BIODIVERSITY CONSEQUENCES OF PREDATION AND HOST PLANT HYBRIDIZATION ON AN APHID–ANT MUTUALISM

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Abstract. We examined the hypothesis that mutualists, predators, and host plant quality act in concert to determine the distribution and abundance of a common herbivore. The aphid, *Chaitophorus populicola,* is found only in association with ants, which provide tending services and protection from predators. As a consequence, aphid abundance declined by 88% on host plants located $\geq$6 m from an ant mound. Differences in host plant quality resulted in aphid fecundity being greatest on narrowleaf cottonwoods, 7–22% less on backcross hybrids, 37–46% less on F_1 hybrids, and 57–61% less on Fremont cottonwoods. Due to the combined effects of these factors, we found that the realized aphid habitat was only 21% of their potential habitat.

On trees where aphids and tending ants are present, aphids and ants greatly outnumber any other arthropod species; therefore, we examined the hypothesis that the factors affecting aphid density and distribution are also determinants of arthropod community structure. On a per-tree basis, observational data showed that arthropod species richness was 51% greater and abundance was 67% greater on trees where aphid–ant mutualists were absent relative to trees where they were present. When aphids were experimentally removed and ants abandoned the tree, we found the same pattern. On a per-tree basis, arthropod species richness increased by 57%, and abundance increased by 80% where aphid–ant mutualists were removed, relative to control trees. Overall, a total of 90 arthropod species were examined in this study: 56% were found only on trees without aphid–ant mutualists, 12% were found only on trees with aphid–ant mutualists, and 32% were common to both. Specific guilds were also affected; the aphid–ant mutualism had a negative effect on herbivores, generalist predators, and other species of tending ants, and a positive effect on specialist enemies of aphids. These results suggest that, by examining the factors responsible for the population dynamics of a common herbivore, we may also uncover mechanisms that determine arthropod community structure. Furthermore, studies that address the role of mutualism in shaping communities are underrepresented in the literature; these results emphasize the importance of mutualism in ecological communities.

Key words: aphid–ant mutualism; biodiversity; Chaitophorus populicola; *community structure;* Formica propinqua; *herbivory; host plant quality; hybridization;* Populus fremontii $\times$ P. angustifolia; *predation.*

Introduction

Top-down (Hairston et al. 1960, Menge and Sutherland 1976, Oksanen et al. 1981, Fretwell 1987, Strong 1992), bottom-up (Root 1973, White 1978, Price et al. 1987), and lateral effects from organisms on the same trophic level (Faeth 1985, 1986, Karban 1986, Ritchie and Tilman 1993, Merrill et al. 1994, Brown and Weis 1995, Hougen-Eitzman and Karban 1995) affect herbivore survival and performance. However, relatively few studies have examined how these factors might act in concert to produce a complex web of interactions that determine the distribution of a herbivore (but see review by Harrison and Cappuccino 1995). Furthermore, if a herbivore is abundant and/or affects other species and trophic levels, community structure may be altered (e.g., Dickson and Whitham 1996). Our stud-

ies have two major goals: (1) to quantify the major factors that affect the local and geographical distribution of the free-feeding aphid, *Chaitophorus populicola,* and (2) to examine how the distribution of aphids directly and indirectly affects other trophic levels. This study represents an effort to understand how the selective forces acting upon a population subsequently extend to the community via direct and indirect pathways. As other studies have suggested, the community-level consequences of indirect interactions may equal or exceed the importance of direct interactions, yet they are poorly understood (e.g., Martinsen et al. 1998).

Aphids are well suited to observationally and experimentally address community-level effects of herbivore population dynamics (see Plate 1). Numerous studies have shown that aphid populations are structured by top-down, bottom-up, and lateral factors, but we are unaware of any studies that have integrated these factors. Free-feeding aphids often depend on a mutu-

PLATE. 1. Aphids, ants, predators, and parasites are shown interacting in close proximity on the same cottonwood stem. The ant in the upper left of the photograph is tending a colony of aphids. Below the colony, a large white syrphid maggot can be seen feeding on aphids, and the white eggs of this predator can be seen in the center of the photograph. The bloated, dark-colored aphid to the right of the syrphid eggs has been "mummified" by a parasitic wasp. Photograph by Thomas Whitham.

alistic interaction with ants. Aphids provide tending ants with sugar-rich honeydew (Way 1963), and the primary service that ants provide is protection from predators (Banks and Macauley 1967, Tilles and Wood 1982). This mutualism is important to aphid abundance and survival (Pontin 1978, Seibert 1992) because predators may extirpate aphid populations before they become well established (Way 1963, Banks and Macaulay 1967, Bradley and Hinks 1968, Sanders and Knight 1968, Addicott 1978, 1979, Chiverton 1986, Buckley 1987). Thus, aphid populations are both positively and negatively affected by organisms on higher trophic levels. Host plant traits that contribute to the success of aphid populations include leaf age and photosynthetic efficiency (Hartnett and Bazzaz 1984), plant height, growth, and flower occurrence (Service 1984a, Larson and Whitham 1991), shoot size (Addicott 1978), tree architecture (Larson and Whitham 1997), host plant genotype (Service 1984b, Blackman 1990), host plant species or hybrid type (Whitham 1989, Floate and Whitham 1993), and secondary host plant chemistry (van Emden 1978). Host plant quality is often one of the most important factors influencing host selection in aphids (Blackman 1990); and host plant species or hybrid type has been shown to determine the distribution and survival of a galling aphid (*Pemphigus betae*) in the same system as *C. populicola*. Hybrid or pure status also affects two other galling aphid species in the same system (Floate and Whitham 1993), and could have similar effects on populations of *C. populicola*. Last, aphids may be displaced through intraspecific (Whitham 1978, 1987) and interspecific competition (Moran

and Whitham 1990). Not only do aphids interact with aphids and other insects, but they are also affected by large herbivorous mammals (Danell and Huss-Danell 1985, Messina et al. 1993).

Having examined the factors affecting aphid distribution, we then sought to determine how aphid distribution affected other community members. This extension is important because several studies have demonstrated that aphids have the potential to act as a keystone species. For example, the abundance of birds, fungi, and insects decreased on cottonwoods when the galling aphid, *Pemphigus betae,* was removed (Dickson and Whitham 1996). However, species of aphids tended by ants may have the opposite effect on the surrounding arthropod community. Homopteran-tending ants have been shown to reduce the diversity of other herbivorous insects (Fowler and Macgarvin 1985) including many species of destructive defoliators (Nickerson et al. 1977, Messina 1981, Skinner and Whittaker 1981, Ito and Higashi 1991).

To examine the factors that affect the distribution of a common herbivore and its community-level implications, we addressed four major questions: (1) How do ant mutualists, predators, and host plant species or hybrid type act separately to determine the fecundity and distribution of *C. populicola*? (2) How do these three factors interact to determine aphid habitat usage? (3) How do the abundance and distribution of this aphid affect arthropod community structure and biodiversity? (4) Do distinct arthropod feeding guilds respond differently to the presence or absence of aphids?

Methods and Materials

Experimental organisms

The free-feeding aphid, *C. populicola,* is cyclically parthenogenetic and spends its entire life cycle on poplars (Richards 1972). They typically feed as a colony on terminal shoots where they are tended by ants (*Formica* spp.). From 1994–1998, we studied a natural population along the Weber River near Ogden, Utah. At lower elevations, the riparian zone is dominated by Fremont cottonwood, *Populus fremontii,* at high elevations the riparian zone is dominated by narrowleaf cottonwood, *P. angustifolia,* and at their common boundary both hybridize to form a 13-km hybrid and overlap zone (Keim et al. 1989, Whitham 1989). The hybrid zone contains both pure species, F_1 hybrids, and backcross hybrids.

Ant mutualists

Formica propinqua usually builds large colonies and is very aggressive. To examine the effects of these ant mutualists on aphid distribution, we censused the number of aphids on 15 trees that ranged from 1 to 15 m from ant mounds. For this data set and subsequent data sets where normality and/or equality of variance assumptions were not met, a square root transform was performed before we analyzed the data. Data were analyzed using a linear regression.

To experimentally control for plant genotype and initial aphid densities, we placed potted backcross cottonwoods at ground level at each of three set distances from ant mounds (1, 6, and 16 m). We replicated this design at six ant mounds, in which trees were randomized according to genotype, and blocked by ant mound. These six mounds were selected because of their large size and a lack of adjacent mounds that could complicate our analyses of distance effects. Approximately 20 aphids were transferred onto each potted tree. To ensure that aphids became established before predators removed them, aphids were protected with mesh enclosures for the first day and removed on the following day. Two weeks later, we counted the total number of aphids and tending ants on each tree. To test for both treatment (distance) and blocking effects (ant mound), aphid data were transformed and then analyzed using a Quade Test (Conover 1980). For this data set and subsequent data sets where transformed data did not meet normality assumptions, we performed a nonparametric test. Ant data were analyzed using a χ^2 test due to the abundance of zero counts.

Predators

Because declining aphid populations may result from aphid dispersal and/or predation, we designed an experiment that examined the effects of predation in the absence of aphid dispersal. We transferred aphids onto two branches on each of 13 trees and kept them in a mesh enclosure overnight to ensure that all began feeding prior to the experiment. On one branch, we continued to protect aphids using a mesh enclosure and obtained data on their performance in the absence of predation. On the second branch, the mesh enclosure was removed leaving aphids exposed to predators. On this second set of branches, aphids were prevented from dispersing by applying a thin layer of Tangle-trap (The Tanglefoot Company, Grand Rapids Michigan, USA) at the base of the branch with a syringe (all aphids were wingless). Previous experiments have shown that a very narrow and thin layer of Tangle-trap prevents aphid movement, but does not prevent larger predators from either stepping over the barrier or flying onto the branch. We counted aphid numbers at 0900, 1300, and 1800 for three days and noted any predators found feeding on the aphids. This design was replicated for 13 trees and data were analyzed using repeated-measures ANOVA.

To address whether protection from predators was the only service ants provided, we manipulated established aphid–ant associations in the field. We used three treatments with 12 replicate blocks. On one branch we left the aphid–ant relationship intact. On a second branch we caged aphids so that they were protected from predators but were not tended by ants. On a third branch we applied a thin, but broader layer of Tangle-trap so that aphids could not disperse or be protected by ants, but were still exposed to winged predators. Aphid abundance was quantified after 7 d; data were transformed and analyzed using two-way ANOVA.

Host plant species and hybrid type

To determine the effects of host plant species and hybrid type on aphid performance, aphids were transferred onto trees in a common garden, protected from predators using mesh enclosures, and their reproductive success quantified. Trees used in this experiment were 7 yr old, ~4 m tall, and represented Fremont, F_1 type hybrid, backcross hybrid, and narrowleaf cottonwoods. These trees had been cloned from trees growing naturally along the Weber River whose pure and hybrid status had been established using molecular techniques (Keim et al. 1989, Martinsen et al. 2001). In 1996, aphids were transferred onto seven trees of each of the four tree types. Aphids were allowed to feed and asexually reproduce for 10 d, at which time their abundance was measured. Data were transformed and analyzed using a Kruskal-Wallis test. The same experimental procedure was repeated in 1997, but the sample size was increased to 10 trees of each tree type and transformed data met normality assumptions. These data were transformed and analyzed using ANOVA.

To determine the effects of host plant species and hybrid type on the distribution of aphids throughout the ~500 km of the Weber River drainage system, aphids were censused at 37 sites along an elevational gradient. We chose 12 Fremont cottonwood sites, 13 hybrid sites (where we found both pure species, F_1

hybrids, and complex backcrosses), and 12 narrowleaf sites. At each site we randomly selected five cottonwoods of approximately the same size (3–4 m tall) along a 50-m transect and counted the numbers of aphids and their tending ants during a 2-min census. Data were analyzed using a χ^2 test due to the abundance of zero counts.

To determine whether aphid distribution was dependent on the number or type of ant species present in an area, we censused ant species and the number of ants present per square meter for each meter of our 50-m transect. Data were analyzed using a χ^2 test due to the abundance of zeros.

Combined top-down and bottom-up factors

We examined the relative and interactive effects of ant mutualists, host plant species, and hybrid type on aphid distribution. In the three different zones (Fremont, hybrid, and narrowleaf), we recorded both the occurrence of ants and the tree types (Fremont, F_1, backcross, and narrowleaf) on which aphids were present. Data were analyzed using a loglinear regression to account for both ant and host plant effects.

Indirect effects on the community

Chaitophorus populicola may indirectly affect other community members by supporting its aggressive, tending ant. To examine this relationship, we chose 12 trees infested with aphids and 12 trees in the same area that were uninfested. We then surveyed 100 shoots on each of the 24 trees and recorded the number and abundance of each arthropod species present. Because some small trees contained fewer than 100 shoots, species richness and abundance data were standardized per 50 shoots, transformed, and analyzed using an independent samples t test. Because we were unable to control for confounding factors that could affect our data, we then performed an experiment.

To experimentally examine the effect of the aphid–ant mutualism on the surrounding community, we choose 17 ramet pairs that were naturally infested with aphids. We paired ramets according to proximity, size, and initial aphid densities. Each pair was a member of the same cottonwood clone (i.e., individual), and different pairs were located within different clones. On one set of trees, we allowed aphid colonies and ants to freely establish and this set served as our control. On the second set of trees, we performed aphid removals beginning on 12 May 1998. On the removal trees, we wrapped the base of the tree in a thin layer of masking tape and then applied a thin layer of Tangle-trap on top of the masking tape. The masking tape allowed easy removal of the Tangle-trap at a later time. Tangle-trap was necessary at the time of aphid establishment to control their numbers. We then performed hand removals of aphids every-other day for 1 mo. On 30 June 1998, we removed the masking tape and Tangle-trap from the removal trees (which allowed wing-less insect recovery on the removal trees), but we continued our hand removals of aphids. With the removal of aphids, ants largely abandoned the trees. On 15 July 1998, we began our arthropod censuses on aphid removal and control trees. Our surveys of arthropods may be conservative due to the presence of Tangle-trap on aphid-removal trees during the time of aphid colonization. We performed visual censuses and recorded arthropod species and abundance. Censuses were performed once a week over the course of 1 mo, and data were combined for the four census periods. Because we were interested in the effect of the aphid–ant mutualism on the surrounding arthropod community, tending ants on aphid-infested trees were not included in community analyses. Species richness data were analyzed using a paired t test. Arthropod abundance data were transformed, analyzed using a paired t test, and results were adjusted using a Bonferroni correction because we also examined abundance data using a standardization. Because abundance data may be driven by one or a few very abundant species, we standardized each species to their individual maxima (Faith et al. 1987). With this standardization, all species are weighted equally and if the treatment and control groups differed significantly, the differences represent a community-wide pattern rather than a pattern driven by just a few species.

To examine the effect of aphids on different feeding guilds of arthropods, raw abundance data for trees with aphids, and trees with aphids experimentally removed, were transformed and analyzed using a paired t test. Ninety taxa were identified (see Table 1) and separated into broadly defined feeding guilds based upon the literature and/or our personal observations (e.g., Richards 1972, Kaston 1978, Slater and Baranowski 1978, Wheeler and Wheeler 1986, Stehr 1987, Borror et al. 1989). Data for the abundance of general predators, aphid-specific enemies, and tending ants (other than the dominant tending ant, *F. propinqua*) were transformed and analyzed using a Wilcoxon signed-ranks test. Results from these four guilds were adjusted using a Bonferroni correction. Those species that did not actively take part in a feeding guild were designated as "transient" species. Transient species were not placed into feeding guilds because these species were never observed to feed on any component of the cottonwood community, as either immatures or adults, in the past 6 yr we have conducted arthropod censuses.

Including both observational and experimental community studies, 2836 arthropods were censused (not including *C. populicola* and *F. propinqua*). We then used these data to examine the impact of the aphid–ant mutualism on rare species in the community. Rare species were defined as those species that were encountered ≤5 times during the course of our observational and experimental censuses.

TABLE 1. Arthropod community found on observational and experimental trees.

Order	Family	Species	Tree type	Guild
Araneae	Salticidae	species 1, 4, 5, 6	AA	GP
		species 2, 3	C	GP
	Thomisidae	species 1, 2	AA	GP
	Lycosidae	species 1	C	GP
Acari		species 1	AP	—
		species 2	AA	—
Opiliones		species 1	AA	O
Ephemeroptera		species 1	AA	—
Orthoptera	Acrididae	*Melanoplus sanguinipes*	C	H
		Hisperolettix viridus	C	H
	Tettigoniidae	species 1	AA	H
Dermaptera	Forficulidae	species 1	AA	GP
Hemiptera	Pentatomidae	*Podisus* sp.	AA	GP
		Euschistus sp.	AA	H
		Apateticus sp.	AA	GP
		Thyanta sp.	AA	H
	Miridae	species 1, 2	AA	H
		species 5	AA	O
	Reduviidae	*Zelus* sp., species 1	AA	GP
Homoptera	Cixiidae	species 1	C	H
	Delphacidae	species 1	AA	H
	Cicadellidae	species 4, 5, 10	AA	H
		species 2, 3, 6	C	H
		species 11, 12	AP	H
		species 1	AA	O
		species 7	C	O
	Cercopidae	species 2	C	H
		species 3	C	H
	Aphididae	*Chaitophorus* sp.	C	H
		Pemphigus betae	AA	O
		Thecabius sp.	AA	O
	Membracidae	species 1	AA	H
	Diaspididae	species 1	C	H
Thysanoptera		species 1	C	H
Neuroptera	Chrysopidae	species 1	C	AS
		species 2, 3	AA	O
		species 4	AA	AS
Coleoptera	Tenebrionidae	species 1	AA	H
	Scarabaeidae	species 1	AP	H
Coleoptera	Coccinellidae	*Adalia bipunctata*	AA	AS
		Coccinella sp.	AA	AS
		C. septum punctata	C	AS
		species 2	AA	O
	Anthribidae	species 1	AA	O
	Chrysomelidae	*Chrysomela confluens*	AA	H
Diptera	Phoridae	species 1	C	—
	Cecidomyiidae	species 1	C	—
		species 1	AA	—
	Otitidae	species 1	AA	—
	Syrphidae	species 1, 2	AP	AS
	Muscidae	species 1	AA	—
	Sarcophagidae	species 1	AA	O
	Calliphoridae	species 1	AA	—
Lepidoptera	Gracillariidae	species 1, 2	C	H
	Tortricidae	species 1	C	H
		species 2	AA	H
	Notodontidae	species 1	AA	H
	Gelechiidae	species 1	AA	H
	Noctuidae	species 1	C	H
	Geometridae	species 1	AA	H

TABLE 1. Continued.

Order	Family	Species	Tree type	Guild
Hymenoptera	Formicidae	*Liometopum* sp.	C	OTA
		Formica sp. 1	C	OTA
		Formica sp. 2	AA	OTA
		Formica sp. 3	C	OTA
		Tetramorium caespitum	AA	OTA
	Apidae	species 1	AP	O
	Mutillidae	species 1	AP	GP
	Andrenidae	species 1	AP	H
	Sphecidae	species 1	AP	O
	Vespidae	species 1	AP	GP
	Tenthredinidae	species 1, 2	AA	H
		species 3	C	H
	Braconidae	species 1	C	AS

Notes: Of the 90 species surveyed, 56% were found only on trees where aphids and ants were absent (AA), 12% were strictly associated with aphid–ant trees (AP), and 32% were common to both tree types (C). Arthropods are classified into the following broadly defined feeding guilds: herbivores (H), generalist predators (GP), other tending ants exclusive of *Formica propinqua* (OTA), aphid specialists (AS), transient species (—), and those species only appearing during the observational study (O), which were not separated into guilds.

RESULTS

Ant mutualists

Observations and experiments showed that aphid abundance sharply declined with increasing distance from ant mounds. Observational data showed that aphid densities ranged from 500 to 1800 aphids per tree (trees were ~1 m tall) adjacent to ant mounds and declined to zero only 8 m from ant mounds ($r^2 = 0.498$, $n = 15$, $P = 0.003$; Fig. 1A). We then experimentally ex-
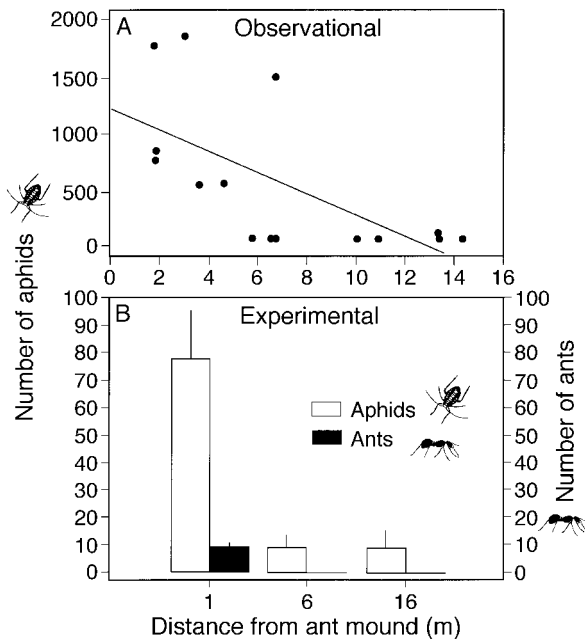

FIG. 1. Aphid distribution in relation to tending ant distribution. (A) Aphid densities on trees at varying distances from ant mounds. (B) Aphid densities on potted plants placed 1, 6, and 16 m from ant mounds (shown are means + 1 SE).

amined this pattern by placing potted cottonwoods at three set distances from ant mounds. In agreement with our observations, our experiment showed that after 2 wk, aphid numbers declined with increasing distance from ant mounds ($T = 8.26$, $n = 6$, $P < 0.05$; Fig. 1B).

Consistent with the decline in aphid numbers with increasing distance from the ant mound, our experiment also showed that tending ants declined with increasing distance from ant mounds ($\chi^2 = 110.02$, $n = 6$, $P < 0.05$). On potted plants, ants were only present 1 m from an ant mound and their abundance dropped to zero at greater distances (Fig. 1B). Apparently, ants are so important that aphid numbers decreased from 79.0 ± 17.77 aphids (mean ± 1 SE) per potted plant in the presence of ants, to 9.2 ± 6.11 aphids in the absence of ants.

The close proximity of aphids to ant mounds is related to two major services provided by ants. First, aphids significantly declined on branches exposed to predators compared to branches protected from predators ($F = 5.16$, $n = 13$, $P = 0.032$; Fig. 2). As expected, we also found a significant time effect ($F = 4.73$, $n = 13$, $P < 0.001$), and a significant time × treatment effect ($F = 2.378$, $n = 13$, $P = 0.018$). We had significant time and time × treatment effects because aphids exposed to predators suffered a 31% decline over the 3-d experiment, whereas aphids protected from predators showed no significant change in abundance (Fig. 2).

Second, ants provide tending services such as the removal of honeydew that has a direct effect on aphid fecundity. After 7 d, we found a significant difference in aphid numbers between ant-tended branches (i.e., ant exclusion of predators), branches where aphids were in mesh enclosures (i.e., predators experimentally excluded but no tending), and branches with Tangle-
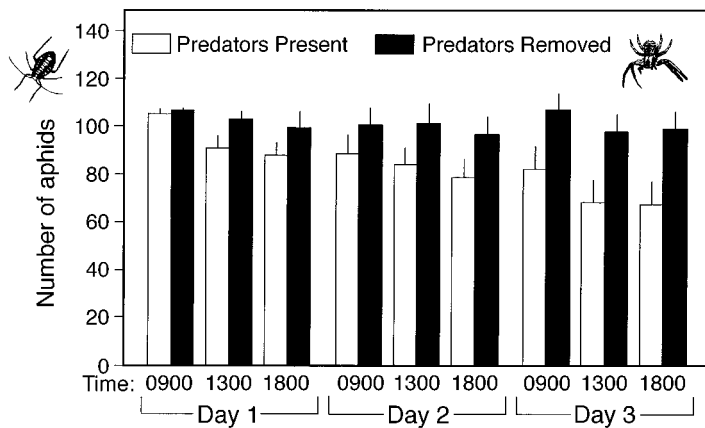
Fig. 2. The effect of predators on aphid populations: aphid densities were measured three times per day over the course of three days on trees that were exposed to predators, and on trees where predators were removed (shown are means + 1 SE).

trap (i.e., exposed to predation and no tending) (Block: $F = 4.362$, $n = 14$, $P = 0.001$; Treatment: $F = 32.289$, $n = 14$, $P < 0.001$). Using Fisher's LSD for pairwise comparisons, we found significant differences between all three treatment groups ($P < 0.05$). Aphid populations were greatest in the presence of ants (498.4 ± 58.4 aphids), intermediate when protected from predators but tending eliminated (286.2 ± 41.4 aphids), and lowest in the absence of protection from predators and tending (167.3 ± 43.3 aphids).

Host plant effects

In two years of common garden experiments we found that both host plant species and hybrid type affected aphid fecundity. In 1996, aphids transferred onto Fremont, F_1, backcross, and narrowleaf cottonwoods
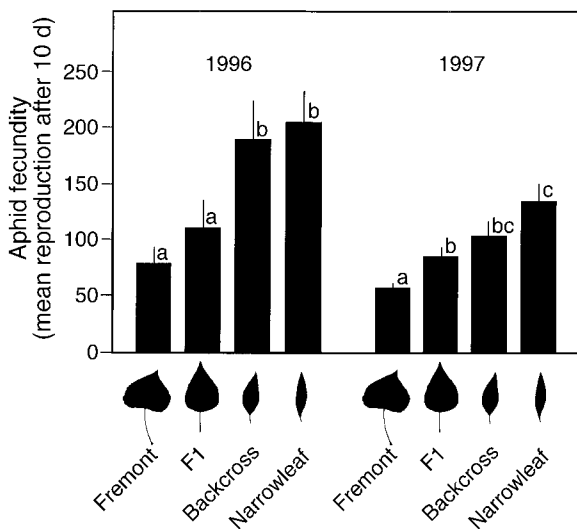

Fig. 3. Aphid fecundity on Fremont, hybrid (F_1 and backcross), and narrowleaf cottonwoods in common garden experiments conducted in 1996 and 1997. Shown are means + 1 SE; different letters indicate significant differences among means.

showed significant differences in reproduction after 10 d ($T = 9.193$, $n = 7$ trees per species or hybrid type, $P = 0.027$; Fig. 3). Using Dunn's test for multiple comparisons, we found that aphid performance varied significantly among groups; aphid fecundity was lowest on Fremont cottonwood, highest on narrowleaf cottonwood, with hybrids showing intermediate differences. In 1997, data met normality assumptions and the same general pattern was observed ($F = 7.638$, $n = 10$ trees per species or hybrid type, $P = 0.001$; Fig. 3). Using Fisher's LSD, we once again found that aphid performance varied significantly among groups; aphid fecundity was again lowest on Fremont cottonwood, highest on narrowleaf cottonwood, and hybrids were intermediate.

The effect of hybridization on aphid performance differed between hybrid types; backcrosses exhibited dominance and F_1's exhibited additive effects. In both years, backcross hybrids (i.e., trees resulting from F_1 × narrowleaf and backcross × narrowleaf crosses; Keim et al. 1989) were not significantly different than narrowleaf cottonwoods, demonstrating a dominance effect on aphid performance. In contrast, F_1 hybrids were significantly different from one, but not the other parent in 1996, but were significantly different from both parents in 1997. This indicates that the effect of F_1 hybrids on aphid performance was additive.

Based upon the experimentally derived differences in aphid performance across cottonwood species and their hybrids, we predicted that differential performance on these hosts would affect the geographical distribution of aphids. Consistent with this prediction, we found the same basic pattern over the 500 km of the Weber River drainage system (Fig. 4A). In censuses of 37 sites (12–13 per zone), we found *C. populicola* aphid colonies in the hybrid and narrowleaf zones, but none could be found in the Fremont zone ($\chi^2 = 455.49$, $n = 183$, $P < 0.05$). Because there were no aphids found in the Fremont zone, we also did not find any ants actively tending aphids in that area. The abundance
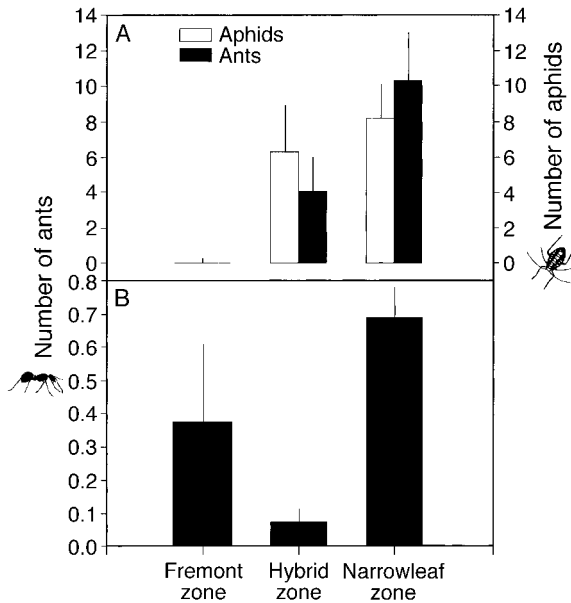
FIG. 4. The distribution of ants and aphids among three zones (Fremont, hybrid, and narrowleaf zones) along the Weber River. (A) The number of aphids, and ants found actively tending these aphids, on trees in the three different zones. (B) Transect data from the forest floor showing the abundance of tending ant species across the three different zones. Vertical bars indicate means + 1 SE.

of actively tending ants was therefore significantly different among the three different zones ($\chi^2 = 64.156$, $n = 12$, $P < 0.001$; Fig. 4A).

The geographical distribution of aphids is consistent with their differential performance on different host types. Alternatively, their geographical distribution could be caused by changes in the presence and abundance of tending ants. However, two lines of evidence argue against this alternative. First, although we did not find ants actively tending aphids in the Fremont zone (because we did not find any aphids), ant species are present in the Fremont zone that have been observed tending aphids in the other two zones (Fig. 4B). We found a significant difference in the abundance of potential tending ants among the three different zones ($\chi^2 = 334.49$, $n = 1850$, $P < 0.05$). In fact, the hybrid zone has the lowest abundance of potential tending ants among the three zones, yet it supports a large aphid population (Fig. 4A, B).

Second, in analyses of ant species composition, two of three ant species (*Tetramorium caespitum, Formica* sp.1, and *Camponotus* sp.) in the Fremont zone have been observed tending aphids in the hybrid and narrowleaf zones, three of three ant species (*Formica propinqua, Tetramorium caespitum,* and *Formica* sp.3) in the hybrid zone tend aphids, and two of two ant species (*Formica* sp.1, *Formica* sp.3) in the narrowleaf zone tend aphids.

Combined top-down and bottom-up effects

Throughout the Weber River drainage system, aphids were positively associated with ants ($z = -4.23$, $n = 41$, $P < 0.001$). On trees where aphids were found, tending ants were present 89% of the time. Host plant species or hybrid type also affected aphid distribution ($z = -3.11$, $n = 41$, $P < 0.001$). Aphids occurred on narrowleaf cottonwoods 68% as often as they did on backcross cottonwoods. We did not find any aphid colonies on either F_1 or Fremont cottonwoods. While both ant distribution and host plant type independently affected aphid distribution, we did not find an interactive effect between ant mutualists and host plant type ($z = -0.80$, $n = 41$, $P = 0.212$).

In combining the above effects, we found that the realized aphid habitat is a fraction of their potential habitat. Through our censuses of aphids at 37 sites along the Weber River, we calculated the proportion of cottonwoods inhabited by aphids with respect to the overall number of trees. We found that the interaction between host plant suitability and the presence of tending ants limits the distribution of aphids to only 21% of their potential habitat space.

Chaitophorus populicola *negatively affects biodiversity*

In an arthropod community composed of 90 species, observational studies showed that biodiversity increased when aphids were absent. Species richness was greater on trees where aphids were absent (2.48 ± 0.46 species), compared to trees with aphids (1.21 ± 0.23 species, $t = 2.01$, $n = 24$, $P = 0.029$). In addition, arthropod abundance was greater on trees where aphids were absent (4.69 ± 1.1 arthropods), compared to trees with aphids (1.56 ± 0.33 arthropods, $t = 2.48$, $n = 24$, $P = 0.01$).

To confirm that the absence of aphids and/or ants was responsible for the observed increase in biodiversity, we experimentally removed aphids and found that biodiversity increased. On aphid removal trees, species richness increased by 57% relative to trees with aphid–ant mutualists ($t = 7.35$, $n = 17$, $P < 0.001$; Fig. 5A). Similarly, on aphid removal trees, arthropod abundance increased by 80% relative to trees with aphid–ant mutualists ($t = 5.736$, $n = 17$, $P < 0.01$; Fig. 5B). Although the pattern of reduced total abundance in the presence of aphids could be driven by a few common species, when we standardized abundance (i.e., each species was standardized to a proportion of its maximum abundance), the same pattern emerged ($t = 5.95$, $n = 17$, $P < 0.01$; Fig. 5C).

Both rare and common species were negatively affected by the aphid–ant mutualism. Of the 90 recorded species, 65 (72% of the community) were considered rare (i.e., they were observed ≤5 times in our censuses and represented 6% of the total numbers of individuals). Of these 65 rare species, 45 were only found on
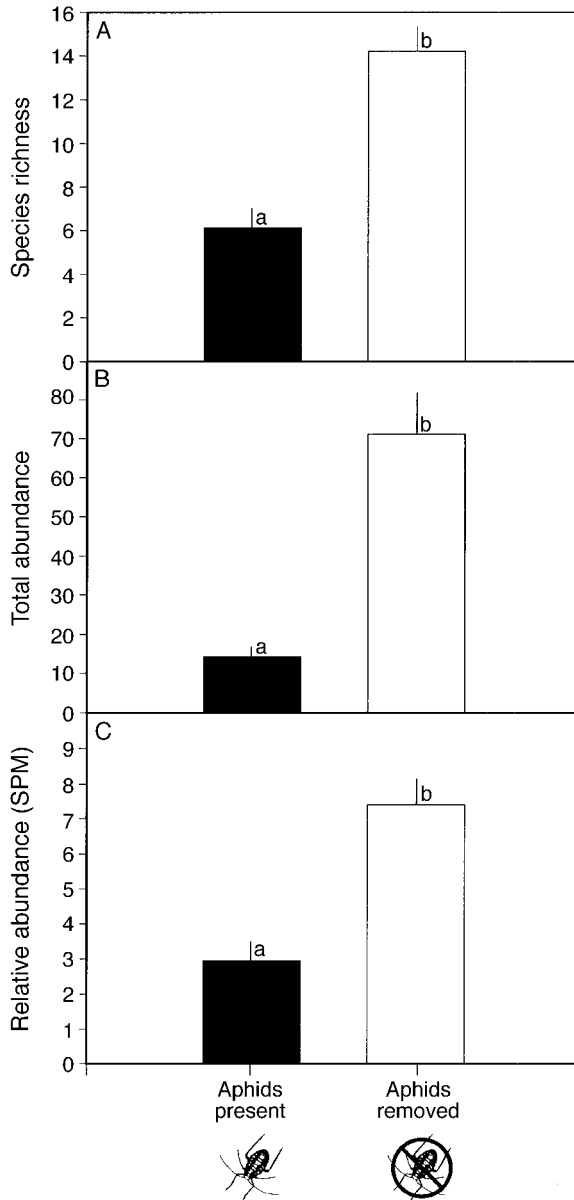
FIG. 5. The effect of the aphid–ant mutualism on the surrounding arthropod community: (A) species richness, (B) abundance, and (C) standardized abundance (SPM = species adjusted to equal maximum abundances) for arthropods found on trees with mutualists compared to trees where aphids were experimentally removed. Shown are means + 1 SE; different letters indicate significant differences between means.

trees without mutualists and only 9 were found on trees with mutualists.

Although the aphid–ant mutualism negatively affects biodiversity on individual trees, the mosaic pattern of trees with and without this mutualism supports the greatest overall biodiversity. In our combined observational and experimental censuses of 29 trees with mutualists and 29 trees without mutualists, the species composition of both groups was markedly different. Of the 90 species surveyed, 11 species (12%) were only found on trees with mutualists, 50 species (56%) were found only on trees without mutualists, and 29 species (32%) were common to both groups.

Indirect effects on different feeding guilds

We predicted that different guilds of arthropods would be affected differently by aphid removal and the subsequent abandonment of trees by aggressive ants. Three patterns were detected. First, because other herbivores and generalist predators have the potential to negatively affect aphid performance, tending ants should remove these guilds. Our aphid removal experiment clearly supports this prediction. On trees where aphids were removed, the abundance of herbivores increased by 76% ($t = 7.075$, $n = 17$, $P < 0.05$; Fig. 6). Tending ants not only remove other herbivores, but also generalist predators. On trees where aphids were removed, we found a 76% increase in predators with a general feeding behavior ($Z = 2.638$, $n = 17$, $P < 0.05$; Fig. 6). Second, we predicted that with aphid removal and the abandonment of the tree by aggressive ants, other species of tending ants would increase in abundance. In support of this prediction, we found a 92% increase in the abundance of tending ants (other than *Formica propinqua*) where aphids were removed ($Z = 3.352$, $n = 17$, $P < 0.05$; Fig. 6).

Third, in contrast to the positive effect of aphid removal on the above guilds, we predicted that specialist predators and parasites of aphids would be negatively affected by the removal of aphids. In support of this hypothesis, we found a 44% decrease in the abundance of predators and parasites that are aphid specialists on trees where aphids were removed ($Z = 2.644$, $n = 17$, $P < 0.05$; Fig. 6).

The negative effect of aphids on the surrounding arthropod community occurs primarily through the activities of its aggressive, tending ant. Ants actively remove arthropods from trees where aphids are present. We emphasize that ants were not excluded from aphid removal trees, but when aphids were removed, ants abandoned the tree (i.e., a very narrow Tangle-trap band is an effective barrier to aphids but not to ants). Ant abundance declined from 1240.7 ± 242.93 ants (mean ± 1 SE) on trees where aphids were present to 7.4 ± 2.85 ants on trees where aphids were removed. Therefore, the effect of aphids on the surrounding arthropod community is in part indirect because the presence of aphids represents a resource that attracts *F. propinqua*.

DISCUSSION

Top-down and bottom-up factors

In our study, both positive and negative top-down effects, and bottom-up effects influenced aphid population size and distribution. Although most studies have focused on single effects (Hunter and Price 1992,

Fig. 6. The effect of aphid–ant mutualists on the abundance of broadly defined feeding guilds. Icons, left to right, represent typical species of each guild: herbivores, other aphid-tending ants, generalist predators, and specialized aphid predators. Shown are means + 1 SE; different letters indicate significant differences between means.
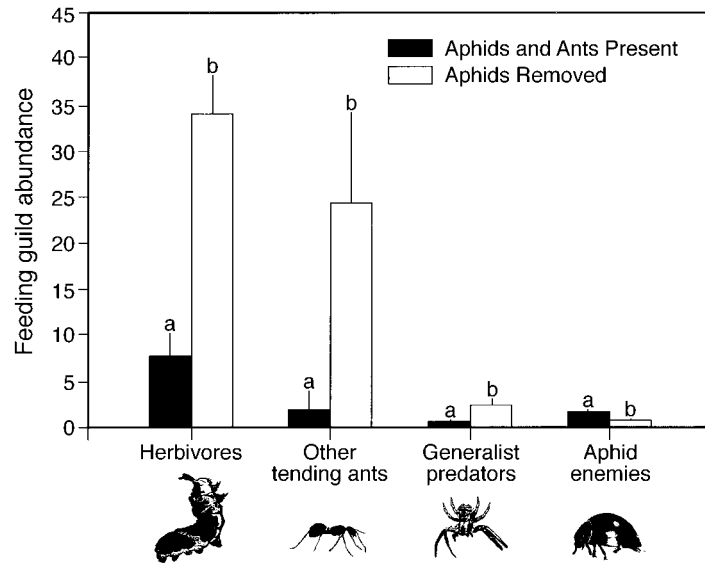
Menge 1992), our findings add to a small but increasing number of studies that have found herbivores to be regulated by multiple factors (Harrison and Cappuccino 1995).

Positive top-down effects due to ant mutualists were important in explaining aphid distribution and abundance. In an observational study, aphid numbers decreased with increasing horizontal distance from ant mounds such that no aphids could be found >8 m from ant mounds (Fig. 1). Experiments confirmed this pattern: aphid numbers dropped by 88% when aphids were located ≥6 m from ant mounds. These results agree with the findings of Seibert (1992) who showed that aphids were most abundant within the foraging range of ants.

The association of aphids with ants is essential to aphid survival because of negative, top-down effects from predators (Fig. 2). Similarly, Sanders and Knight (1968) found that predators extirpated aphid populations before the nymphs were able to mature, and even large colonies were destroyed before they could disperse.

Although protection from predators is probably the most important service provided by ants, other services are provided such as the removal of honeydew. For example, aphid colonies that were protected from predators in mesh enclosures, but not tended by ants, decreased by 34% over the course of a week. This population decline was probably caused by the buildup of honeydew that drowned many aphids. Ant tending has also been demonstrated to increase aphid honeydew production up to 50% (Banks and Nixon 1958), as well as stimulating growth, development, and larviposition (El-Ziady 1960).

The fecundity and distribution of *C. populicola* is also affected by the bottom-up effects of host plant species or hybrid type. Common garden experiments showed that aphid fecundity was greatest on narrowleaf cottonwoods, lowest on Fremont cottonwoods, and hybrids were intermediate (Fig. 3). In agreement with these experiments, in the wild we found that aphids were primarily concentrated in the narrowleaf and hybrid zones, but were not found in the Fremont zone (Fig. 4). Furthermore, the lack of aphids in the Fremont zone cannot be explained by a lack of aphid-tending ants because these ants are found across all plant zones.

Potential and realized distribution of aphids

Over the ~500 km of the Weber River drainage system, we found that host plant suitability based on cottonwood species and hybrid type appears to be most important in determining the geographical distribution of *C. populicola*. However, at the local level, the distribution of ant mutualists and predators is most important. The effects of ant mutualists and host plant type are not connected because ants respond to the presence of aphids, not host plant type. Our observations and experiments suggest that the relationship between ants and aphids seems to be more opportunistic on behalf of the ants. To ensure ant tending, aphids must establish on trees very close to ant mounds where they will be discovered by the ants. Solicitation of ant tending can be one of the most important factors influencing colony survival in free-feeding aphids, and this often leads to highly clumped aphid distributions near tending ant mounds (Pontin 1978, Seibert 1992). Membracid females choose plant stems closest to *Formica* mounds for oviposition to ensure that their offspring will be tended (Messina 1981). The aphid–ant mutualism described in this study is not as specialized as some ant–homopteran relationships, where ants "herd" homopterans onto the most productive plants or plant parts to maximize honeydew production (Holldobler and Wilson 1990).

In a geographical survey of 37 sites dispersed along the Weber River, aphids occupied only 21% of their potential hosts. To survive and prosper aphids require both the right host (i.e., species or hybrid type) and an ant mutualist. While numerous studies have documented the individual importance of top-down and bottom-up effects on aphid populations, we are aware of no studies that have combined these factors to explain aphid population size and distribution.

Indirect and direct effects of aphids on biodiversity

Because indirect effects can have a strong influence on community structure, they have received increasing attention. In Schoener's (1993) review of the importance of indirect effects on communities, 25% of the studies showed indirect effects to be stronger than direct effects. Knowledge of indirect interactions is essential to understanding some communities (Schoener 1993), and may help improve our current perspectives on coevolution (Miller and Travis 1996).

On a per tree basis, aphids had a negative impact on biodiversity, which occurred indirectly through their attraction of tending ants, and directly through their own activities. Observationally, we found that species richness and arthropod abundance were greater on trees without aphid–ant mutualists, compared to trees with aphid–ant mutualists. When aphids were experimentally removed from trees where they were naturally present, we found a similar increase in species richness and arthropod abundance (Fig. 5). Ant–homopteran mutualisms have likewise been found to negatively affect populations of destructive herbivores (Nickerson et al. 1977, Messina 1981, Seibert 1992); however, this study demonstrates that their negative effects extend to an entire community of arthropods representing multiple trophic levels.

Formica propinqua removes potential predators, other herbivores, and other competing ants on trees where aphids are present. The abundance of generalist predators and other herbivores both increased by 76% on aphid removal trees compared to control trees (Fig. 6). Also, on aphid removal trees that were abandoned by the aggressive ant, *F. propinqua,* the number of other aphid-tending ants increased by 92%. Thus, the presence or absence of aphids seems to dictate the territorial relationships between multiple ant species.

In sharp contrast to the ant-tended aphids of our study, in another study of a non-ant-tended aphid (*Pemphigus betae*), the presence of these galling aphids had the opposite effect on the arthropod community. On trees where the galling aphid was present, species richness increased by 31% and the relative abundance of arthropod taxa increased by 26% (Dickson and Whitham 1996). Even though both of these aphids occur at the same study sites and on the same host trees, the impacts of each on the arthropod community are opposite, apparently due to the presence or absence of an aggressive ant mutualist.

C. populicola also directly affects the surrounding arthropod community by supporting aphid-specific predators and parasites. Such specialists (e.g., syrphid flies and braconid wasps) decreased by 44% on aphid removal trees. Both winged parasites and evidence of aphid "mummification" were commonly found on aphid-infested trees. With their specific adaptations that circumvent tending ants (e.g., braconids can chemically mimic aphids), ants will protect them as though they were aphids. On both aspen (Sanders and Knight 1968) and spring barley (Chiverton 1986), aphids were found to attract specialist predators and parasites, particularly during the early phases of colony establishment.

Although the aphid–ant mutualism had a negative impact on the biodiversity of individual trees, at the landscape level, the combined mosaic of trees with and without mutualists enhances overall biodiversity. The presence of these mutualists excluded 56% of the recorded species and because rare species make up such a large proportion of the total (i.e., 65 of 90 species), mutualist impacts on rare species were especially great. In spite of these negative effects, 12% of all species were only found on trees with mutualists. This latter group that benefited from the presence of mutualists were mostly specialist predators of aphids that circumvent tending ants. Thus, a mosaic forest composed of trees with and without mutualists supports the greatest overall biodiversity. In the same system, Waltz and Whitham (1997) found that cottonwood ontogeny (i.e., age-related shifts in plant traits) structures community diversity in much the same way. They found that a mix of juvenile and mature trees supported greater biodiversity than either group alone.

In this study, we have combined the multiple factors that drive herbivore establishment and abundance with the effects of these herbivores on the surrounding arthropod community. Regulation of the abundance and distribution of *C. populicola* is accomplished by an array of interacting forces. Positive top-down effects from ant mutualists, negative top-down effects from predators, and bottom-up effects due to host plant quality all contribute to a complex web of interactions that structure aphid populations. Where aphids occur, they then directly and indirectly influence 90 other herbivores, generalist and aphid-specialist predators, and tending ants of the surrounding arthropod community. These results demonstrate some of the many links between different trophic levels and the need for an integrated approach to studying herbivores and natural communities.

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