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FORUM

Host-plant mediation of insect mutualisms: variable outcomes in herbivore-ant interactions

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Summary. I present and evaluate the hypothesis that host plants indirectly affect the fitness of many homopterans and lepidopterans by mediating the outcome of their interactions with ants. Two conditions must be met to support this contention. First, the attractiveness of herbivores to ants must vary predictably with intra- and/or interspecific changes in host-plant quality. Such variation will occur if a) the chemical composition and/or quantity of ant attractants (excretions and secretions) produced by herbivores varies with changes in host quality and b) ants preferentially tend those herbivores that produce the most nutritionally rewarding attractants. Second, the number of tending ants must have a significant effect on the fitness of herbivores. While there is abundant evidence to support these individual conditions, few studies have examined both conditions for a single herbivore-ant association.

I outline a series of testable predictions based on the host-mediation hypothesis. 1) The effects of host plants will vary with the degree to which herbivores depend on ants. 2) Hosts will affect the ability of herbivores to compete for ant mutualists. 3) Tended herbivores will exhibit host-selection behaviors that increase their ability to attract ants. And most importantly, 4) variation in host quality will predict fluctuations in the strength and sign of herbivore-ant interactions. I present a graphical model to illustrate 1) the ways in which plant-induced variation in the value of attractants to ant colonies can be used to predict switchpoints in the behavior of ants and 2) the effects of distance to servicing ant nests and nutritional status of these colonies on the predictions.

An increasing number of studies demonstrate the variable and context-dependent nature of mutualistic interactions (see Thompson 1982, 1988, Addicott 1984, Jordano 1987, Herrera 1988, Cushman and Addicott in press). The outcome of these interactions varies in space and time in response to a range of biotic and abiotic factors. Unfortunately, very little is known about the extent, mechanisms, and implications of this variation, and such information is essential for developing a realistic understanding of the ecology and evolution of mutualism.

Ants are one of the most ubiquitous mutualists found in nature, forming close and often mutualistic associations with a variety of plants, fungi, and animals, particularly herbivorous insects in the Homoptera and Lepidoptera (Wilson 1971, Carroll and Janzen 1973, Bentley 1977, Thompson 1982, Beattie 1985, Sudd and Franks 1987, Hölldobler and Wilson 1990). While herbivore-ant associations have received considerable attention during the past century (see reviews by Hinton 1951, Nixon 1951, Way 1963, Cottrell 1984, Buckley 1987, Pierce 1987, Sudd 1987), few studies address the influence of host plants on the outcome of herbivore-ant interactions and no study outlines the mechanisms by which such effects can occur.

In this paper, I develop the hypothesis that host plants generate significant variability in the outcome of interactions between herbivores and their tending ants. I argue that such host-plant mediation can influence these interactions, and the selection pressures which accompany them, in two fundamentally different ways. First, the strength of mutualistic interactions can fluctuate from strong to weak (++ to +). In these situations, selection pressures will be weak but consistent (i.e., in the same direction). By contrast, the sign of interactions can fluctuate from mutualism to antagonism (+ to -). When such reversals occur, the actual direction of selection changes and selection becomes a disruptive force, favoring traits (behaviors and morphologies) that facilitate the association in certain situations and favoring very different and perhaps opposing traits in others.

Here, I present and evaluate the mechanisms by which host plants can indirectly mediate herbivore-ant interactions. I then use this framework to address various implications of host-plant mediation, with particular emphasis on how plants alter the strength and sign of these insect interactions.
Herbivore-ant associations

Both homopteran-ant and lepidopteran-ant associations are common mutualisms found in temperate and tropical regions. In homopteran-ant associations, ants tend phloem-feeding homopterans (primarily those in the Aphididae, Membracidae, Coccidae, and Pseudococcidae) and harvest their excretions (“honeydew”). In lepidopteran-ant associations, ants tend leaf-chewing butterfly larvae (those in the Lycaenidae and Riodinidae), and harvest their secretions (see also DeVries and Baker 1989) who document that larvae of a riodinid species consume their host's extrafloral nectar). Through their tending, ants can provide a range of beneficial services to both homopterans and lepidopterans, particularly protection from natural enemies, but also increased feeding rates, decreased emigration, reduced fungal infections, construction of protective shelters, and provision of parental care (see reviews by Hinton 1951, Nixon 1951, Way 1963, Cottrell 1984, Beattie 1985, Buckley 1987, Pierce 1987).


Direct and indirect effects of plants on tended herbivores

Host plants can directly and indirectly affect the fitness of their ant-tended herbivores. Phloem fluids directly affect the survival, growth, and reproduction of homopterans (Auclair 1963, Dixon 1985) and the chemical composition of leaf tissue directly influences the fitness of lepidopterans (Mattson 1980, Crawley 1983, Hill and Pierce 1989). Other plant characteristics, such as surface type and architecture, can directly affect the ability of herbivores to acquire food resources (Juniper and Southwood 1986).

While a number of studies evaluate the direct effects of host plants on herbivores (Price et al. 1980, Crawley 1983, Strong et al. 1984), few have considered the indirect effects of host plants on herbivore fitness via ant associates. There are at least two mechanisms by which host plants can have such effects. First, as noted by Buckley (1987), host plants bearing extrafloral nectaries can mediate herbivore-ant interactions by attracting ants independently. Herbivore aggregations that form on plants with extrafloral nectaries will be more likely to be located and subsequently tended by ants than aggregations forming on hosts without such structures. This is supported by Buckley (1983), Maschwitz et al. (1984), and Sudd and Sudd (1985) who show or suggest that ants commonly switch from visiting extrafloral nectaries to visiting tended herbivores (although see Becarra and Venable (1989) who claim that the reverse can also occur). Given that oviposition by many lycanid species is dependent upon the presence of ants (Atsatt 1981b, Pierce and Elgar 1985, Smiley et al. 1988, Baylis 1989, Baylis and Pierce in press), host plants with extrafloral nectaries may influence tended lepidopterans in a similar fashion.

In this paper, I examine a second and potentially more common mechanism for indirect host mediation that involves the response of ants to herbivore excretions and secretions of variable composition and quantity. Clearly, other indirect effects can also operate in such associations, but I will not discuss them because they concern the ways in which host plants can indirectly benefit from being infested by ant-tended homopterans (Messina 1981, Buckley 1983, 1987, Fritz 1983, Beattie 1985, Compton and Robertson 1988).

Mechanisms and evidence

Two conditions must be met to document that host plants indirectly mediate the fitness of tended herbivores via ants. First, the attractiveness of herbivores to ants must vary predictably with intra- and/or interspecific changes in host-plant quality. Such variation will occur if a) the chemical composition and/or quantity of ant attractants produced by herbivores varies with changes in host-plant quality and b) ants preferentially tend those herbivores that produce the most nutritionally rewarding attractants. Second, the number and/or attentiveness of ants must have a significant effect on the fitness of herbivores.

Plant-mediated variation in herbivore attractiveness to ants

Influence of host plants on herbivore attractants

The influence of plants on homopteran honeydew is well established. Many studies show that genotypic and phenotypic variation in host plants (within individual plants, within species, and among species) can affect the amount of honeydew produced as well as the identity and concentration of sugars, amino acids, and other compounds in these excretions (Mittler 1958a, b, Auclair 1963, Dixon 1985, Holt and Wratten 1986, Klingauf 1987).

By comparison, the relationship between host-plant
quality and the composition and quantity of lepidopteran secretions is poorly understood. To my knowledge, only one study has provided direct evidence that host plants influence secretion characteristics. Fiedler (1990) showed that the ability of a lycaenid (Polyommatinus icarus) to secrete ant attractants was significantly reduced when their larvae fed on a woody host plant (Robinia pseudacacia). Baylis (1989) and Baylis and Pierce (in press) have shown that larvae of the lycaenid Jalmenus evagoras are more attractive to ants when feeding on fertilized host plants. Presumably, the mechanism for this result is that larvae are able to produce more nutritionally rewarding secretions when feeding on high-quality host plants. Pierce (1984, 1985) also hypothesized such effects.

**Variation in attractants and ant recruitment**


Four studies provide more direct evidence that the recruitment response of ants is strongly influenced by the nutritional content and quantity of herbivore attractants. Working with the lycaenid Jalmenus evagoras, Pierce (1984, 1989) detected a positive correlation between the number of ants tending butterfly pupae and the amino acid concentrations of their secretions (especially serine). Edinger (1985) found that the ant Camponotus noveboracensis was more aggressive when tending large colonies of the aphid Chaetophorus populicola, presumably because these aggregations produced larger quantities of honeydew. In addition, C. noveboracensis more aggressively tended colonies of C. populicola than other aphid species producing less rewarding honeydew. Third, Fiedler (1990) showed that larvae of the lycaenid Polyommatinus icarus were more attractive to ants when feeding on herbaceous legumes than a woody species. Fourth, Bristow (in press) has shown that feeding sites used by aphid colonies strongly influence their ability to attract ants. Colonies of the aphid Aphis nerii on oleander (Nerium oleander) were more frequently tended by ants when feeding on flower buds than on leaf tips. This pattern occurred within individual host plants, independent of aphid colony size, and throughout the season.

**Ant tending levels and herbivore fitness**

Variation in herbivore attractants and recruitment behavior of ants is important only if there is a positive correlation between the number or attentiveness of tending ants and herbivore fitness. While many species of homopterans and lepidopterans benefit from ant tending and have evolved a variety of morphological and behavioral traits which encourage this association (reviews by Way 1963, Blackman 1974, Heie 1980, Atsatt 1981a, Cottrell 1984, Pierce 1984, 1985, 1987, Buckley 1987, Sudd 1987), the precise relationship between ant tending level and herbivore fitness is less clear (e.g., are 10 ants per aggregation more beneficial to the herbivores than 6?). This situation results from a strong bias towards performing ant-exclusion rather than ant-reduction and ant-enhancement experiments. This practice seems particularly surprising given that the complete exclusion of ants rarely occurs in nature. More realistically, the number of ants tending herbivores varies in space and time in response to numerous factors, including plant-induced variation in the excretions and secretions of herbivores.

Two studies have shown that ant tending levels significantly affect homopteran fitness. First, Cushman and Addicott (1989) presented correlative data suggesting that colonies of the aphid Aphis varians acquired great-

![Behavior of ants towards tended herbivores](image)

Fig. 1. Proposed relationships for how plant-induced variation in the nutritional content and quantity of rewards provided to ants, in association with other factors, predicts the behavior of ants towards tended herbivores. When herbivores feed on low-quality host plants and produce rewards of low nutritional content and/or quantity, ant colonies are predicted to acquire greater fitness by acting as predators than as mutualists. Alternatively, when herbivores feed on high-quality hosts and produce rewards of high nutritional content and/or quantity, ant colonies are predicted to gain more by acting as mutualists. The first switchpoint (SP₁) represents a hypothetical level of reward at which ant colonies act as predators of herbivores feeding on host plants far away from their nests and mutualists of herbivores on hosts close to their nests. The second switchpoint (SP₂) represents the level of reward after which ant colonies with high protein demand act as mutualists.
er benefit (presumably protection from natural en-
emies) when the ants *Formica cinerea* and *F. fusca* were
in greater abundance. Second, by performing ant-re-
duction experiments, Cushman and Whitham (in press)
demonstrated that greater numbers of the membracid
*Pubilia modesta* survived and matured into adults when
tended by increased numbers of the ant *F. altipetens*.
Greater membracid fitness was associated with reduced
abundance of the predatory salticid spider *Pellenes* sp.

Information on the relationship between lepidopo-
tan fitness and the density of tending ants is less clear.
The only direct evidence comes from Baylis (1989) and
Baylis and Pierce (in press) who demonstrated that the
lycaenid *Jalmenus evagorus* acquires greater benefit
from an increased abundance of tending ants (*Iridomyr-
max* sp.). In addition, Pierce (1984, 1985) hypothesized
that the fitness of lycaenid larvae in general is increased
by attracting more tending ants.

**Overall evidence of host-plant mediation**

While many studies have addressed various aspects of
the hypothesis that host plants mediate herbivore-ant
interactions (see conditions above), only one study pro-
vides clear evidence for this possibility in a single herb-
ivore-ant association. With field experiments, Baylis
(1989) and Baylis and Pierce (in press) documented that
1) fifth-instar larvae of the lycaenid *Jalmenus evagorus*
attract a greater number of ants when feeding on fertili-
ized host plants (*Acacia decurrens*) than on unfertilized
controls and 2) larvae attracting more ants survive bet-
ter than larvae receiving less attention. Baylis and
Pierce also demonstrated that *J. evagorus* more com-
monly oviposited on fertilized host plants (see discus-
sion in Pierce 1989, Pierce et al. in press). Although
these results were obtained by manipulating host-plant
quality experimentally, Auclair's (1963) review of the
literature suggests that similar variation also occurs nat-
urally.

An additional study provides less direct but more
general support for the host-mediation hypothesis.
Pierce (1984, 1985) presented data suggesting that host-
plant quality has strongly influenced the evolution of
ant-tended lycaenids. She documented that tended.ly-
caenid larvae usually feed on nitrogen-fixing and/or pro-
tein-rich host plants whereas non-tended species do not
exhibit such patterns. Pierce goes on to hypothesize that
selection has favored the use of protein-rich hosts by
tended lycaenids because their larvae (and sometimes
pupae) produce secretions that are more attractive to
ants and that the increased attention results in greater
fitness.

**Implications of host-plant mediation**

If host plants are significant mediators of insect interac-
tions, then there are a number of testable predictions
that can be made which have important implications for
the ecology and evolution of herbivore-ant associations.
The first prediction based on the host-mediation hy-
pothesis is that the indirect influence of host plants will
vary with the degree to which herbivores depend on
ants. Effects should be minimal for herbivores that form
facultative associations with ants and influential for
more obligate species. Second, as emphasized by Cushman
and Addicott (1989, in press), host plants should
influence the ability of tended herbivores to compete
with neighboring plants and herbivores for ant mu-
tualists.

The predictions that I discuss in this section suggest
that host-plant selection by ant-tended herbivores will
be an important and complex process. Herbivores asso-
ciating with ants must select hosts that simultaneously
maximize their nutritional intake and their ability to
attract ants. Indirect effects of host plants on habitat
selection should be especially important for herbivores
with extreme dependencies on ants, such as the scale
*Saissetia zanzibarensis* (Way 1954) and the lycaenid *Jal-
menus evagorus* (Pierce 1987). For example, as men-
tioned earlier, female *J. evagorus* prefer to oviposit on
fertilized hosts, as such hosts make their larvae more
attractive to ants (Baylis 1989, Baylis and Pierce in
press), and tended lycaenids in general exhibit strong
preferences for nitrogen-rich host plants (Pierce 1984,
1985).

The fourth prediction of the plant-mediation hypo-
thesis concerns variability in the strength and sign of
herbivore-ant interactions. The behavior of ants to-
wards herbivores will be determined in part by the
nutritional content and quantity of rewards that they
receive from herbivores. I predict that differences in the
rewards will cause significant variation in the strength
and sign of herbivore-ant interactions (i.e., whether
ants act as mutualists or predators). In Fig. 1, I present
a simple graphical model that illustrates these predicted
relationships. When herbivores feed on low-quality host
plants and offer attractants of low nutritional content
and/or quantity, ant colonies will acquire greater fitness
by acting as predators rather than mutualists. Conver-
sely, when herbivores feed on high-quality host plants
and the nutritional content and/or quantity of their re-
wards is high, ant colonies will gain more by acting as
mutualists (i.e., tending herbivores and harvesting their
excretions/secretions).

The value of herbivore attractants to ant colonies will
be a complex function of various factors, in addition to
host-mediated variation in the nutritional content and
quantity of attractants. These include the distance of
tended herbivores from servicing ant colonies (McEvoy
1979, Sudd 1983), nutritional requirements of ant colo-
nies, age and size of ant colonies, and the availability of
alternative food sources, such as insect prey, extrafloral nectar (Buckley 1983), and the attractants produced by neighboring herbivores (Cushman and Addicott 1989, Cushman and Whitham in press). These factors should interact with the content and quantity of rewards to change the position of curves predicted in Fig. 1, thereby producing a more complex range of ant behaviors. For example, I predict that the curve will shift down when tended herbivores feed on host plants that are far away from servicing ant nests and shift up when infested hosts are close to nests. Thus, when herbivores feed on host plants that result in the reward content and quantity specified by the first switchpoint in Fig. 1 (SP1), the model predicts that ants will act as predators of herbivores on hosts located far away from their nest and mutualists of herbivores on hosts close to their nest. In addition, I predict that ant colonies with a high demand for protein will act as mutualists only at extremely high content and/or quantity of rewards (after SP).

Ants can switch between acting as predators and mutualists of tended homopterans, although variation in host-plant quality has not been considered to be the driving mechanism for these switchpoints (Way 1963, Sudd 1987). Pontin (1958, 1978) reported that colonies of the ant Lasius flavus rely on the honeydew of root-feeding aphids during early summer but then prey on the same aphid species latter in the growing season. Although not evaluated by Pontin, this switch in behavior may be explained by seasonal changes in the honeydew requirement of ant colonies and/or plant-induced changes in the content or quantity of honeydew.

Edinger (1985) provides additional evidence for behavioral switchpoints in ants. He found that the ant Lasius neoeiger preyed on a tended aphid species producing small quantities of honeydew more frequently than it preyed on the more productive aphid Chaitaphorous populicola. In addition, Edinger elegantly showed that when C. populicola was experimentally deprived of phloem fluids (by girdling the vascular tissue of its host), L. neoeiger preyed on them twice as often as controls.

Way (1954) also demonstrated that ants switch between acting as homopteran mutualists and predators. When honeydew appeared to be in excess of its needs, the ant Oecophylla longinoda began to prey on the scales (Saissetia zanzibarensis) that it normally tends. In the laboratory, Way (1954) was also able to experimentally induce and suppress ant predation of scales by manipulating the availability of honeydew. When honeydew was in abundance, ants acted as predators while they acted as mutualists when honeydew was in short supply. This result suggests that the model in Fig. 1 can be amended to include a fourth curve which never (or rarely) rises above the switchpoint line at zero. When honeydew requirements of an ant colony become saturated, no value of reward will be sufficient to deter workers from acting as predators.

The outcome of species interactions is strongly dependent upon the physical and biological setting in which they occur (Thompson 1988, Cushman and Whitham 1989, Cushman and Addicott in press). Here, I have argued that host plants represent an important and largely overlooked form of biological setting that varies sufficiently to alter the outcome of herbivore-ant interactions, potentially explaining significant variation in the occurrence and strength of mutualism in these associations.

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