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Geographic and taxonomic distribution of a positive interaction: ant-tended homopterans indirectly benefit figs across southern Africa

Abstract Although species pairs and assemblages often occur across geographic regions, ecologists know very little about the outcome of their interactions on such large spatial scales. Here, we assess the geographic distribution and taxonomic diversity of a positive interaction involving ant-tended homopterans and fig trees in the genus *Ficus*. Previous experimental studies at a few locations in South Africa indicated that *Ficus sur* indirectly benefited from the presence of a homopteran (*Hilda patruelis*) because it attracted ants (primarily *Pheidole megacephala*) that reduced the effects of both pre-dispersal ovule gallers and parasitoids of pollinating wasps. Based on this work, we evaluated three conditions that must be met in order to support the hypothesis that this indirect interaction involves many fig species and occurs throughout much of southern Africa and Madagascar. Data on 429 trees distributed among five countries indicated that 20 of 38 *Ficus* species, and 46% of all trees sampled, had ants on their figs. Members of the *Sycomorus* subgenus were significantly more likely to attract ants than those in the *Urostigma* subgenus, and ant-colonization levels on these species were significantly greater than for *Urostigma* species. On average, each ant-occupied *F. sur* tree had 37% of its fig crop colonized by ants, whereas the value was 24% for other *Ficus* species. *H. patruelis* was the most common source for attracting ants, although figs were also attacked by a range of other ant-tended homopterans. *P. megacephala* was significantly more common on figs than other ant species, being present on 58% of sampled trees. Ant densities commonly exceeded 4.5 per fig, which a field experiment indicated was sufficient to provide protection from ovule gallers and parasitoids of pollinators. Forty-nine percent of all colonized *F. sur* trees sampled had ant densities equal to or greater than 4.5 per fig, whereas this value was 23% for other *Ficus* species. We conclude that there is considerable evidence to suggest that this indirect interaction occurs across four southern African countries and Madagascar, and involves many *Ficus* species.

Key words Ant-plant-homopteran interactions · *Ficus* · Geographic distribution of interactions · Indirect effects · Positive interactions

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Introduction

Species pairs and assemblages can occur across large geographic regions, although very little is known about the degree to which this occurs and the outcome of species interactions across such spatial scales. Nevertheless, ecologists and evolutionary biologists commonly draw conclusions about interspecific interactions after studying them at one or a few sites. This practice is quite understandable given the immense practical problems associated with large-scale studies, particularly when they involve experiments. However, the outcome of interactions can exhibit considerable spatial variation (Herrera 1988; Thompson 1988; Cushman and Addicott 1991), and it is therefore important to determine the geographic distribution of these outcomes. Such infor-

mation is critical for understanding evolutionary and coevolutionary processes (Thompson 1994), as well as the influence of species interactions on foraging behavior, population dynamics, and community structure.

Here, we propose a practical approach for studying the occurrence and outcome of interactions across large geographic scales. The method comprises (1) experimentally documenting the outcome of an interaction on a local scale, (2) using these results to identify conditions that must be met in order to show non-experimentally that the interaction occurs, and (3) evaluating these conditions on a geographic scale to estimate the distribution of the interaction, and thus its potential importance. Clearly, this approach is not a substitute for conducting field experiments on a geographic scale or along abiotic gradients (e.g., elevation) that mirror much of the variation that occurs on a geographic scale. However, there are formidable logistical difficulties associated with such efforts, and hence studies of this nature rarely occur. Consequently, we employ this approach mindful of its limitations, but also aware of the need for studies that begin to explore the geographic distribution of interactions.

We use this approach to study an indirect interaction. Despite a growing appreciation for their importance (Vandermeer 1980; Wilson 1980; Kerfoot and Sih 1987; Strauss 1991; Wootton 1994), previous studies have not considered the geographic distribution of indirect interactions or the possibility that suites of related species participate in them. This is particularly true for interactions that involve indirect facilitation, in which one species benefits another through its effect on a third (Boucher et al. 1982; Addicott 1984; Beattie 1985; Boucher 1985).

Numerous studies have shown that plants can indirectly benefit from hosting ant-tended homopterans (Room 1972; Nickerson et al. 1977; Laine and Niemela 1980; Messina 1981; Skinner and Whitaker 1981; Buckley 1983, 1987; Compton and Robertson 1988, 1991; Bach 1991; Ito and Higashi 1991; Rashbrook et al. 1992; although see Fritz 1983). These studies demonstrate that ants can reduce the amount of damage that non-homopteran herbivores inflict on their host plants. If the decrease in herbivory exceeds the increase in damage caused by ant-tended homopterans themselves, then the net effect on the host plant will be positive (Carroll and Janzen 1973).

Here, we assess the geographic distribution and taxonomic diversity of a plant-homopteran-ant interaction studied previously by Compton and Robertson (1988, 1991) and Zachariades (1994). Using manipulative field experiments, these authors demonstrated that the Cape fig (*Ficus sur*) can indirectly benefit from the presence of a homopteran (*Hilda patruelis*, Tettigometridae) because this herbivore attracts ants (mainly *Pheidole megacephala*) that reduce the effects of both pre-dispersal seed predators and the parasitoids of pollinating wasps (see Fig. 1). These three studies were conducted at a few sites located in the eastern Cape Province of South Africa.
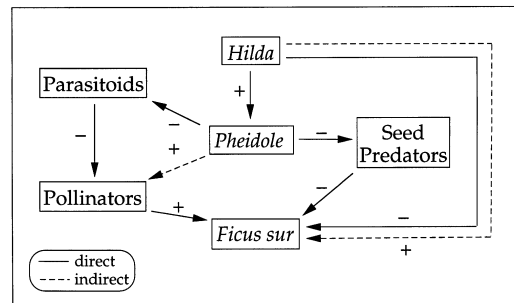

Fig. 1 A schematic diagram summarizing the direct and indirect interactions occurring within the *Ficus sur* system in southern Africa. Based on the experimental studies of Compton and Robertson (1988, 1991) and Zachariades (1994)

However, *F. sur*, *Hilda*, and *Pheidole* all occur throughout much of southern and central Africa (and the invasive *Pheidole* now has a nearly global distribution). In addition, *Hilda* and other ant-tended homopterans are known to feed on a variety of *Ficus* species. Therefore, this form of indirect interaction has the potential to occur over large geographic areas and involve many fig tree species.

In this paper, we present a test of three conditions that must be met in order to support the hypothesis that indirect benefits in the fig-homopteran-ant system are geographically widespread and taxonomically diverse. Regardless of the region or tree species involved, we need to show that (1) fig trees are attacked by a range of non-pollinating wasps whose larvae feed on developing ovules or parasitize pollinating wasps (i.e., fig trees have significant ecological 'problems' that tending ants may be able to solve); (2) ants commonly occur on the figs of trees; and (3) ant densities on figs commonly reach levels that significantly reduce the negative effects of non-pollinating wasps. Hawkins and Compton (1992) have already addressed the first condition for a wide variety of *Ficus* species that occur in southern Africa. They showed that *Ficus* supports diverse assemblages of non-pollinating fig wasps that are detrimental to reproductive success, reducing both male and female components of fitness. For example, at least 15 species of non-pollinators are known to be associated with *F. sur* across its range, and individual trees may support as many as four galling and seven parasitoid species, with combined densities that commonly exceed the number of pollinators (Hawkins and Compton 1992).

Natural history of fig systems

Fig trees (*Ficus*, Moraceae) and their fig-wasp pollinators (Agaoninae, Agaonidae, Hymenoptera) are participants in an obligate mutualism. Female agaonines are the exclusive pollinator of the trees, which in turn provide the wasps with food (in the form of ovules) for their developing larvae (Galil 1977). The relationship is highly species specific, with each of the approximately 750 tree

species typically pollinated by only one wasp species and each wasp species associated with only one tree species (Ramirez 1970; Janzen 1979; Wiebes 1979; Wiebes and Compton 1990).

In addition to the agaonines, figs are host to a range of non-pollinating wasps from other agaonid subfamilies as well as other families in the Hymenoptera. These wasp species include both gall-forming herbivores and parasitoids. The galling species either enter figs through the ostiole (an opening in each fig used by pollinating wasps) and lay their eggs inside developing ovules ('internal' ovipositors) or use long ovipositors to lay eggs into ovules from outside the figs ('external' ovipositors). Parasitoid species attack both pollinator and non-pollinator galling wasps, and always oviposit from outside the fig. Tree specificity of these non-pollinating wasp groups also appears to be well developed, although it may not be as extreme as for pollinators (Boucek et al. 1981; Wiebes 1982; Boucek 1988).

In the eastern Cape of South Africa, *F. sur* supports at least six wasp species. In addition to a species-specific pollinator (*Ceratosolen capensis*), there is a second ovule-galling species (*Sycophaga cyclostigma*) that oviposits internally. There are probably three closely related and undescribed species of ovule-galling species in the genus *Apocryptophagus* that oviposit externally. The parasitoid *Apocrypta guineensis* also oviposits externally and attacks all of the other five wasp species. Because of their mode of oviposition, *Apocryptophagus* and *Apocrypta* females are much more exposed to attack by ants than *Ceratosolen* or *Sycophaga*.

Methods

Large-scale fig sampling

During five field trips from June 1990 to December 1992, we traveled extensively through Madagascar, Malawi, South Africa, Zambia, and Zimbabwe, sampling all fig trees that we encountered which were producing figs. The *Ficus* species were members of two subgenera as outlined by Berg (1990): *Sycomorus* and *Urostigma*. For each fig-bearing tree sampled, we recorded the following information: (1) location and habitat type; (2) size of the fig crop and its developmental stages (pre-pollination, pollination, post-pollination, or a combination); (3) presence or absence of ants on the figs; (4) species of ant(s) present on figs; (5) proportion of figs in the crop with ants; (6) ant densities on a random sample of five occupied figs per tree; and (7) source(s) of ant attraction to figs (e.g., honeydew-producing homopterans such as *Hilda*, aphids, coccids and pseudococcids, as well as plant exudates and unknown sources).

Data from our large-scale sampling were analyzed with contingency table and ANOVA tests using StatView 4.1. We used Bonferroni/Dunn multiple comparisons to test for differences among treatment levels in all significant ANOVAs.

Ant densities and wasp production

We conducted an ant-exclusion experiment in order to determine the number of ants per fig required to significantly decrease the number of deleterious wasps (non-pollinating ovule gallers and parasitoids) emerging from figs and increase the number of bene-ficial wasps (pollinators) emerging from figs. We selected between one and five branch pairs with young, pre-pollinated figs on each of five *F. sur* trees at sites in and around Grahamstown, South Africa. In total, our analysis is based on data from 24 branches. Throughout the course of this experiment, *Pheidole* was by far the most common ant species tending the homopteran *Hilda*. We excluded ants from one branch of each pair using Formex Insect Barrier (Ciba-Geigy). At approximately 2-week intervals throughout crop development, we recorded the numbers of figs and ants on the branches, as well as the species of ants present. On each sampling occasion, we divided the number of ants on a branch by the number of figs it contained to generate a mean ant density per fig. We used these data to calculate the mean number of ants per fig for the entire sampling period.

We collected figs from trees just prior to the time that wasp progeny were due to emerge. We then placed a random sample of five figs per branch into gauze-covered containers to capture emerging adult wasps and counted the number of individuals of each wasp species per fig. The three putative *Apocryptophagus* species were combined because we were unable to distinguish among their males. For each branch, we calculated the mean number of each wasp species per fig.

For each of the four wasp taxa emerging from figs, we performed a two-way ANOVA, using ant treatment (present or absent) and tree (fig trees one through five) as the grouping factors and mean number of emerging wasps per fig per branch as the response variable. In this analysis, we were not interested in the tree effect, but wanted to remove the influence of trees from the data. If we detected significantly beneficial effects of ants on figs (i.e., reduced abundance of non-pollinating ovule gallers and/or parasitoids and increased abundance of pollinators), then the mean ant densities on unmanipulated figs could serve as an estimate of the number of ants required for figs to receive indirect benefits.

Results

Occurrence of ants on figs

Data from 429 trees distributed across five African countries showed that 20 of the 38 *Ficus* species sampled (53%), and 197 of the 429 trees sampled (46%), had their figs colonized by ants (Table 1). The figs of *F. sur* were frequently colonized by ants throughout its range in Malawi, South Africa, Zambia, and Zimbabwe, with the value for each country averaging 80% of the trees sampled (Fig. 2A; *F. sur* is not found on Madagascar). With respect to other *Ficus* species, members of the *Sycomorus* subgenus were significantly more likely to have ants on their figs than species from the *Urostigma* subgenus (54% vs 35%; $\chi^2 = 12.09$, $df = 1$, $P < 0.0005$; Table 1, Fig. 3A).

The four sources for attracting ants to figs occurred at significantly different frequencies ($\chi^2 = 114.9$, $df = 3$, $P < 0.001$). The homopteran *Hilda* was by far the most common source for attracting ants to figs (47%), followed by other homopterans (25%), plant exudates (2.5%), and unknown sources (25%). We may have underestimated the importance of homopterans as ant-attraction sources, given that exudates coming from figs may have been due to the recent removal of homopteran mouthparts and 'unknown sources' may have corresponded to mobile homopterans (e.g., *Hilda*) that temporarily moved off figs when disturbed during sampling. Trees in the *Sycomorus* subgenus were signifi-

Table 1 Species-specific distributions of sampled *Ficus* trees among five African countries. Data are presented for 38 species and 429 individual trees. Numbers in parentheses in the total column correspond to the number of trees with ant-colonized figs

Ficus species	Total	Madagascar	Malawi	South Africa	Zambia	Zimbabwe
Subgenus *Sycomorus*						
F. sycomorus "sakalavarum"	10 (5)	10	0	0	0	0
F. sycomorus sycomorus	49 (35)	21	3	12	9	4
F. sycomorus gnaphalocarpa	9 (5)	0	7	0	2	0
F. sur	54 (45)	0	5	22	8	20
F. vallis-choudae	5 (2)	0	3	0	2	0
F. tiliifolia	2 (1)	2	0	0	0	0
F. polyphlebia	8 (1)	8	0	0	0	0
F. botryoides	26 (10)	26	0	0	0	0
Subgenus total	163 (104)	67	18	34	21	25
Subgenus *Urostigma*						
F. ingens	20 (7)	0	4	16	0	0
F. cordata salicifolia	9 (5)	0	0	6	0	3
F. verruculosa	11 (2)	0	0	1	9	0
F. madagascariensis	3 (3)	3	0	0	0	0
F. menabeensis	4 (2)	4	0	0	0	0
F. humbertii	2 (2)	2	0	0	0	0
F. lutea	10 (2)	0	1	9	0	0
F. bussei	6 (0)	0	4	0	2	0
F. glumosa	15 (5)	0	6	8	0	1
F. stuhlmannii	23 (10)	0	0	7	16	0
F. nigro-punctata	3 (2)	0	0	0	3	0
F. tettensis	11 (3)	0	0	11	0	0
F. abutilifolia	34 (24)	0	7	27	0	0
F. trichopoda	5 (1)	0	0	5	0	0
F. grevei	4 (2)	4	0	0	0	0
F. rubra	2 (0)	2	0	0	0	0
F. marmorata	4 (4)	4	0	0	0	0
F. fischeri	6 (0)	0	0	0	6	0
F. craterostoma	4 (1)	0	0	0	1	3
F. natalensis	3 (2)	0	2	0	0	1
F. burtt-davyi	24 (4)	0	0	24	0	0
F. antandronarum	2 (0)	2	0	0	0	0
F. reflexa	1 (0)	1	0	0	0	0
F. thonningii	43 (6)	0	7	24	12	0
F. cyathistipula	1 (0)	0	0	0	1	0
F. scassellatii	1 (1)	0	0	0	1	0
F. ottoniifolia	4 (2)	0	0	0	3	1
F. tremula	1 (0)	0	0	1	0	0
F. polita	2 (0)	1	0	1	0	0
F. bizanae	1 (1)	0	0	1	0	0
F. sansibarica	5 (2)	0	0	1	4	0
F. bubu	1 (0)	0	0	1	0	0
Subgenus total	266 (93)	23	31	143	58	10
Genus total	426 (197)	90	49	177	79	35

cantly more likely to be attacked by *Hilda* than trees in the *Urostigma* subgenus (59% vs 34%, respectively; $\chi^2 = 11.57$, $df = 1$, $P < 0.0001$).

Ants were present on figs throughout most of their development, with the stage of figs not significantly affecting the probability of ant colonization ($\chi^2 = 1.83$, $df = 5$, $P = 0.87$). We also failed to detect significant relationships between crop size or tree height and probability of trees having ants (tree height, $F_{1,420} = 0.21$, $P = 0.65$; crop size, $F_{1,407} = 0.34$, $P = 0.56$).

Each tree categorized as ant-colonized had ants on a substantial portion of their figs. For *F. sur*, 37% of the fig crop of an individual tree was colonized on average.

A one-way ANOVA indicated that this varied significantly among countries ($F_{3,42} = 4.42$, $P = 0.009$), with Bonferroni/Dunn multiple-comparison tests indicating that the colonization level for South Africa was significantly less than for Zambia ($P = 0.005$) and Zimbabwe ($P = 0.004$; Fig. 2B). For the other *Ficus* species, an average of 24% of the fig crops on sampled trees were colonized by ants, with the two subgenera not differing significantly with respect to colonization frequency (Fig. 3B; $F_{1,147} = 0.03$, $P = 0.87$). Trees in the subgenus *Sycomorus* were therefore more likely to be ant-colonized than those in the subgenus *Urostigma*, but ants were equally abundant on colonized trees. A two-way ANOVA revealed that the percentage of each tree's
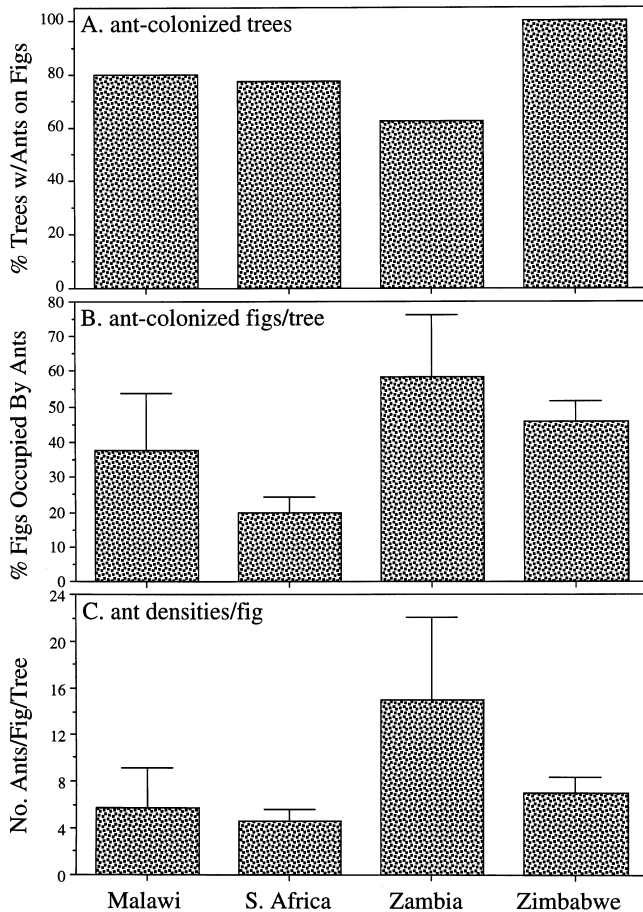
Fig. 2 Data for *Ficus sur* across four southern African countries, illustrating the percentage of sampled trees with ant-colonized figs (**A**), the percentage of figs per tree that were colonized by ants (**B**), and the average number of ants per fig per tree (**C**). (*F. sur* does not occur in Madagascar and this country is therefore not included in the graph.) *Vertical bars* correspond to 1 SE. Numbers of trees sampled in each country are shown in Table 1

Fig. 3 Data from *Ficus* trees in the subgenera *Sycomorus* (excluding *F. sur*) and *Urostigma* across four southern African countries and Madagascar, illustrating the percentage of sampled trees with ant-colonized figs (**A**), the percentage of figs per tree that were colonized by ants (**B**), and the average number of ants per fig per tree (**C**). *Vertical bars* correspond to 1 SE. Numbers of trees sampled in each subgenus and country are shown in Table 1

fig crop colonized by ants varied significantly among countries ($F_{4,139} = 8.42$, $P < 0.0001$) but not subgenera ($F_{1,139} = 0.89$, $P = 0.35$; the interaction term was not significant). Bonferroni/Dunn multiple-comparison tests indicated that the proportion of figs colonized by ants was significantly lower in Madagascar compared to South Africa ($P < 0.0001$), with insignificant trends in this direction for Malawi ($P = 0.044$), Zambia ($P = 0.037$), and Zimbabwe ($P = 0.041$).

Ant species

Ant-colonized trees were significantly more likely to have *Pheidole* on their figs than all other ant species combined ($\chi^2 = 3.96$, $df = 1$, $P < 0.05$). This ant species was present alone on 53.8% of the trees sampled and together with other species on 4.6% of the trees. In contrast, we found the following ants on colonized trees much less frequently: *Anoplolepis* sp. (6.1%), *Crema-*
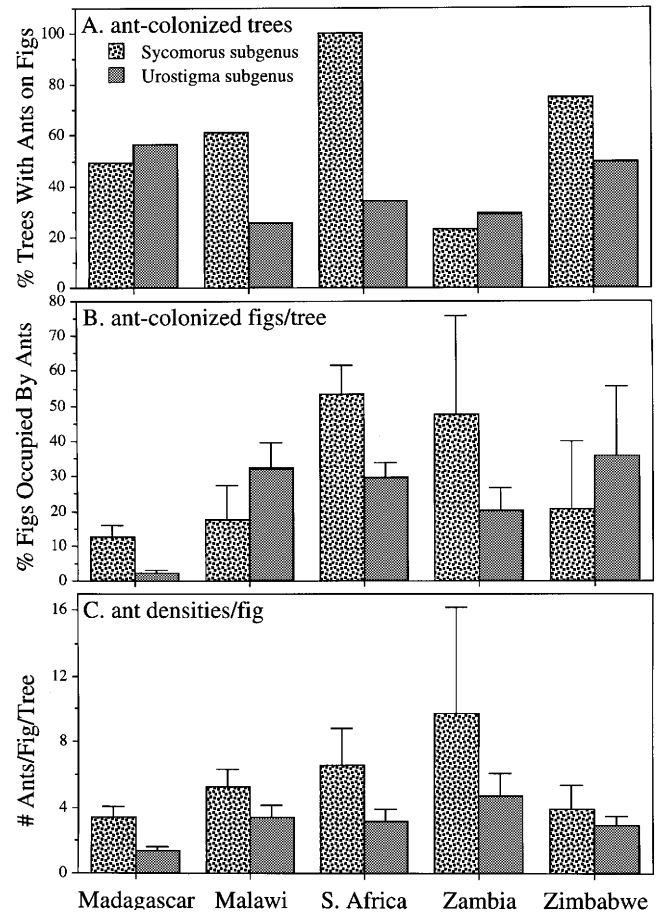
togaster sp. (5.3%), *Campanotus* sp. (3.0%), *Polyrachis schistacea* (0.8%), *Odontomachus troglodytes* (0.8%), *Oecophylla longinoda* (0.8%), and unidentified species (25.8%).

Ant densities and wasp production

For three of the four wasp taxa, the ant-exclusion experiment indicated that an average of 4.5 ants per fig resulted in considerable benefits for *F. sur* in South Africa (Fig. 4). Significantly more pollinating wasps (*C. capensis*) emerged from ant-tended figs (with an average of 4.5 ants/fig) compared to untended figs ($F_{1,18} = 21.3$, $P = 0.0002$), and emergence of parasitoid wasps (*A. guineenis*) from ant-tended figs was significantly reduced relative to controls ($F_{1,18} = 7.9$, $P = 0.012$). The number of externally ovipositing ovule-gallers emerging (the three *Apocryptophagus* species) was also reduced significantly when ants were
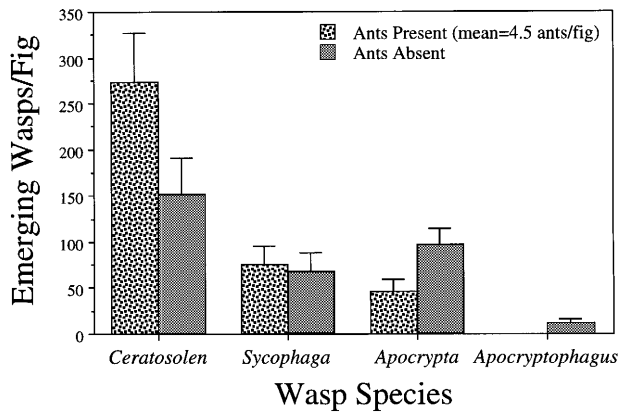
Fig. 4 Influence of the presence or absence of ants on the number of individual wasps from four taxa emerging from the figs of *Ficus sur*. *Vertical bars* correspond to 1 SE. Data are from 12 fig-bearing branches per treatment

Fig. 5 The mean number of ants on figs as a function of four attraction sources. In most, but not all cases, the ants on figs were *Pheidole megacephala*. Data are from 197 individual *Ficus* trees distributed among 20 species. *Vertical bars* represent 1 SE. *Numbers above bars* correspond to fig tree sample sizes

present ($F_{1,18} = 5.8$, $P = 0.027$). However, numbers of the internally ovipositing ovule-galler, *S. cyclostigma*, were not influenced by the presence or absence of ants ($F_{1,18} = 0.13$, $P = 0.718$).

Our large-scale sampling indicated that ant densities per fig commonly exceeded the 4.5 level found experimentally to provide figs with indirect benefits. For *F. sur* trees, ant densities averaged 6.9 per fig, with 49% of the individual trees sampled having ant densities per fig equal to or greater than 4.5. Average ant densities per fig for *F. sur* were above 4.5 in all countries (Fig. 2C), with significant variation among countries ($F_{3,42} = 2.87$, $P = 0.048$).

For the other *Ficus* species, ant densities per fig for the sample as a whole were less than the 4.5 level, averaging 3.7 per fig. However, a two-way ANOVA indicated that ant densities varied significantly among *Ficus* subgenera ($F_{1,134} = 5.1$, $P = 0.026$), averaging 4.5 for trees in the *Sycomorus* subgenus and 3.2 in the *Urostigma* subgenus (Fig. 3C). Twenty-three percent of the non-*F. sur* trees had ant densities per fig equal to or greater than 4.5 (39% for the *Sycomorus* subgenus and 13% for the *Urostigma* subgenus). Ant densities per fig also varied substantially among countries ($F_{1,134} = 2.23$, $P = 0.069$; the subgenus × country interaction term was not significant).

Our data indicated that the source of ant attraction had a significant influence on the number of ants recruiting to figs (Fig. 5; one-way ANOVA, $F_{3,186} = 6.71$, $P = 0.0003$). Bonferroni/Dunn multiple-comparison tests indicated that *Hilda* attracted significantly more ants to figs than other homopterans ($P < 0.007$) and unknown sources ($P < 0.0001$), but not plant exudates (presumably due to the small sample size for plant exudates). None of the tests indicated significant differences among other homopterans, plant exudates, and unknown sources of attraction. There was no significant difference between the two *Ficus* subgenera with respect to the number of ants visiting the different attraction sources ($F_{3,182} = 0.23$, $P = 0.874$), although there was
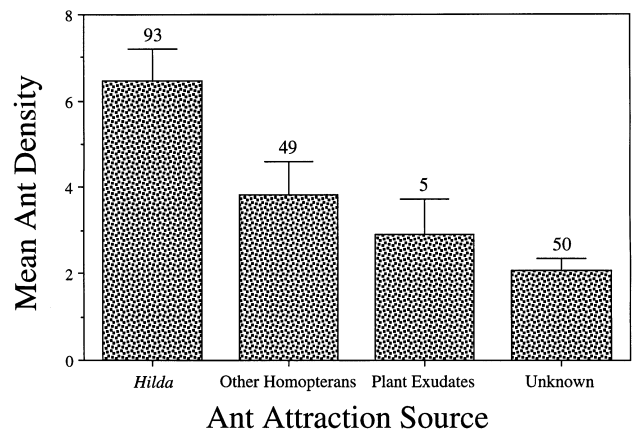
a trend for *Hilda* to attract more ants when feeding on trees in the subgenus *Sycomorus* compared to *Urostigma*.

Discussion

In this paper, we have proposed and tested the hypothesis that positive indirect effects in a fig-homopteran-ant system are geographically widespread and involve numerous fig species. Based on the field experiments of Compton and Robertson (1988, 1991) and Zachariades (1994), we have outlined three conditions that must be met in order to support this hypothesis and present data to evaluate each of them. Although we detected substantial variation, our data generally support the hypothesis that many fig species, particularly those in the subgenus *Sycomorus*, commonly benefit from being fed upon by ant-tended homopterans. The data strongly suggest that the benefits to fig trees, particularly those in the subgenus *Sycomorus*, persist across a large portion of southern Africa (although they are less frequent on Madagascar). We also show that non-*Hilda* homopterans and plant exudates can attract ants to figs, although at lower densities than for *Hilda* and often in insufficient numbers for indirect benefits to occur.

The net effect of ant-tended homopterans on their host plants will be positive if the indirect benefits of protective ants exceeds the direct negative effects of homopteran herbivores (Carroll and Janzen 1973; Messina 1981). Studies by Zachariades (1994) strongly indicate that this condition is met for phloem-feeding *Hilda* on *F. sur* in South Africa. His experiments showed that the presence of *Hilda* did not significantly affect fig diameter (which is correlated with seed number), the number of mature figs per fruiting branch, or rates of seed germination. He concluded that, if *Hilda* does have direct negative effects on the reproductive success of *F. sur*, they are exceedingly small relative to the indirect

beneficial effects of this species. Although we lack similar data for other *Ficus* species and regions of Africa, the strength of the indirect benefits found in this study combined with the findings of Zachariades (1994) suggest that the net effect of hosting ant-tended *Hilda* (and possibly other homopterans) will often be positive for *Ficus* species.

The importance of this positive interaction, for each fig species or subgenus, will be a joint function of the degree to which figs and pollinators are attacked by antagonistic wasps (ovule-gallers and parasitoids, respectively), the probability that trees attract ants to their figs, the level of ant infestation per tree, fig size, and the abundance of ants per fig. There will undoubtedly be considerable temporal and spatial variation in many of these variables and thus in the frequency and intensity of the indirect interaction. The strength of the interaction will also vary according to the number of antagonistic wasps species (and the number of individuals of each species) that attack a particular tree.

An important requirement for the occurrence of indirect benefits is that ants be present on figs during the developmental stages that are susceptible to attack by antagonistic wasps. With regard to ovule-galling species, figs should benefit from ant protection during all stages because these wasps can oviposit before, during, or after pollination (S.G. Compton, personal observation). With respect to parasitoids, figs should benefit from protection of their pollinators only after the pollination stage (i.e., when future pollinators are developing inside figs). Our data show that ants were found on figs during all their developmental stages and thus were present to protect both figs and pollinators from attack.

There are several potential explanations for why species belonging to the subgenus *Sycomorus* were more commonly involved in the fig-homopteran-ant interaction than those in the *Urostigma* subgenus. The most probable of these is simply that *Hilda* and other ant-tended homopterans prefer to feed on figs in the *Sycomorus* subgenus. Our data offer partial support for this view, as *Hilda* was found on figs significantly more often for *Sycomorus* species than *Urostigma* species. Another explanation is that they produce honeydew on *Sycomorus* species that is more rewarding to ants, either in terms of quality and/or quantity (see Cushman 1991; Cushman and Addicott 1991).

For at least four reasons, we feel we may have underestimated the importance of positive interactions in these fig-homopteran-ant associations. First, our tree-sampling methods were conservative because it is likely that we failed to locate ants on trees when they were actually present (this may have been especially true for larger trees). Second, our estimate of 4.5 ants per fig is not the minimum number of ants required for protection of individual figs – it is simply the average density that we know from experiments can lead to the occurrence of indirect benefits. Third, by focusing on *F. sur*, we may have overestimated the ant densities that are required to provide protection. This is because fig diameters are generally larger in the *Sycomorus* subgenus than in the *Urostigma* subgenus, and the figs of *F. sur* are among the largest in our survey (S.G. Compton, personal observation). Trees with larger figs presumably require more ants to patrol the greater surface area of their figs. The majority of tree species in our sample produce figs that are considerably smaller than those of *F. sur*, and thus may require fewer ants per fig to provide protection. Fourth, it is possible that this positive interaction occurs over more of the African continent than we sampled. *Ficus* species are found throughout the continent, as is *Pheidole*. While the distribution of *Hilda* is not well documented, we have records of the homopteran being tended by ants on fig trees in Uganda (East Africa), Cameroon (West Africa), and the Comoro Islands (off the coast of Mozambique; S.G. Compton, personal observation).

Given that a number of studies have shown that plant species can indirectly benefit from hosting ant-tended homopterans (see Beattie 1985; Compton and Robertson 1988; Bach 1991), it is relevant to consider the factors that would lead to such interactions being geographically widespread. We suspect the most important determinant will be that host plants must have significant and spatially consistent 'problems' with their enemies. While this appears to be the case for fig species, it may not be the case for many plant species that host ant-tended herbivores. For example, Messina (1981) showed that goldenrod (*Solidago altissima*) could benefit from being fed on by ant-tended membracids because ants reduced the effect of a far more detrimental beetle herbivore. However, beetle densities may rarely reach the levels necessary for indirect benefits to occur. Thus, because beetles probably constitute a variable and ephemeral 'problem' for goldenrods, we hypothesize that the indirect effect will occur sporadically in this system.

Species pairs and assemblages regularly occur across large geographic regions, but for understandable reasons, ecologists usually study these associations and the resulting interactions on a much smaller scale – usually at one or a few sites. The work presented here offers contributions to ecology on three fronts. First, we have outlined and applied a simple method for attaining geographic-scale data on species interactions. Second, we have documented that an ant-plant-homopteran association occurs over an extensive geographic range and involves at least 20 host plant species. Simply showing that a species association occurs on such a large scale – regardless of the interaction's outcome – has rarely been demonstrated and thus represents an important advance. Third, we have presented data suggesting that the outcome of this species association often involves indirect benefits for the various host plant species. Such large-scale data are essential for understanding the evolutionary and coevolutionary consequences of species interactions, as well as the influence of these interactions on population dynamics and community structure.

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