (ca. 1 mm^2) where pedicels of a bud cluster join. Mealybugs, usually only one or two, also were found under sepals, their wax-coated dorsum appressed to the inner, viscid surfaces. Single mature females occasionally were observed on external surfaces of viscid corollas, apparently dead or unable to move. When we returned to an "embedded" individual ca. 30 min later, we found that it occupied a different position on the corolla. Under stereomicroscopy, mealybugs thought to be stuck were observed walking so slowly that movement would have been imperceptible in the field. If legs became embedded in exudates, the mealybug arched its body, pressing the tip of its abdomen to the substrate, which elevated the head and forelegs from the sticky surface; in addition, wax from anal-ring pores apparently was applied to the plant surface. The forelegs, thus freed from exudates, were lowered to the surface, and walking resumed; when necessary, the behavior was repeated.

Dead ants on mealybug-infested versus uninfested stems

Our counts of dead ants on haphazardly selected stems of sticky ericas show that dead ants were more abundant on mealybug-infested stems ($n = 53$), compared with stems lacking mealybug infestation [Fig. 3, $F(df = 1) = 9.54$, $n = 65$, $p = .0025$].

Other arthropods on sticky ericas

Except for the immigrant mealybug *D. confusus*, the only other herbivores that appeared to be reproducing on sticky ericas were a tiny aphid (*Aphis* sp.), a seed-feeding lygaeid bug (*Kleidocerys* sp.), an undetermined thysanopteran, and a microlepidopteran whose larvae fed on floral buds. Live and embedded (Fig. 4b) adults of the chrysomelid *Altica prasina prasina* ($n = 9$) also were observed, but the presence on viscid ericas of this *Populus*- and *Salix*-feeding beetle (LeSage 1995) probably is incidental.

Honey bees visited flowers of sticky ericas; a dead adult was stuck on a corolla. Honey bees more often appeared to visit flowers of nonsticky species such as *E. baueri and E. cruenta*. A bumble bee (*Bombus vosnesenskii*) visited flowers of *E. caffra*, another nonviscid species.

Among predatory taxa, a dead adult anthocorid bug was embedded in exudates, as were adults of the lady beetles *C. septempunctata* ($n = 2$) and *Exochomus quadripustulatus* ($n = 6$). Two adults of *E. quadripustulatus* also probed mealybug-infested bud clusters. This Palearctic lady beetle was introduced to California from Italy for the biological control of scale insects (Clausen 1956; Gordon 1985). The immature harvestmen (Opiliones) that were embedded in exudates ($n = 4$) might forage nocturnally for entrapped insects.

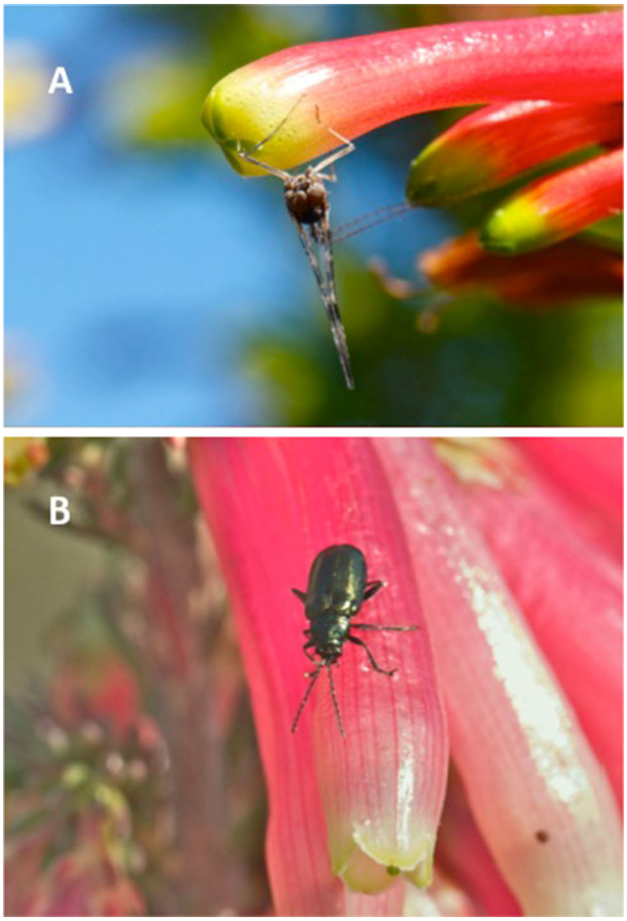

Fig. 4 Large insects stuck to sticky *Erica* flower: **a** mayfly and **b** chrysomelid beetle (*Altica prasina*)

Discussion

We observed a system comprised of adventive taxa—ant, mealybug, and both nonsticky and sticky species of *Erica*. Two other studies of ant–hemipteran interactions or mutualisms also comprise non-native species (Helms et al. 2011; Stanley et al. 2013), although their systems involved nonviscid plants. In our study, the ant–mealybug association—a possible mutualism—was established on nonviscid species of *Erica*. On sticky ericas, however, ants were precluded from tending mealybugs, except on small buds not yet coated with exudates. Certain thistles (*Cirsium* spp.) undergo a similar development of stickiness; involucral bracts begin to become sticky before buds open, late-stage buds are >75 % sticky, and stickiness is retained throughout the flowering period (Willson et al. 1983).

The immigrant South African mealybug (*D. confusus*) in our system previously was thought to have been eradicated from California nurseries and not established in the state (Miller and Giliomee 2011). Exotic trophobionts in invaded areas often are tended by invasive ants (Ness and Bronstein 2004). Because mutualism and facilitation can play a role in the success of invasive species (Simberloff and Von Holle 1999), synergistic interactions between the invasive Argentine ant and the adventive *D. confusus* on nonviscid ericas might have facilitated the latter's establishment in the UCSC Arboretum. Availability of novel food resources, such as hemipteran honeydew, at introduced locales not only may promote the abundance of Argentine ants (Helms et al. 2011), but also might be crucial in facilitating colony establishment from low propagule pressure (Shik and Silverman 2013).

Massive insect deaths on sticky plants similar to those of ants and other insects on ericas have been reported, but not within the context of ant–hemipteran mutualisms. Darwin's (1875) observations of a viscid nyctaginaceous plant (*Mirabilis longiflora*) appearing "dusted" with entrapped beetles and flies were followed by those of Stone (1881) on dead and dying ants stuck on stems of the caryophyllaceous *Silene viscaria.* The myrmecologist W. M. Wheeler (1906) provided additional examples of maladaptive ant behavior resulting in death, but none involved entrapment on sticky plants. Exudates on bracts of thistles in Minnesota, USA, trapped insects, mostly two ant species; one tended thistle-feeding aphids (Willson et al. 1983), but possible disruption of an ant–aphid mutualism by host-plant stickiness was not suggested. In Brazil, more than 90 % of ants observed on a sticky asteraceous shrub (*Trichogoniopsis adenantha*) were entrapped in the plant's sticky trichomes, although large ants in the genus *Camponotus*, which tended treehoppers (Hemiptera: Membracidae), were not affected by host-plant stickiness (Romero and Vasconcellos-Neto 2003). Ants also were among the most common insects entrapped in sticky exudate on flowers of a bromeliad (*Vriesea bituminosa*) in Brazil (Monteiro and Macedo 2014). Argentine ants visiting sticky flowers of *Silene lanceolata* in Hawaii can become entrapped, but others are able to access nectar by crawling over carcasses of conspecifics (Slemmons 2008), similar to how Argentine ants breach Tanglefoot® (Phil Ward, pers. comm.). We did not observe similar bridging behavior by Argentine ants on viscid ericas. Argentine ants in a South African study of proteas were attracted to, and showed a preference for, sticky bracts as a nectar source on inflorescences, even though ants sometimes became entrapped (Lach 2013). The proteas in Lach's (2013) study might not have been as sticky as the ericas in our system.

The abundance of dead Argentine ants and other insects on sticky ericas in the UCSC Arboretum might attract facultative scavengers. Such detritivores can affect food webs and community structure (Wilson and Wolkovich 2011; Krimmel and Pearse 2013). We did not, however, observe feeding on insect carrion in the arboretum. Potential scavengers, such as lady beetles (coccinellids are opportunistic necrophages; Wheeler 1971), and the typically nocturnal (Allard and Yeargan 2005) opilionids, sometimes succumbed to the stickiness of erica buds and corollas.

Insect species richness of nonviscid and viscid species of *Erica* in the arboretum was low. We suggest that the lack of insect diversity on ericas should not be attributed mainly to adverse effects from Argentine ants, but rather to absence of *Erica* specialists in the local fauna and minimal recruitment of local generalist herbivores, as well as the stickiness of certain *Erica* species.

The Argentine ant and mealybug, the most numerous insects on ericas in the arboretum, contrast in their ability to survive on sticky species. Certain insects have evolved adaptations allowing them to move safely over sticky plant surfaces (Voigt and Gorb 2008; Wheeler and Krimmel 2015). Evolutionary history is considered a key predictor in whether insects are able to exploit plant resources (e.g., Pearse and Hipp 2009), and this may be particularly important in well-defended plants, such as sticky plants. On sticky ericas, consideration of probable evolutionary histories of the Argentine ant and South African mealybug might help explain why the ant becomes entrapped in exudates, whereas the mealybug, which presumably shares an evolutionary relationship with endemic Cape ericas, does not.

Insect diversity in South African fynbos, once considered low relative to adjacent biomes, is comparably species-rich (Davies 1988a, b; Wright and Samways 1998; Procheş and Cowling 2006). The relatively scant information on insect herbivory in fynbos (Johnson 1992) has focused mainly on proteaceous plants (Coetzee 1989; Visser et al. 1996). A lack of knowledge regarding plant-feeding insects in fynbos apparently extends to South African species of *Erica*, including mealybugs and other scale insects. The feeding of an unidentified scale insect (subsequently identified to family level: Coccidae; G. L. Miller, pers. comm.) resulted in dead branches and death of ericas in the Western Cape in 2006 (Maneveldt 2008). No published record from endemic Cape heaths is available for the mealybug *D. confusus*, which now is established in the UCSC Arboretum. The South African National Collection of Insects, Pretoria, however, has specimens with labels indicating the mealybug's collection from *E. sessiliflora* in the Cape Region (J. L. Giliomee, pers. comm.). Although *E. sessiliflora* has nonviscid flowers, sticky ericas also might serve as hosts of the mealybug.

The behavior of *D. confusus* appears to minimize its vulnerability to viscid host exudates. After stickiness is initiated on viscid ericas, mealybugs typically occupy the small pubescent area ("crotch") at the base of multipedicelled flower buds, which provides a nonsticky substrate. When walking on sticky corollas, the mealybugs move so slowly as to appear stuck in exudates. Unlike many other mealybugs, species of *Delottococcus* lack a circulus (adhesive organ on the abdominal venter), which adheres to a substrate on which walking becomes difficult, such as a smooth surface; with the circulus appressed to the substrate, the legs move exploratorily to secure a foothold so that forward movement can resume (Lloyd and Martini 1957; Gullan and Kosztarab 1997). Although lacking a circulus, *D. confusus* apparently can extricate itself from sticky surfaces by pressing the tip of the abdomen against the substrate, which raises the head and forelegs. During this behavior, the mealybug appeared to apply wax from its abdominal area to the surface. Some individuals of *D. confusus* feed between a sepal and flower, with their dorsum against the sepal's viscid inner surface. The mealybug's largely sedentary habits would minimize the risk of becoming stuck in exudates. The waxy coating of mealybugs that is thought to protect against desiccation, natural enemies, and contamination by their honeydew (Gullan and Kosztarab 1997) also might help prevent entrapment in sticky exudates. Mealybug wax might function similarly to scales on a moth wing that serve as "detachable 'powder'" upon contact with sticky silk of spider webs. Viscid strands of silk that become coated with lepidopteran scales lose their adhesiveness (Eisner 2003). Insects coated with powdery wax also are less likely to become stuck in spider webs (Eisner et al. 1964).

The mealybug *D. confusus* in its behavior and morphology appears adapted to living on sticky plants. A somewhat similar combination of behavioral and physical attributes allows a reduviid bug (*Stenolemus lanipes*) to live in spider webs without becoming stuck in sticky silk (Snoddy et al. 1976). The sedentary habit and waxy coating of adult female mealybugs are adaptations for a plant-parasitic lifestyle (Gullan and Kosztarab 1997). Whether the apparent ability of *D. confusus* to free itself when stuck in exudates is unusual in the Pseudococcidae is not known. We are unaware of studies on the use of sticky plants by mealybugs. Even so, the ability of this South African mealybug to circumvent host stickiness and live on sticky ericas in a novel environment supports our supposition of an evolutionary relationship with viscid species of *Erica* in its native Cape Region of South Africa.

Argentine ants are broadly omnivorous, colonize plants having diverse surface features, and lack an evolutionary history with glandular species of *Erica* in South Africa, which might explain their inability to walk on sticky ericas. Clearly, there is a cost to the ant colony in terms of lost workers. The ants' interaction, however, might not be detrimental but result in a neutral or positive outcome if the energy they derive from mealybugs before plants become sticky balances or outweighs the costs of their mortality. Further work is needed to determine the fitness consequences for all three players involved in this interaction. Presumably, homopteran-tending ant species native to the Santa Cruz area would face similar challenges on sticky *Erica* flowers, although we did not observe native ants in the arboretum.

Ants do not merely collect homopteran honeydew but, in food patches, can assess nutritive quality and mortality risks (e.g., other ant species); their foraging thus tends to maximize colony fitness (Nonacs and Dill 1990; Nonacs and Calabi 1992; Stadler and Dixon 2005). Ants, however, might not be able to perceive risks of foraging on sticky plants. In the case of *L. humile*, adapting to specific plant defenses such as stickiness might impair the fitness of a generalist forager. Some native ant in the South African Cape might be better adapted for dealing with sticky ericas than is the Argentine ant; future work is needed to test this.

It is difficult to place our observations in an adaptive framework because not all the interacting species share an evolutionary history. Yet, our observation that the Argentine ant mostly was excluded from sticky ericas, coupled with its determent of pests' natural enemies that allows pest populations to increase (Haney et al. 1987), supports the conventional view that stickiness and other plant defenses exclude potentially damaging insects. It is less clear how stickiness affects the mealybugs, particularly with ants being excluded from tending them. Exclusion could be costly to the mealybugs; parasites, predators, and pathogens might become more of a threat on untended plants (e.g., Bartlett 1961). The mealybugs might also lose the potential for dispersal benefits from the ants. But if the stickiness of ericas excludes most predators, then benefits to the mealybugs of ant attendance would be greatest before stickiness is expressed. If ants prey on the mealybugs, in addition to feeding on their honeydew, the mealybugs could benefit from excluding ants once the plants become sticky and other predators are excluded. Tests of these hypotheses await future research.

Stickiness in plants is dynamic due to plant development and myriad environmental factors such as rain, wind, and dust (Obrycki and Tauber 1984). Our study highlights how a dynamic system can affect species interactions. In our study, plants facilitated mealybug–ant interactions before floral development. As flower buds emerged and became coated in sticky secretions, the same plants no longer were suitable for ant–mealybug interactions. Our study also demonstrates how a single plant trait—stickiness—has divergent effects on different species of insects. The mealybug continued feeding on plants when they became sticky, whereas the Argentine ants became entrapped and died. That the mealybug is from the same region as the sticky ericas, but the ant is not, might explain this difference.

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