

CHAPTER SEVENTEEN

Multitrophic interactions in a neotropical savanna: ant–hemipteran systems, associated insect herbivores and a host plant

PAULO S. OLIVEIRA

Universidade Estadual de Campinas

KLEBER DEL-CLARO

Universidade Federal de Uberlândia

Introduction

In many habitats ants form a major part of the arthropod fauna found on vegetation, and recent studies have shown that the abundance and diversity of ant–plant associations is particularly remarkable in the tropical region. For instance, one-third of the plant species in a Panamanian forest (Schupp & Feener 1991) and over 20% of the woody species in a Brazilian savanna (Oliveira & Oliveira-Filho 1991) were found to produce ant rewards. Furthermore, 312 ant–plant interactions were recorded in one Mexican coastal site (Rico-Gray 1993), and the ant–plant community in an Amazonian rainforest comprised 377 plants per ha (Fonseca & Ganade 1996). In the tropics many ant species use plant surfaces as a foraging substrate to search for both live and dead animal prey, as well as for different types of plant-derived food products (Carroll & Janzen 1973). Ant activity on foliage can be promoted by the occurrence of predictable and immediately renewable food sources, including extrafloral nectar, honeydew from phloem-feeding hemipterans, and secretions from lepidopteran larvae (see Way 1963; Bentley 1977; Buckley 1987; Koptur 1992; Pierce *et al.* 2002). In fact, plant- and insect-derived liquid foods appear to provide a large amount of the energy supply of foliage-dwelling ants (Tobin 1994; Davidson *et al.* 2003). Although food resources located on foliage are probably more often found and exploited by arboreal species, ground-nesting ants frequently extend their foraging areas onto the plant substrate as well (Rico-Gray 1993; Blüthgen *et al.* 2000; Davidson *et al.* 2003). Intense ant activity on vegetation has resulted in a multitude of ant–plant–herbivore interactions, ranging from facultative to obligate associations (reviewed by Beattie 1985; Davidson & McKey 1993; Bronstein 1998). From the

plant's standpoint, the outcomes of many of these interactions are largely mediated by how ant behavioural patterns can affect herbivore performance on a given host plant (Chapters 15 and 16, this volume).

Ant patrolling activity on leaves may affect insect herbivores in different ways, and this in turn may result in positive, negative or neutral consequences for plants (Bronstein 1994a, b; Beattie & Hughes 2002). The distribution of ants within the plant crown and their behaviour towards herbivores may depend on the nature of the food source being exploited by the foragers (e.g. McKey 1984; Völkl 1992; Oliveira 1997, this volume). For instance, liquid food is typically supplied on foliage in the form of extrafloral nectar and insect honeydew, and general aggression exhibited by ants at these two sources ('ownership behaviour', see Way 1963) can have consequences that are markedly variable, both for the herbivore and for the plant (Oliveira *et al.* 2002; Beattie & Hughes 2002, and citations therein). By showing aggressive behaviour towards herbivores on extrafloral nectary-bearing plants, visiting ants can positively affect plant fitness by decreasing herbivore damage to vegetative and reproductive plant parts (reviewed by Koptur 1992). On the other hand, by protecting sap-feeding hemipterans from their natural enemies, honeydew-gathering ants can negatively affect plant fitness by increasing hemipteran damage to the host plant (Rico-Gray & Thien 1989). However, the outcomes of such plant-ant-herbivore systems may not always be so straightforward; whereas some studies have demonstrated that ant visitation to extrafloral nectaries may afford no apparent benefit to plants, others have shown that ant-Hemiptera interactions may be beneficial to the host plant (see reviews in Beattie 1985; Koptur 1992; Beattie & Hughes 2002).

Three decades ago, Carroll and Janzen (1973) first suggested that honeydew-producing hemipterans could function as insect analogues of extrafloral nectaries because of tending ants' deterrence of other herbivores associated with the plant. In short, ant-Hemiptera interaction could positively affect plant fitness if the benefits of ant-derived protection from herbivory outweighed the losses incurred by hemipteran feeding (Carroll & Janzen 1973; Janzen 1979). In theory, in order for the ant-hemipteran association to affect plant fitness positively, the ant-tended partner should not be the primary herbivore, and the ants should effectively deter non-hemipteran herbivores (Messina 1981; see also Horvitz & Schemske 1984 on ant-tended lepidopteran larvae).

A number of factors (e.g. time, habitat type, identity, abundance and behaviour of species partners, and severity of herbivore damage) may influence the final results of plant-ant-herbivore associations, and only by considering the variation of associated costs and benefits inherent in these systems can we understand their complex dynamics and the range of possible outcomes (Thompson 1988; Cushman 1991; Bronstein 1994a, b; Gaume *et al.* 1998). Although mutualism is defined as an interaction between two species that is beneficial to both (Boucher *et al.* 1982), some mutualisms can only be understood in the context of the



Figure 17.1 Schematic outline of the interaction system involving ants and *Guayaquila xiphias* treehoppers on shrubs of *Didymopanax vinosum* in the cerrado savanna of Brazil. (A) *G. xiphias* prefers to aggregate at the apex of the single reproductive branch. Tending ants collect honeydew from treehoppers day and night, and have a positive impact on treehopper survival. Ant presence reduces the abundance of the principal natural enemies of *G. xiphias*, (B) salticid spiders, (C) predatory syrphid flies and (D) parasitoid

community, and by assessing the influence of other species and other trophic levels on the pairwise relationship (reviewed by Bronstein & Barbosa 2002) (this volume).

In this chapter we report on our research on ant–plant–herbivore interactions in the cerrado savanna of Brazil, with special emphasis on ant–Hemiptera interactions and their effects on associated insect herbivores. We first present the natural history of the study system, present experimental data supporting ant-derived benefits to hemipterans, and describe the relevant behavioural aspects involving the participant species. In the second part we examine the ways through which ant–hemipteran associations can affect damage from different types of associated herbivores, illustrate the intricacy of the effects and infer the consequences of such multitrophic systems for the host plant. Finally, we emphasize the relevance of multitrophic systems for community ecology and conservation of biodiversity.

Ant–Hemiptera interactions in the cerrado savanna

The treehopper Guayaquila xiphias and its ant attendants

In the cerrado of Mogi-Guaçu (SE Brazil; 22° 18' S, 47° 10' W), aggregations of *Guayaquila xiphias* (Fabr.) (Membracidae) commonly infest shrubs of *Didymopanax vinosum* March. (Araliaceae), where they are tended by a diverse assemblage of honeydew-gathering ants. The vegetation consists of a dense scrub of shrubs and trees, known as cerrado *sensu stricto* (Oliveira-Filho & Ratter 2002). Treehoppers occur on *D. vinosum* throughout the year, and levels of infestation on a plant range from one female with her egg mass to over 200 individuals in a single aggregation (mean \pm SD = 18.8 \pm 23.6; no. of aggregations $N = 222$). Although females of *G. xiphias* show parental care by guarding the egg mass and young nymphs, in the presence of ants they may abandon the first brood to ants and produce an additional clutch. Nymphs complete their development about 3 weeks after hatching, and newly emerged adults disperse from natal aggregations. The treehoppers are normally located on stems and feed near growing meristems, but in the flowering season (March to September) they tend to aggregate close to the inflorescence at the apex of the single reproductive branch (Fig. 17.1). Across diurnal and nocturnal censuses, a total of 21 ant species have been recorded collecting honeydew from *Guayaquila* aggregations, the most frequent ones being *Camponotus rufipes* Fabr., *C. crassus* Mayr, *C. renggeri* Emery

← wasps. (E) Untended or poorly tended treehopper aggregations and brood-guarding females attract ants by flicking accumulated honeydew onto lower leaves and beneath the host plant. Upon discovering scattered honeydew droplets on the ground, alerted ants eventually find the treehoppers as they climb onto the plant, and begin tending activities at the newly discovered food source. See text for further details.

(Formicinae) and *Ectatomma edentatum* Roger (Ponerinae). Daily turnover of ant species at a given treehopper aggregation occurs frequently (an account of the whole ant assemblage is given by Del-Claro & Oliveira 1999). The relevance of hemipteran honeydew as an energy (and perhaps water) supply for cerrado ants is such that some species (*C. rufipes* and *E. edentatum*) tend *Guayaquila* on a round-the-clock basis, and *C. rufipes* may even build satellite nests of dry grass to house groups of treehoppers. Indeed, even after having discovered an alternative sugar source on the host plant, honeydew-gathering ants do not desert *Guayaquila* aggregations and keep tending levels unchanged (Del-Claro & Oliveira 1993).

Treehoppers are attacked by three main types of natural enemies on shrubs of *D. vinosum* (see Fig. 17.1). A total of 15 species of salticid spiders may prey on nymphs and adults. Predatory larvae of *Ocyrtamus arx* (Fluke) (Diptera: Syrphidae) suck empty the entire body contents of the treehoppers, and occasionally feed on egg masses if no nymph or adult treehopper is present on the plant. Treehopper egg masses are parasitized by *Gonatocerus* wasps (Myrmaridae).

How tending ants benefit *Guayaquila xiphias*

A series of controlled ant-exclusion experiments performed in the cerrado enabled us to assess the nature of the benefits afforded by tending ants to *G. xiphias*, and identify the variable outcomes of the interaction (Del-Claro & Oliveira 2000). In March 1992 and 1993 we tagged 44 *D. vinosum* shrubs (1–2 m tall). Each plant had one incipient aggregation (*G. xiphias* female with her brood), and was randomly assigned to a control (ants present; $N = 22$ plants) or treatment group (ants excluded; $N = 22$ plants). Ants were prevented from climbing onto treated plants by applying sticky Tanglefoot resin to the trunk base, and pruning grass bridges within 0.5 m. Treehoppers and their natural enemies were censused every 2–3 days on control and treatment plants during 16 days (08.00 to 16.00 h). The occurrence of a second egg mass laid by the resident treehopper female was also recorded in each plant class. In both years of experimental manipulations the initial size of treehopper aggregations did not differ between control and treatment plants.

Increased ant density near *Guayaquila* aggregations markedly affected the spatial distribution and foraging behaviour of spiders, syrphid flies and parasitoid wasps on the host plant. Spiders were not only warded off from the vicinity of the treehoppers by tending ants, but also jumped off the plants after attacks by large ants such as *C. rufipes* and *E. edentatum*. The two ant species were also seen attacking adult syrphid flies near treehopper aggregations. Aggression by tending ants was strong enough to keep parasitoid wasps away from brood-guarding females, and significantly decreased their success in approaching the egg mass. Whereas on ant-excluded plants the wasps were more frequent near (< 5 cm) hemipteran egg masses, on ant-visited plants they were seen mostly on leaves (Fig. 17.2).

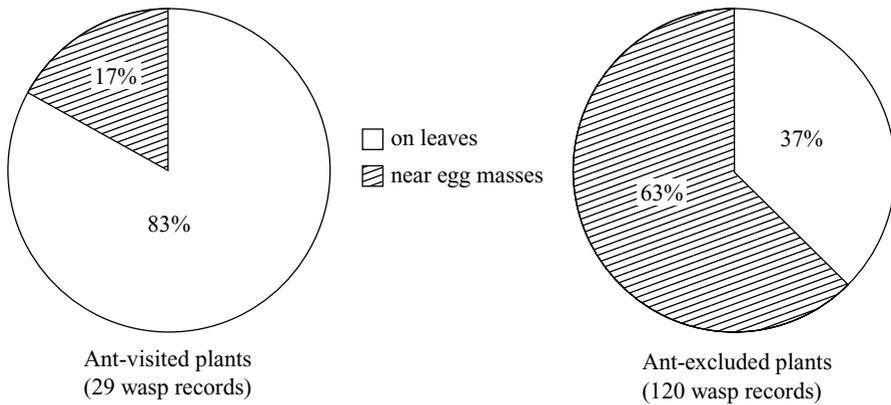


Figure 17.2 Distribution of parasitoid wasps (*Gonatocerus* sp.) on shrubs hosting *Guayaquila xiphias* treehoppers in the presence or absence ($N = 22$ plants in each group) of tending ants. The spatial distribution of wasps (on leaves versus near egg masses) is significantly affected by ant attendance to brood-guarding females ($\chi^2 = 17.46$, $P = 0.001$, d.f. = 1). Modified from Del-Claro & Oliveira (2000).

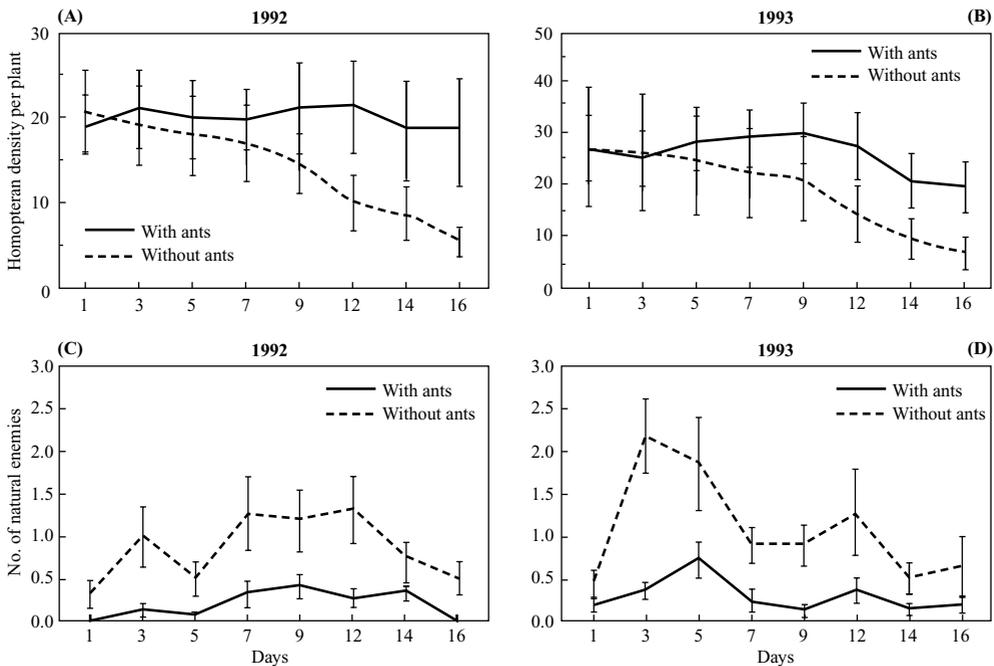


Figure 17.3 Density of *Guayaquila xiphias* treehoppers per plant through time in the presence or absence of tending ants ($N = 22$ plants in each group), in (A) March 1992 and (B) 1993. Ant tending had a positive effect on treehopper survival in 1992 (treatment \times time: $F = 4.33$, d.f. = 7, $P = 0.0001$), but not in 1993 ($F = 1.11$, d.f. = 7, $P = 0.35$). Ant presence decreased significantly the abundance of natural enemies of *Guayaquila* on plants, in (C) 1992 (treatment: $F = 11.54$, d.f. = 1, $P = 0.0015$) and (D) 1993 ($F = 11.51$, d.f. = 1, $P = 0.0015$). Values are means ± 1 SE. Repeated-measures ANOVA performed on square-root transformed data. Modified from Del-Claro & Oliveira (2000).

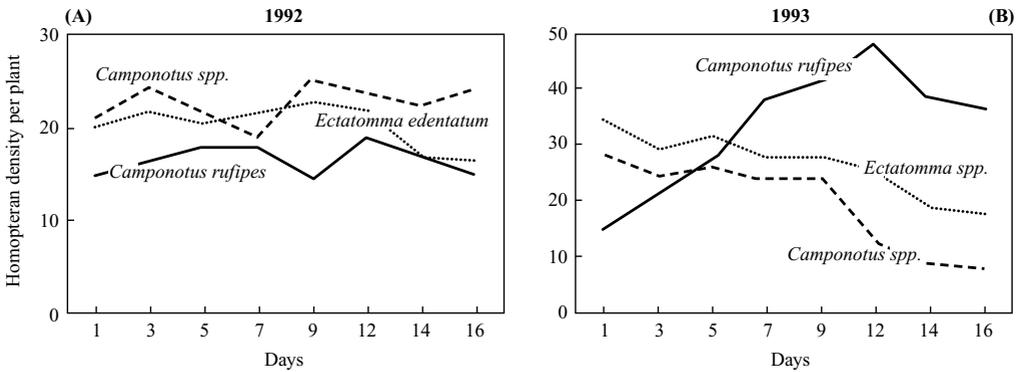


Figure 17.4 Density of *Guayaquila xiphias* treehoppers per plant through time as a function of the species identity of ant partners. (A) 1992: Group 1. *Camponotus rufipes* ($N = 6$); Group 2. *C. crassus*, *C. renggeri*, and *C. sp.* ($N = 7$); Group 3. *Ectatomma edentatum* ($N = 9$). (B) 1993: Group 1. *C. rufipes* ($N = 6$); Group 2. *C. crassus*, *C. aff. blandus*, and *C. renggeri* ($N = 7$); Group 3. *E. edentatum* and *E. planidens* ($N = 9$). While in 1992 all ants had a positive impact on *Guayaquila* (treatment \times time: $F = 0.5$, d.f. = 14, $P = 0.93$), in 1993 ant-derived benefits to homopteran survival differed among the species (treatment \times time: $F = 5.16$, d.f. = 14, $P = 0.0001$). Values are means. Repeated-measures ANOVA performed on square-root transformed data. Modified from Del-Claro & Oliveira (2000).

The ant-exclusion experiments unequivocally demonstrated that tending ants have a positive impact on treehopper survival, and decrease the abundance of the natural enemies of *Guayaquila* on the host plant (Fig. 17.3). Two years of experimental manipulations, however, have shown that ant-derived effects on hemipteran survival can vary both with time and with the species of tending ant (Figs. 17.3, 17.4). Whereas in 1992 *Camponotus* and *Ectatomma* species were equally beneficial to *Guayaquila*, in 1993 only *C. rufipes* had a positive effect on treehopper survival (Fig. 17.4). The experiments also revealed that ant-tending can positively affect treehopper fecundity, because brood-guarding females transfer parental care to ants and lay an additional clutch more often than untended females (91% vs. 54% of the cases; $N = 22$ females in each group; $P = 0.018$, $\chi^2 = 5.61$, d.f. = 1).

Enhancement of interaction through treehopper behaviour

Accumulated honeydew can be flicked by untended phloem-feeding hemipterans with the hind legs or caudae, or by contraction of the rectum or entire abdomen (Hölldobler & Wilson 1990). Although the occurrence of scattered honeydew droplets beneath untended or poorly tended hemipterans has long been noted (e.g. Way 1954; Douglas & Sudd 1980), only more recently has the flicking of honeydew been investigated experimentally and its consequences for ant-Hemiptera interaction evaluated in greater detail (Del-Claro & Oliveira 1996). Aggregations

of *Guayaquila xiphias* are never seen unattended by ants in the cerrado, and constancy of ant-tending is due largely to the treehopper's capacity to provide cues that promote contact with potential ant partners on the host plant. Upon oviposition, while sitting on egg masses, or while guarding newly enclosed nymphs, females of *G. xiphias* commonly flick accumulated honeydew onto lower leaves and onto the ground beneath the host plant (Fig. 17.1). We first speculated that honeydew flicking by the female could function to attract ants at early stages of brood development (Del-Claro & Oliveira 1993). We noted, however, that developing nymphs in poorly tended aggregations also show the same behaviour. In view of the important benefits afforded by ant-tending to both female and brood (see above), promotion of early contact with ants would presumably be highly advantageous for *Guayaquila*. Indeed, field observations of ants (*Camponotus*, *Cephalotes* and *Ectatomma*) at flicked honeydew strongly supported the hypothesis of ant attraction. Upon discovering the droplets on the ground, the alerted scout ant typically searches around the immediate vicinity and eventually climbs onto the host plant (Fig. 17.1). While ascending the plant the forager further licks additional flicked honeydew scattered on lower foliage (Fig. 17.1), and eventually encounters the female and her brood near the apical meristem. The ant then collects some secretion from the nymphs and returns directly to the nest nearby, where additional workers are recruited to exploit the newly discovered food source. The ant colony then establishes a long-term fidelity to the path leading to the treehoppers, and tending activities endure as the nymphs develop. In a series of field experiments we were able to demonstrate that flicked honeydew induces ground-dwelling ants to climb onto the host plant and begin tending activities. Pieces of honeydew-soaked filter paper placed beneath treehopper-free plants induced significantly more ground-dwelling ants to climb onto the plant than did control water-soaked papers (Del-Claro & Oliveira 1996).

Ant-*Guayaquila* interactions, associated herbivores, and host plant

Damage by associated herbivores to Didymopanax vinosum

Shrubs of *D. vinosum* are infested by four principal non-hemipteran insect herbivores: (1) *Liothrips didymopanicis* Del-Claro & Mound (Thysanoptera: Phlaeothripidae): thrips consume the apical leaf primordia and young leaves. Feeding damage alters host-plant architecture by causing folding of leaves, and by leading to growth of lateral shoots due to death of the apical meristem (Fig. 17.5A, B). Severe damage by thrips may cause death of the host plant (Del-Claro & Mound 1996). While moving between folded leaves and shoot tips, the thrips may become vulnerable to tending ants, and predation by *Camponotus rufipes* and *Cephalotes pusillus* (Klug) was observed twice on plants with *Guayaquila* treehoppers. (2) *Caralauca olive* Jesmar (Coleoptera: Chrysomelidae): adults mate on the host plant and feed mainly on mature adult leaves. Chewing activity

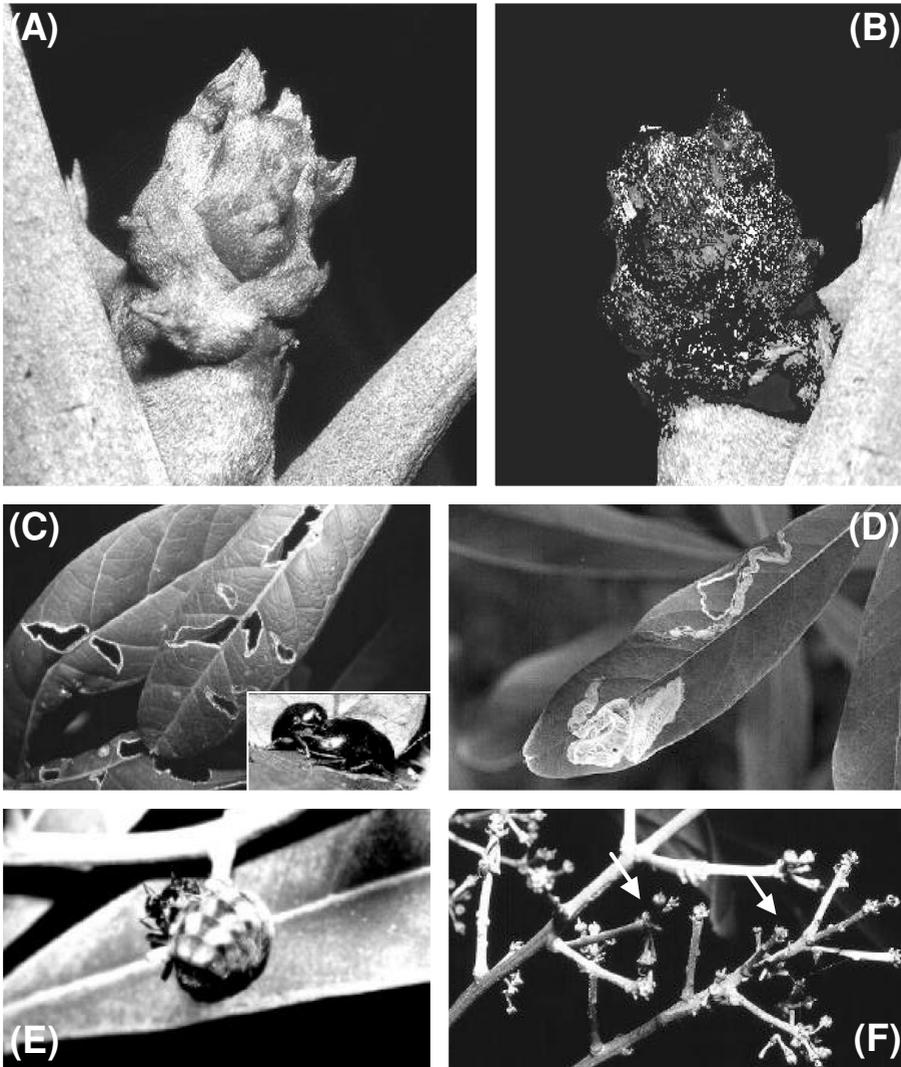


Figure 17.5 Types of herbivore damage to *Didymopanax vinosum* shrubs in cerrado savanna. (A) An intact meristem and (B) an apical meristem entirely destroyed by *Liothrips didymopanicis* thrips. (C) Leaves with characteristic chewing marks made by *Caralauca olive* beetles (inset), and (D) mines made by developing lepidopteran larvae. (E) A larva of *Panthiades polibetes* resting on a floral bud while tended by *Camponotus*. (F) Inflorescence of *D. vinosum* presenting signs of floral damage (arrows) by *P. polibetes* feeding activity.

by the beetles produces characteristic marks on leaf blades (Fig. 17.5C). (3) Leaf-miners (Lepidoptera, undetermined family): mining/feeding activity by developing larvae leaves easily detectable tunnels within the leaf blade (Fig. 17.5D). (4) *Panthiades polibetes* Cramer (Lepidoptera: Lycaenidae): larvae feed on floral buds (diameter 2 mm). The cryptic caterpillars rest on floral buds and are tended

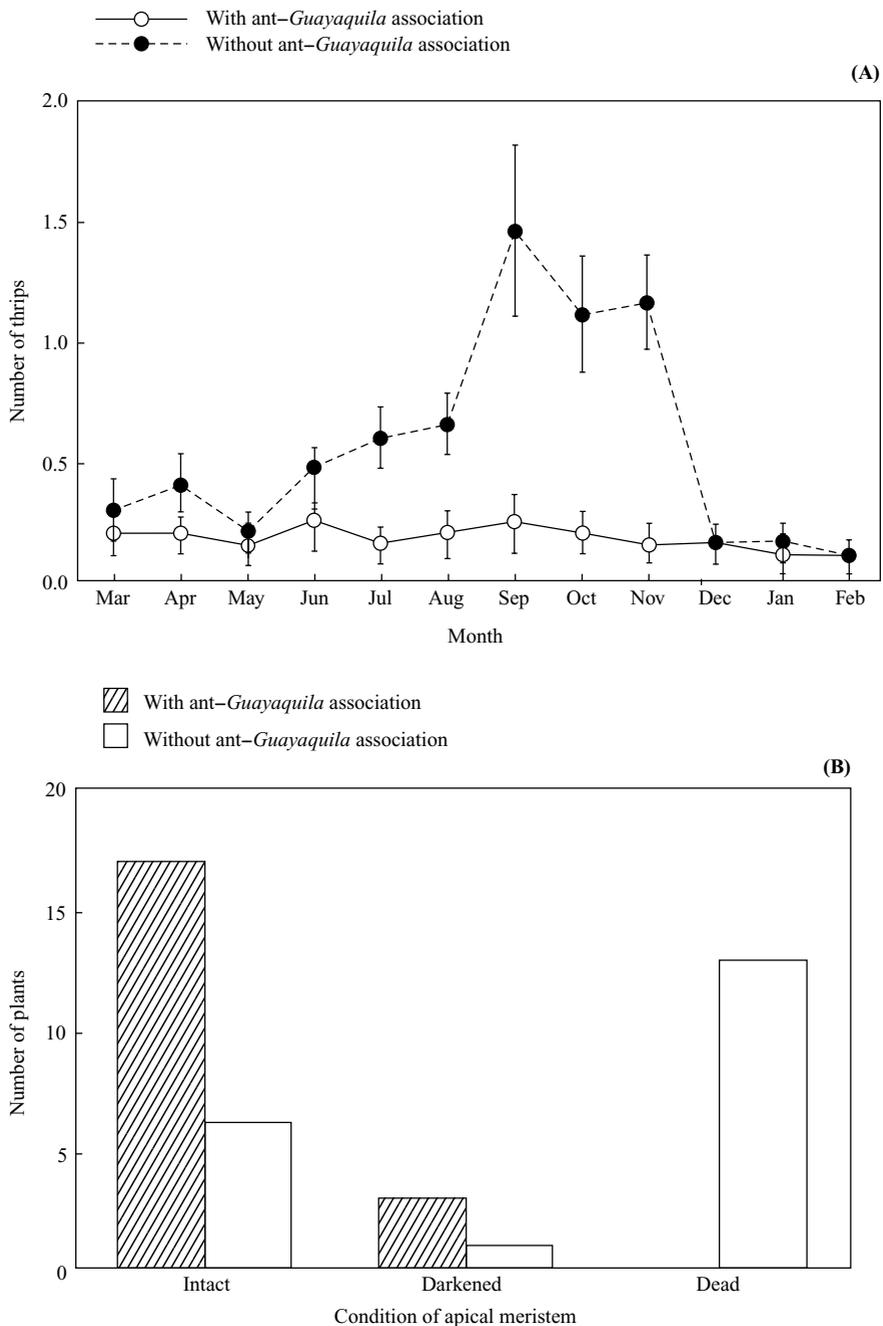


Figure 17.6 (A) Infestation levels by the thrips *Liothrips didymopanicis* on *Didymopanax vinosum* shrubs through time, in the presence (control) or absence (treatment) of an ant-*Guayaquila xiphias* association on the plant ($N = 20$ plants in each group). Thrips abundance is negatively affected by ant-treehopper interactions ($F = 19.33$, d.f. = 1, $P = 0.0001$). Values are means ± 1 SE. Repeated-measures ANOVA performed on square-root transformed data. (B) After 12 months of experimental exclusion, damage to the apical meristem by thrips was significantly greater on plants without ants and *G. xiphias* than on plants with the association ($\chi^2 = 19.26$, d.f. = 2, $P = 0.0001$, $N = 20$ plants in each group).

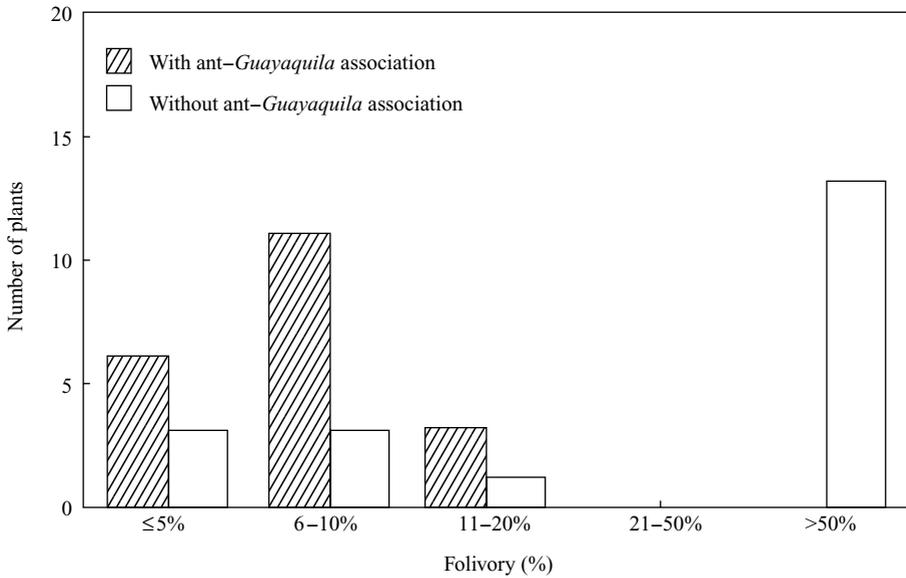


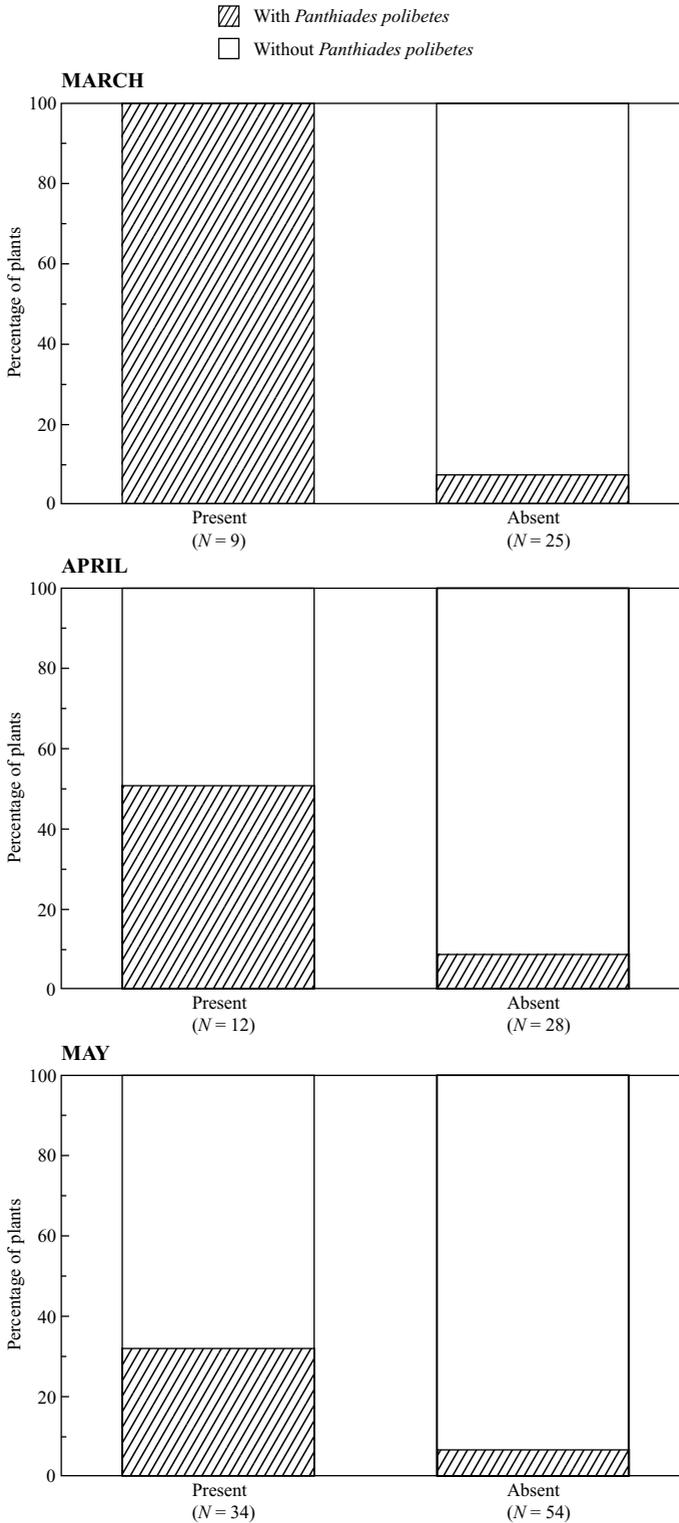
Figure 17.7 Levels of folivory (pooled for *Caralauca olive* beetles and leaf-mining lepidopteran larvae) on *Didymopanax vinosum* shrubs, in the presence (control) or absence (treatment) of an ant-*Guayaquila xiphias* association on the plant ($N = 20$ plants in each group). After 12 months of experimental exclusion, percentage of leaf surface damaged was significantly higher on plants without ants and *G. xiphias* than on plants with the association ($\chi^2 = 19.27$, d.f. = 4, $P = 0.0007$).

from the earliest instars by at least seven ant species (*Camponotus* spp., *Cephalotes clypeatus* (Fabr.) and *Ectatomma edentatum*) that feed on larval secretions (Fig. 17.5E). Worker ants from a single colony may simultaneously tend and collect liquid from both *Panhiades* and *Guayaquila* if these co-occur on a given shrub of *D. vinosum*. The inflorescences of plants infested by *Panhiades* may have several buds destroyed by larval feeding (Fig. 17.5F).

How ant-*Guayaquila* interactions affect associated herbivores

The effect of ants tending *Guayaquila* on associated herbivores was evaluated in monthly censuses on shrubs of *D. vinosum* from March 1992 to February 1993. Plants were tagged at the beginning of the dry season (March), when

Figure 17.8 Monthly infestation pattern by larvae of the myrmecophilous *Panhiades polibetes* butterflies on experimental *Didymopanax vinosum* shrubs, in the presence (control) or absence (treatment) of an ant-*Guayaquila xiphias* association on the plant. In all months the butterflies infested in preference the plants hosting ant-tended treehoppers. March ($\chi^2 = 21.56$, d.f. = 1, $P = 0.001$), April ($\chi^2 = 7.15$, d.f. = 1, $P = 0.007$), May ($\chi^2 = 9.29$, d.f. = 1, $P = 0.002$).



Ant-Guayaquila association

growing meristems are intact (Fig. 17.5A), leaf and bud expansion begin, and herbivore activity is very low (Del-Claro & Mound 1996; Del-Claro & Oliveira 1999). Shrubs were approximately the same height (1–2 m tall), had similar numbers of leaves, and were c. 4 m from each other. Infestation levels and/or damage by associated herbivores were measured on experimentally manipulated plants, with and without ant-*Guayaquila* associations (hereafter ‘with AG’ and ‘without AG’, respectively). After dispersal of newly emerged adult treehoppers from natal aggregations, with-AG plants were repeatedly re-infested by gravid *Guayaquila* females from March 1992 to February 1993. In the period, sequential occupation of such plants by ant-*Guayaquila* associations lasted 9.4 ± 2.4 months (mean \pm SD). The assemblage of tending ants on tagged with-AG plants included *Camponotus crassus*, *C. renggeri*, *C. rufipes*, *Cephalotes pusillus* and *Ectatomma edentatum*. To avoid establishment of ant-hemipteran association on without-AG treatment plants, occasional scout ants were excluded by applying sticky Tanglefoot resin to the trunk base. Upon landing on such ant-excluded plants, potentially colonizing *Guayaquila* females would normally feed on plant sap and flick accumulated honeydew (see above) for nearly 1 hour before abandoning the plant.

Infestation by thrips was monitored monthly during 1 year by counting the number of adults on the plants ($N = 20$ in each experimental group). In March 1992 all plants had intact growing meristems. After 1 year the condition of the apical meristem relative to damage by thrips was re-evaluated as intact, darkened or dead (see Fig. 17.5A, B). Damage by beetles and leaf-mining caterpillars was pooled under ‘folivory’, which was estimated visually as the percentage leaf area eaten and/or covered by mines (Fig. 17.5C, D). In March 1992 all plants had 5% folivory or less. After 1 year, levels of folivory were re-evaluated under five categories (5%, 6–10%, 11–20%, 21–50%, > 50%). Folivore damage was evaluated on the same plants used to investigate abundance and damage by thrips ($N = 20$ in each experimental group).

The effect of ant-*Guayaquila* interaction on infestation of *D. vinosum* shrubs by *Panthiades polibetes* (Fig. 17.5E, F) was investigated by monitoring with-AG and without-AG plants (different from the ones described above) from March to May 1992. At the beginning of each month, we tagged groups of plants in these two categories bearing young inflorescences (bud diameter 2 mm) and free from *Panthiades*. The numbers of plants in with-AG and without-AG groups each month were, respectively, 9 and 25 (March), 12 and 28 (April), and 34 and 54 (May). Tagged plants were free from attack by thrips (see above), lateral vegetative shoot tips were not present; and the stem’s apical meristem originated the inflorescence axis (Fig. 17.1). With-AG plants were visited by *Camponotus crassus*, *C. aff. blandus* Fr. Smith, *C. renggeri*, *C. sericeiventris* Guerin, *C. abdominalis* Fabr. and *Ectatomma edentatum*. A band of Tanglefoot was applied to the base of each without-AG plant. Tagged plants of both groups were re-checked for *P. polibetes* infestation on the last day of each month, and were not re-used

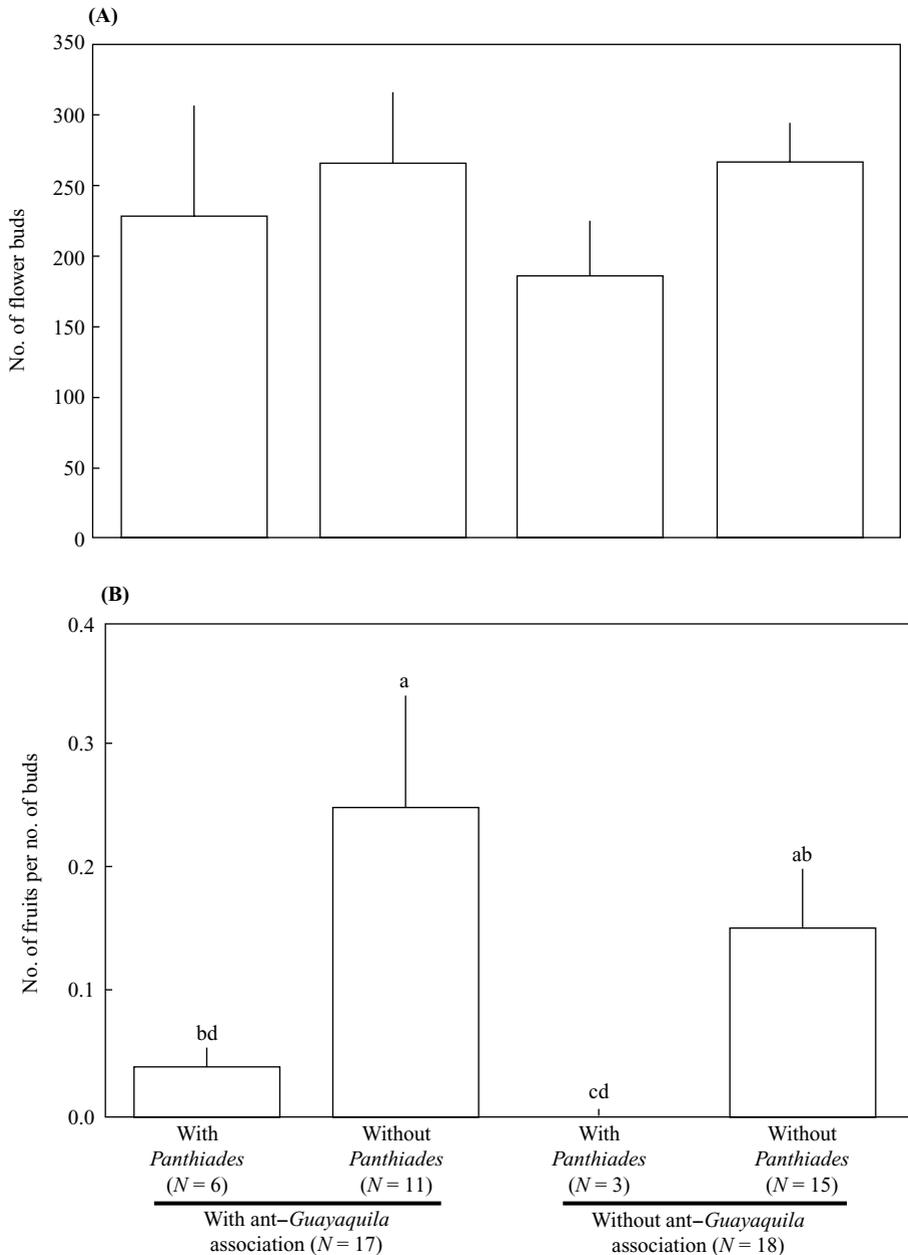


Figure 17.9 Production of flower buds and fruit set in experimental *Didymopanax vinosum* shrubs, in the presence (control) or absence (treatment) of an ant-*Guayaquila xiphias* association on the plant, and as a function of infestation by myrmecophilous bud-consuming *Panthiades polibetes* caterpillars. **(A)** Production of floral buds did not differ among treatments (Kruskal-Wallis test, $H = 1.83$, d.f. = 3, $P = 0.609$). **(B)** Fruit set differed significantly among the four groups ($H = 10.32$, d.f. = 3, $P = 0.016$); treatments designated by the same letter above bars are not significantly different. Values are means ± 1 SE.

in subsequent months. Results are presented as the percentage of with-AG and without-AG plants infested by *P. polibetes* in each month. The effect of bud-destroying *P. polibetes* on the reproductive output of experimental plants was evaluated by dividing the number of fruits by the number of buds produced by each shrub of *D. vinosum*.

Results show that occurrence of ant-*Guayaquila* interactions can have variable effects on the abundance and/or damage caused by associated herbivores of *D. vinosum*. Damage by thrips to the apical meristem, and by chewing and mining insects to leaves, were both significantly lower on with-AG plants than on without-AG plants (Figs. 17.6, 17.7). The lycaenid *P. polibetes*, on the other hand, preferentially infested plants with ant-*Guayaquila* interactions (Fig. 17.8). Presence of *P. polibetes* larvae on a plant led to lower fruit production, and a higher proportion of with-AG plants had lycaenid larvae than did without-AG plants. On with-AG plants bud consumption by ant-tended larvae of *P. polibetes* reduced the reproductive output of *D. vinosum* by 84% (Fig. 17.9).

Discussion

The association between *Guayaquila xiphias* and tending ants on shrubs of *Didymopanax vinosum* in the cerrado savanna can be summarized as follows. Hemipteran honeydew is an important promoter of ant activity on foliage, and the treehoppers are also able to attract potential tending ants by flicking accumulated honeydew beneath the host plant. Ownership behaviour and aggression by ants in the vicinity of the treehoppers keep parasitoid wasps away from brood-guarding *Guayaquila* females. Presence of tending ants decreases the abundance of predators and parasitoids on the host plant, and has a positive impact on hemipteran survival over time. Moreover, ant tending confers a direct reproductive benefit to *G. xiphias* females, which can transfer parental care to ants and lay an additional clutch. Two years of field experiments revealed that the outcomes of ant-*G. xiphias* associations are dynamic in nature, and that benefits from ant tending may vary with time and/or with the species of ant partner. Similar findings have been reported for other ant-Hemiptera systems (e.g. McEvoy 1979; Bristow 1983; 1984; Cushman & Whitham 1989; Cushman & Addicott 1991; Buckley & Gullan 1991; Völkl & Kroupa 1997). Additional aspects of the ecology and natural history of ant-*G. xiphias* systems, in the context of related research in the area, can be found in our earlier work (Del-Claro & Oliveira 1993; 1996; 1999; 2000).

New insights in the study of the evolutionary ecology of ant-Hemiptera and ant-Lepidoptera systems, including reviews of the most important works, can be found in the recent literature (e.g. Morales 2000; Billick *et al.* 2001; Beattie & Hughes 2002; Bronstein & Barbosa 2002; Oliveira *et al.* 2002; Pierce *et al.* 2002; Billick & Tonkel 2003). In the remainder of this discussion we will focus on the interactions generated by the presence of ant-Hemiptera associations on plants,

with emphasis on the impacts of tending ants on associated herbivores, and on the consequences of such effects for the host plant.

Ant behaviour on foliage, and herbivore deterrence

Ant behaviour required to deter herbivores from feeding or ovipositing on plants is similar to that needed to protect ant-tended insects from their natural enemies, and in both cases ownership behaviour by the ants is sufficient to expel intruders from the ants' immediate foraging area (Way 1963; Bentley 1977). Indeed, several ant species associated with extrafloral nectaries or honeydew-producing insects probably confer protection on the plants and the insects through similar behaviours (DeVries 1991; Koptur 1992). For instance, the aggressive *Camponotus rufipes*, an abundant ant on cerrado foliage (Oliveira & Brandão 1991), is very effective at both removing potential herbivores from plants with extrafloral nectaries (Oliveira *et al.* 1987), and protecting *Guayaquila* treehoppers from their natural enemies (Del-Claro & Oliveira 2000). Ant aggressiveness, however, is not an essential trait for herbivore deterrence on foliage. For instance, 'timid' minute *Petalomyrmex* ants efficiently protect *Leonardoxa* trees from chewing and sucking herbivores (Gaume *et al.* 1997), and 'passive' *Pheidole* may confer protection on ant-inhabited *Piper* saplings by removing eggs of insect folivores (Letourneau 1983).

Although not fortuitous, ant-derived protection against herbivores on plants hosting ant-hemipteran associations can be regarded as a by-product of the increased alertness and general aggression shown by ants near the hemipterans. It is also possible that honeydew-gathering ants are protein-limited, leading to increased searching for insect prey and thereby to increased plant protection.

Effects on host plants by honeydew-gathering ants

Since the hypothesis was first proposed by Carroll and Janzen (1973), several studies have supported the idea that honeydew-producing hemipterans can protect plants by attracting tending ants that deter other herbivores. Room (1972) showed that *Crematogaster* ants tending hemipterans on a mistletoe species protect the plant from other herbivores and allow increased shoot growth of the mistletoe. *Formica* ants associated with *Publilia* treehoppers attack leaf-chewing beetles and reduce defoliation to goldenrod (*Solidago*), resulting in increased seed production and growth by stems bearing membracids (Messina 1981). Another type of benefit conferred to a scale's host plant by tending ants was reported by Bach (1991), who demonstrated that sanitation by honeydew-gathering ants reduces leaf death and abscission caused by fungal infection on accumulated honeydew (see also Queiroz & Oliveira 2001).

Herbivore deterrence by tending ants has also been recorded on plants that regularly house ant colonies, and that produce food rewards for ants. Stout (1979) reported that *Myrmelachista* ants tending mealybugs inside *Ocotea* trees

can remove insect eggs from young stems and leaves, and suggested that ant inhabitants could protect the plant from herbivores. *Crematogaster* ants inhabiting *Macaranga* trees tend scales inside the stems, and not only remove herbivores from leaves but also prune foreign plants that come in contact with their host plant (Fiala *et al.* 1989). Finally, benefits to a plant may be mediated by the type of honeydew-producing hemipteran tended by ant inhabitants. Gaume *et al.* (1998) have shown that net benefits against herbivory conferred by *Aphomomyrmex* ants on myrmecophytic *Leonardoxa* vary with the type of sap-sucking hemipteran (coccids or pseudococcids) tended by resident ants inside the tree's hollow twigs.

Negative effects to host plants caused by ants tending honeydew-producing insects have also been documented by several authors both in temperate and tropical habitats, and indicate that other secondary interactions may complicate potential ant-derived benefits to the plant. For example, Fritz (1983) has demonstrated that although *Formica* ants tending *Vanduzea* treehoppers reduced adult density and oviposition by leaf-mining beetles on black locust, they also indirectly protected beetle larvae by excluding their main hemipteran predator. As a result of the ants' opposite effects on adult and immature beetles, Fritz (1983) found no apparent benefit or harm to black locust in having ants tending *Vanduzea*. In the system studied by Buckley (1983) in Australia, *Iridomyrmex* ants feeding on honeydew from *Sextius* treehoppers also collected extrafloral nectar from the host plant (*Acacia*). Because ants were more attracted to treehoppers than to nectaries, ant-derived protection against other herbivores was disrupted and resulted in an overall negative effect of the ant-Hemiptera interaction on plant growth and seed set (Buckley 1983; see also DeVries & Baker 1989). Similar results were obtained by Rico-Gray and Thien (1989) in Mexican sand-dune communities, where honeydew-producing mealybugs shift ant attention away from the extrafloral nectaries of *Schomburgkia* orchids, resulting in increased damage to plant reproductive organs and reduced fruit set. In the same type of habitat, however, the impact of ant-aphid interactions on *Paullinia* seed set varies among years from negative to neutral (Rico-Gray & Castro 1996). How patterns of ant attendance at extrafloral nectaries versus honeydew-producing hemipterans on a given plant can affect the herbivore-deterrent effects of ants is still debatable, and probably depends on the plant and insect species involved (see Becerra & Venable 1989; Fiala 1990; Rashbrook *et al.* 1992; Del-Claro & Oliveira 1993; Gaume *et al.* 1997; 1998).

In perhaps the most detailed study to date of the interactions involving a plant with extrafloral nectaries (*Calathea*), visiting ants, and ant-tended lepidopteran larvae (*Eurybia*), Horvitz and Schemske (1984) emphasized the variable and interdependent character of the components of such complex insect-plant systems, and the variable magnitude of positive and negative effects on plants. Their experiments show that in the absence of ants, damage to reproductive tissues by *Eurybia* caterpillars lowered *Calathea* seed production by 66%, far more than

the 33% reduction in the presence of tending ants. Given that *Eurybia* is a specialist herbivore capable of frequently infesting *Calathea*, the ant–*Eurybia* association seems advantageous for the plant even though seed set is greatest without the caterpillars. Species-specific variation in ant effects on seed production and among-site differences in ant communities further increase the unpredictability of the outcomes in such a complex interaction system (Horvitz & Schemske 1984).

The multispecies system around ant–Guayaquila associations

The results presented here on the system involving ant–*Guayaquila* associations on *Didymopanax* shrubs revealed that effects of tending ants on other species of herbivores ranged from negative to positive. Three types of herbivores (thrips, chewing beetles and leaf-mining caterpillars) were negatively affected by ants, and their damage was reduced on plants hosting ant–*Guayaquila* associations. The bud-destroying lycaenid *Panhiades polibetes*, on the other hand, not only preferentially infested plants with ants and *Guayaquila* but also shifted ant attention partly away from treehoppers towards liquid-rewarding caterpillars. This multitrophic interaction system is unique in its complexity because it involves four types of herbivores, each exploiting plant tissue in a distinct mode, and all being affected by a focal ant–Hemiptera association. As opposed to typical ant–plant systems in which ant-derived protective effects on plants are mediated by plant traits inducing ownership behaviour by ants (e.g. extrafloral nectaries, food bodies, ant domatia; reviewed by Beattie and Hughes 2002), the multispecies interactive system around ant–*Guayaquila* associations is similar to those treated by other studies in that the analyses of pairwise interactions cannot predict the overall impact on the plant from all species involved (see Price *et al.* 1980; Thompson 1988; Cushman 1991; Bronstein 1998; and citations therein).

The full range of effects inherent in multispecies mutualistic systems, in which other species and trophic levels affect the nature and outcome of pairwise interactions, has recently been addressed by Bronstein and Barbosa (2002), who looked at examples from numerous studies. We have shown that ants tending *Guayaquila xiphias* aggregations can have contrasting impacts on damage caused by other herbivores, with varying consequences for *Didymopanax vinosum* shrubs. To understand the net interactive effects of each component in such a complex multitrophic system, one should consider the factors acting both together and separately (e.g. Horvitz & Schemske 1984; Gaume *et al.* 1998). Although an evaluation of the net effects of each component in our system was not possible because of constraints for establishing different treatment groups of appropriate size, a range of potential interactive effects could be identified in the studied system. Some of these are indicated below.

By reducing damage to leaves and shoot tips of *D. vinosum*, tending ants may indirectly benefit the *Guayaquila* by preserving plant quality (see Messina 1981;

Fritz 1982; Bach 1991). Indeed, increased thrips activity on plants free from ant-tended *Guayaquila* increased the probability of mortality of the plant's principal apical meristem. Such damage can kill the host plant (Del-Claro & Mound 1996). Since severe damage by thrips impedes inflorescence development in *D. vinosum*, deterrence by tending ants is likely to be beneficial for *Guayaquila* treehoppers because they normally feed at the apex of the single reproductive branch (Fig. 17.1; see Del-Claro & Oliveira 1999).

The infestation pattern of the myrmecophilous *Panhiades polibetes* on *D. vinosum* shrubs indicates that presence of ant-*Guayaquila* interaction can act as a strong stimulus inducing oviposition by the butterfly, resulting in decreased fruit set. Because myrmecophilous lycaenids may use ants as cues for oviposition, the presence of ant-tended treehoppers may further increase the stimulus by increasing ant density on foliage (see Atsatt 1981a; Pierce & Elgar 1985; a negative effect of ant presence on butterfly oviposition has been shown by Freitas and Oliveira 1996). By efficiently attracting tending ants onto the host plant through honeydew flicking, *Guayaquila* treehoppers create a potentially enemy-free space (Atsatt 1981b) for colonization by competing myrmecophilous *Panhiades*. Therefore the presence of ant foragers promotes species coexistence of ant-tended insects on the host plant. Whether ants are a limited resource on cerrado foliage, and whether competition for their services can adversely affect coexisting *Guayaquila* and *Panhiades*, are questions that remain to be addressed (see Addicott 1978; Cushman & Addicott 1989).

One might also expect a range of reciprocal interactive effects among the species of associated herbivores of *D. vinosum*. For example, early attack by thrips to apical meristem and young leaves (altering plant architecture, and leaf quality) should directly affect subsequent use of the host plant by both chewing and mining insects, and vice versa. Similarly, because ant-tended larvae of *Panhiades* depend on floral resources for growth, host-plant use by the butterfly should also be negatively associated with previous damage by thrips to the apical meristem and to young leaves.

To summarize, the variable character of the numerous components of the complex multitrophic system described here requires sampling at different sites and times for a more realistic evaluation of the impact of the interactions on the host plant. The combination of negative and positive effects among participant species, and their interdependence, should probably result in temporal and spatial variation in the overall impact of the interactions on plants (see Horvitz & Schemske 1984; Thompson 1988; 1994).

At this point, we briefly comment on the uniqueness of the cerrado for research on interaction systems involving ants. At least two factors account for the prevalence of ants on cerrado foliage, and make ant-plant-herbivore interactions especially pervasive in this biome. First, many arboreal ant species

use hollowed-out stems as nest sites, and this per se causes intense ant-patrolling activity on leaves (Morais & Benson 1988). Second, the wide occurrence of predictable food rewards in the form of extrafloral nectaries and insect-derived secretions further promotes ant foraging on cerrado foliage. In the study area in Mogi-Guaçu for example, species with extrafloral nectaries represented 20% of the woody flora (21 of 104 species) surveyed by Oliveira and Leitão-Filho (1987), whereas ant-tended treehoppers occurred on 30% of the 93 plant species examined by Lopes (1995). We are just beginning to understand the role of natural enemies, ants in particular, in structuring herbivore communities and controlling herbivory levels in the cerrado. A range of potential interactive effects of herbivory and abiotic factors on plant fitness and plant population dynamics further provides excellent opportunities for future experimental work (Marquis *et al.* 2002). Thus current available information clearly suggests that cerrado vegetation is unique in providing promising scenarios for research on ant-plant-herbivore interactions (see Oliveira *et al.* 2002; and included references).

Final considerations

Terrestrial communities based on living plants involve at least three interacting trophic levels: plants, herbivores and natural enemies of herbivores (Price *et al.* 1980). In recent decades it has become increasingly apparent that consideration of the third trophic level is essential for understanding not only insect-plant interactions but also whole communities (Thompson 1994). Reports on a variety of interaction systems, including herbivory (Lawton and McNeill 1979; Price *et al.* 1980), mutualism (Gilbert 1980), seed predation and seed dispersal (Heithaus *et al.* 1980), pollination (Horvitz & Schemske 1988) and competition (Price *et al.* 1986), have all emphasized the multispecific character of the interactions, the relevance of the effects from some third species or trophic level, and the need for analysing plant-animal interactions within a broader community context (Chapter 15). Despite the inherent complexity of multitrophic interactions, one current goal in community ecology is to identify across different trophic levels which populations are limited by resource availability (bottom-up forces) and which are limited by consumption by higher trophic levels (top-down forces), and how trophic controls vary at both local and global spatial scales (see Thompson 2002; Dyer & Coley 2002; and citations therein).

Programs for conservation of biodiversity have been concerned primarily with the maintenance of species diversity and ecosystem functions, and the preservation of genetic variation within populations. However, as priorities have moved towards a more landscape-level view of biodiversity, the so-called 'interaction biodiversity' has received greater attention (Thompson 1997; this volume). The numerous studies reported in this chapter have shown in various ways that interspecific interactions can shape the organization of communities, and therefore

act as links between species and ecosystems. Biodiversity should be viewed and evaluated also in ways that embrace the extreme richness inherent to plant–animal interactions, including the species' ecological roles, the kinds of interactions and their outcomes, trophic web structure, selection pressures, habitat heterogeneity and geographical variation (Price 2002). Conservation of 'interaction biodiversity' (Thompson 1997) should therefore be regarded as an integral part of strategies to maintain viable conserved communities.

Acknowledgements

We thank David Burslem and the Organizing Committee for the invitation to participate in the Special Symposium of the British Ecological Society in Aberdeen. The final version of the manuscript was considerably improved by the comments of two anonymous referees, and by the editing of Susan Hartley. H. P. Dutra, K. S. Brown, A. V. L. Freitas, R. Cogni, V. Rico-Gray and H. L. Vasconcelos provided helpful suggestions on early versions of the manuscript; J. R. Trigo and A. X. Linhares helped with the statistical analyses. Our studies in the cerrado were supported by Brazilian Federal (CNPq, CAPES) and State (FAPEMIG) agencies, and by research grants from the Universidade Estadual de Campinas (FAEP). We thank the Instituto de Botânica de São Paulo for permission to work in its cerrado reserve.

References

- Addicott, J. F. (1978) Competition for mutualists: aphids and ants. *Canadian Journal of Zoology*, **56**, 2093–2096.
- Atsatt, P. R. (1981a) Ant-dependent food plant selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia*, **48**, 60–63.
- (1981b) Lycaenid butterflies and ants: selection for enemy-free space. *American Naturalist*, **118**, 638–654.
- Bach, C. E. (1991) Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). *Oecologia*, **87**, 233–239.
- Beattie, A. J. (1985) *The Evolutionary Ecology of Ant-Plant Mutualisms*. Cambridge: Cambridge University Press.
- Beattie, A. J. & Hughes, L. (2002) Ant–plant interactions. In *Plant–Animal Interactions: An Evolutionary Approach* (ed. C. M. Herrera & O. Pellmyr). Oxford: Blackwell Science, pp. 211–235.
- Becerra, J. X. & Venable, D. L. (1989) Extrafloral nectaries: a defense against ant–Homoptera mutualism? *Oikos*, **55**, 276–280.
- Bentley, B. L. (1977) Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics*, **8**, 407–428.
- Billick, I. & Tonkel, K. (2003) The relative importance of spatial vs. temporal variability in generating a conditional mutualism. *Ecology*, **84**, 289–295.
- Billick, I., Weidmann, M. & Reithel, J. (2001) The importance of ant-tending to maternal care in the membracid species, *Publilia modesta*. *Behavioral Ecology and Sociobiology*, **51**, 41–46.
- Blüthgen, N., Verhaagh, M., Goitía, W., Jaffé, K., Morawetz, W. & Barthlott, W. (2000) How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia*, **125**, 229–240.

- Boucher, D. H., James, S. & Keeler, K. H. (1982) The ecology of mutualism. *Annual Review of Ecology and Systematics*, **13**, 315–347.
- Bristow, C. M. (1983) Treehoppers transfer parental care to ants: a new benefit of mutualism. *Science*, **220**, 532–533.
- (1984) Differential benefits from ant attendance to two species of Homoptera on New York iron weed. *Journal of Animal Ecology*, **53**, 775–826.
- Bronstein, J. L. (1994a) Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution*, **9**, 214–217.
- (1994b) Our current understanding of mutualism. *Quarterly Review of Biology*, **69**, 31–51.
- (1998) The contribution of ant-plant protection studies to our understanding of mutualism. *Biotropica*, **30**, 150–161.
- Bronstein, J. L. & Barbosa, P. (2002) Multitrophic/multispecies mutualistic interactions: the role of non-mutualists in shaping and mediating mutualisms. In *Multitrophic Level Interactions* (ed. T. Tscharrntke & B. A. Hawkins). Cambridge: Cambridge University Press, pp. 44–66.
- Buckley, R. C. (1983) Interaction between ants and membracid bugs decreases growth and seed set of host plant bearing extrafloral nectaries. *Oecologia*, **58**, 132–136.
- (1987) Interactions involving plants, homoptera, and ants. *Annual Review of Ecology and Systematics*, **18**, 11–138.
- Buckley, R. C. & Gullan, P. (1991) More aggressive ant species (Hymenoptera: Formicidae) provide better protection for soft scales and mealybugs (Homoptera: Coccidae, Pseudococcidae). *Biotropica*, **23**, 282–286.
- Carroll, C. R. & Janzen, D. H. (1973) Ecology of foraging by ants. *Annual Review of Ecology and Systematics*, **4**, 231–257.
- Cushman, J. H. (1991) Host-plant mediation of insect mutualisms: variable outcomes in herbivore–ant interactions. *Oikos*, **61**, 138–144.
- Cushman, J. H. & Addicott, J. F. (1989) Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. *Oecologia*, **79**, 315–321.
- (1991) Conditional interactions in ant–plant–herbivore mutualisms. In *Ant–Plant Interactions* (ed. C. R. Huxley & D. F. Cutler). Oxford: Oxford University Press, pp. 92–103.
- Cushman, J. H. & Whitham, T. G. (1989) Conditional mutualism in membracid–ant association: temporal, age-specific, and density-dependent effects. *Ecology*, **70**, 1040–1047.
- Davidson, D. W., Cook, S. C., Snelling, R. R. & Chua, T. H. (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, **300**, 969–972.
- Davidson, D. W. & McKey, D. (1993) The evolutionary ecology of symbiotic ant–plant relationships. *Journal of Hymenoptera Research*, **2**, 13–83.
- Del-Claro, K. & Mound, L. A. (1996) Phenology and description of a new species of *Liothrips* (Thysanoptera: Phlaeothripidae) from *Didymopanax* (Araliaceae) in Brazilian cerrado. *Revista de Biologia Tropical*, **44**, 193–197.
- Del-Claro, K. & Oliveira, P. S. (1993) Ant–homoptera interaction: do alternative sugar sources distract tending ants? *Oikos*, **68**, 202–206.
- (1996) Honeydew flicking by treehoppers provides cues to potential tending ants. *Animal Behaviour*, **51**, 1071–1075.
- (1999) Ant–Homoptera interactions in neotropical savanna: the honeydew-producing treehopper *Guayaquila xiphias* (Membracidae) and its associated ant fauna on *Didymopanax vinosum* (Araliaceae). *Biotropica*, **31**, 135–144.
- (2000) Conditional outcomes in a neotropical treehopper–ant association: temporal and

- species-specific effects. *Oecologia*, **124**, 156–165.
- DeVries, P. J. (1991) Mutualism between *Thisbe irenea* butterflies and ants, and the role of ant ecology in the evolution of larval–ant associations. *Biological Journal of the Linnean Society*, **43**, 179–195.
- DeVries, P. J. & Baker, I. (1989) Butterfly exploitation of a plant–ant mutualism: adding insult to herbivory. *Journal of the New York Entomological Society*, **97**, 332–340.
- Douglas, J. M. & Sudd, J. H. (1980) Behavioral coordination between an aphid and the ant that tends it: an ethological analysis. *Animal Behaviour*, **28**, 1127–1139.
- Dyer, L. A. & Coley, P. D. (2002) Tritrophic interactions in tropical versus temperate communities. In *Multitrophic Level Interactions* (ed. T. Tscharrntke & B. A. Hawkins). Cambridge: Cambridge University Press, pp. 67–88.
- Fiala, B. (1990) Extrafloral nectaries versus ant–Homoptera mutualism: a comment on Becerra and Venable. *Oikos*, **59**, 281–282.
- Fiala, B., Maschwitz, U., Pong, T. Y. & Helbig, A. J. (1989) Studies of a South East Asian ant–plant association: protection of *Macaranga* trees by *Crematogaster borneensis*. *Oecologia*, **79**, 463–470.
- Fonseca, C. R. & Ganade, G. (1996) Asymmetries, compartments and null interactions in an Amazonian ant–plant community. *Journal of Animal Ecology*, **65**, 339–347.
- Freitas, A. V. L. & Oliveira, P. S. (1996) Ants as selective agents on herbivore biology: effects on the behaviour of a non–myrmecophilous butterfly. *Journal of Animal Ecology*, **65**, 205–210.
- Fritz, R. S. (1982) An ant–tended treehopper mutualism: effects of *Formica subsericea* on survival of *Vanduzeeia arquata*. *Ecological Entomology*, **7**, 267–276.
- (1983) Ant protection of a host plant’s defoliator: consequence of an ant–membracid mutualism. *Ecology*, **64**, 789–797.
- Gaume, L., McKey, D. & Anstett, M.-C. (1997) Benefits conferred by ‘timid’ ants: active anti–herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. *Oecologia*, **112**, 209–216.
- Gaume, L., McKey, D. & Terrin, S. (1998) Ant–plant–homopteran mutualism: how the third partner affects the interaction between a plant–specialist ant and its myrmecophyte host. *Proceedings of the Royal Society of London B*, **265**, 569–575.
- Gilbert, L. E. (1980) Food web organization and the conservation of neotropical diversity. In *Conservation Biology: An Evolutionary–Ecological Perspective* (ed. M. E. Soulé & B. A. Wilcox). Sunderland: Sinauer, pp. 11–33.
- Heithaus, E. R., Culver, D. C. & Beattie, A. J. (1980) Models of some ant–plant mutualisms. *American Naturalist*, **116**, 347–361.
- Hölldobler, B. & Wilson, E. O. (1990) *The Ants*. Cambridge, MA: Harvard University Press.
- Horvitz, C. C. & Schemske, D. W. (1984) Effects of ants and ant–tended herbivore on seed production of a neotropical herb. *Ecology*, **65**, 1369–1378.
- (1988) A test of the pollinator limitation hypothesis for a neotropical herb. *Ecology*, **69**, 200–206.
- Janzen, D. H. (1979) New horizons in the biology of plant defenses. In *Herbivores: Their Interactions with Secondary Plant Metabolites* (ed. G. A. Rosenthal & D. H. Janzen). New York: Academic Press, pp. 331–350.
- Koptur, S. (1992) Extrafloral nectary–mediated interactions between insects and plants. In *Insect–Plant Interactions*. Vol. 4 (ed. E. Bernays). Boca Raton: CRC Press, pp. 81–129.
- Lawton, J. H. & McNeill, S. (1979) Between the devil and the deep blue sea: on the problem of being a herbivore. *Symposium of the British Ecological Society*, **20**, 223–244.

- Letourneau, D. K. (1983) Passive aggression: an alternative hypothesis for the *Piper-Pheidole* association. *Oecologia*, **60**, 122–126.
- Lopes, B. C. (1995) Treehoppers (Homoptera: Membracidae) in the southeast Brazil: use of host plants. *Revista Brasileira de Zoologia* **12**, 595–608.
- Marquis, R. J., Morais, H. C. & Diniz, I. R. (2002) Interactions among cerrado plants and their herbivores: unique or typical? In *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (ed. P. S. Oliveira & R. J. Marquis). New York: Columbia University Press, pp. 306–328.
- McEvoy, P. B. (1979) Advantages and disadvantages to group living in treehoppers (Homoptera: Membracidae). *Miscellaneous Publications of the Entomological Society of America*, **11**, 1–13.
- McKey, D. (1984) Interaction of the ant-plant *Leonardoxa africana* (Caesalpinaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica*, **16**, 81–99.
- Messina, F. J. (1981) Plant protection as a consequence of ant–membracid mutualism: interactions on Goldenrod (*Solidago* sp.). *Ecology*, **62**, 1433–1440.
- Morais, H. C. & Benson, W. W. (1988) Recolonização de vegetação de cerrado após queimada, por formigas arborícolas. *Revista Brasileira de Biologia*, **48**, 459–466.
- Morales, M. A. (2000) Mechanisms and density dependence of benefit in an ant–membracid mutualism. *Ecology*, **81**, 482–489.
- Oliveira, P. S. (1997) The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). *Functional Ecology*, **11**, 323–330.
- Oliveira, P. S. & Brandão, C. R. F. (1991) The ant community associated with extrafloral nectaries in Brazilian cerrados. In *Ant-Plant Interactions* (ed. D. F. Cutler & C. R. Huxley). Oxford: Oxford University Press, pp. 198–212.
- Oliveira, P. S., Freitas, A. V. L. & Del-Claro, K. (2002) Ant foraging on plant foliage: contrasting effects on the behavioral ecology of insect herbivores. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (ed. P. S. Oliveira & R. J. Marquis). New York: Columbia University Press, pp. 287–305.
- Oliveira, P. S. & Leitão-Filho, H. F. (1987) Extrafloral nectaries: their taxonomic distribution and abundance in the woody flora of cerrado vegetation in southeast Brazil. *Biotropica*, **19**, 140–148.
- Oliveira, P. S. & Oliveira-Filho, A. T. (1991) Distribution of extrafloral nectaries in the woody flora of tropical communities in Western Brazil. In *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (ed. P. W. Price, T. M. Lewinsohn, G. W. Fernandes & W. W. Benson). New York: John Wiley & Sons, pp. 163–175.
- Oliveira, P. S., Silva, A. F. da & Martins, A. B. (1987) Ant foraging on extrafloral nectaries of *Qualea grandiflora* (Vochysiaceae) in cerrado vegetation: ants as potential antiherbivore agents. *Oecologia*, **74**, 228–230.
- Oliveira-Filho, A. T. & Ratter, J. A. (2002) Vegetation physiognomies and woody flora of the cerrado biome. In *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna* (ed. P. S. Oliveira & R. J. Marquis). New York: Columbia University Press, pp. 91–120.
- Pierce, N. E., Braby, M. F., Heath, A. *et al.* (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annual Review of Ecology and Systematics*, **47**, 733–771.
- Pierce, N. E. & Elgar, M. A. (1985) The influence of ants on host plant selection by *Jalmenus evagora*, a myrmecophilous lycaenid butterfly. *Behavioral Ecology and Sociobiology*, **16**, 209–222.

- Price, P. W. (2002) Species interactions and the evolution of biodiversity. In *Plant-Animal Interactions: An Evolutionary Approach* (ed. C. M. Herrera & O. Pellmyr). Oxford: Blackwell Science, pp. 3-25.
- Price, P. W., Bouton, C. E., Gross, P., McPherson, B. A., Thompson, J. N. & Weis, A. E. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41-65.
- Price, P. W., Westoby, M., Rice, B. *et al.* (1986) Parasite mediation in ecological interactions. *Annual Review of Ecology and Systematics*, **17**, 487-505.
- Queiroz, J. M. & Oliveira, P. S. (2001) Tending-ants protect honeydew-producing whiteflies (Homoptera: Aleyrodidae). *Environmental Entomology*, **30**, 295-297.
- Rashbrook, V. K., Compton, S. G. & Lawton, J. H. (1992) Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. *Ecology*, **73**, 2167-2174.
- Rico-Gray, V. (1993) Use of plant-derived food resources by ants in the dry tropical lowlands of coastal Veracruz, Mexico. *Biotropica*, **25**, 301-315.
- Rico-Gray, V. & Castro, G. (1996) Effect of an ant-aphid interaction on the reproductive fitness of *Paullinia fuscegens* (Sapindaceae). *Southwestern Naturalist*, **41**, 434-440.
- Rico-Gray, V. & Thien, L. B. (1989) Ant-mealybug interaction decreases reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae) in Mexico. *Journal of Tropical Ecology*, **5**, 109-112.
- Room, P. M. (1972) The fauna of the mistletoe *Tapinanthus bangwensis* growing on cocoa in Ghana: relationships between fauna and mistletoe. *Journal of Animal Ecology*, **41**, 611-621.
- Schupp, E. W. & Feener, D. H. (1991) Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. In *Ant-Plant Interactions* (ed. C. R. Huxley & D. F. Cutler). Oxford: Oxford University Press, pp. 175-197.
- Stout, J. (1979) An association of an ant, a mealy bug and an understorey tree from a Costa Rican rain forest. *Biotropica*, **11**, 309-311.
- Thompson, J. N. (1988) Variation in interspecific interactions. *Annual Review of Ecology and Systematics*, **19**, 65-87.
- (1994) *The Coevolutionary Process*. Chicago: University of Chicago Press.
- (1997) Conserving interaction biodiversity. In *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity* (ed. S. T. A. Pickett, R. S. Ostfeld, M. Shachak & G. E. Likens). New York: Chapman & Hall, pp. 285-293.
- (2002) Plant-animal interactions: future directions. In *Plant-Animal Interactions: An Evolutionary Approach* (ed. C. M. Herrera & O. Pellmyr). Oxford: Blackwell Science, pp. 236-247.
- Tobin, J. E. (1994) Ants as primary consumers: diet and abundance in the Formicidae. In *Nourishment and Evolution in Insect Societies* (ed. J. H. Hunt & C. A. Nalepa). Oxford: Westview Press, pp. 279-308.
- Völkl, W. (1992) Aphids and their parasitoids: who actually benefits from ant-attendance? *Journal of Animal Ecology*, **61**, 273-281.
- Völkl, W. & Kroupa, A. S. (1997) Effects of adult mortality risks on parasitoid foraging tactics. *Animal Behaviour*, **54**, 349-359.
- Way, M. J. (1954) Studies of the association of the ant *Oecophylla longinoda* and the scale insect *Saissetia zanzibarensis*. *Bulletin of Entomological Research*, **45**, 113-134.
- (1963) Mutualism between ants and honeydew-producing homoptera. *Annual Review of Entomology*, **8**, 307-344.