

The effects of the invasive Argentine ant (*Linepithema humile*) and the native ant *Prenolepis imparis* on the structure of insect herbivore communities on willow trees (*Salix lasiolepis*)

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Abstract. 1. We examined the relative effects of the invasive Argentine ant, *Linepithema humile*, and a common native ant, *Prenolepis imparis*, on the community of herbivorous insects occurring on willow trees, *Salix lasiolepis* in Northern California, U.S.A.

2. Using paired control and treatment branches from which we excluded ants and other non-volant predators, we found that effects of Argentine ants on the herbivore community were generally similar to those of *P. imparis*. Argentine ants and *P. imparis* suppressed the damage by skeletonising insects by 50%, but had little effect on most other external-feeding or internal-feeding guilds.

3. The abundance of aphids was 100% greater in the presence of Argentine ants, but there was no effect on aphid numbers in the presence of *P. imparis*. Late season aphid numbers were substantially higher in the presence of Argentine ants, but not *P. imparis*.

4. The effects of Argentine ants on skeletonising insects and aphids combined with the overwhelming abundance of Argentine ant workers, suggests that they may have substantial, but often overlooked, effects on the herbivore communities on other plant species in or near riparian habitats in which they invade.

Key words. Argentine ants, aphids, feeding guilds, herbivores, invasive ants, native ants, *Salix*, willow.

Introduction

The spread and impact of the invasive Argentine ant (*Linepithema humile* Mayr, Hymenoptera: Formicidae) has disrupted ecosystems worldwide (Holway *et al.*, 2002a). It displaces native ants and has community-wide impacts on a variety of ground-dwelling arthropods (Ward, 1987; Human & Gordon, 1996, 1997; Holway *et al.*, 2002a). The direct effects of Argentine ants on native ants and other ground-dwelling arthropods can indirectly alter plant community structure (Bond & Slingsby, 1984; Christian, 2001, Carney *et al.*, 2003) and affect vertebrate predators of native ants (Suarez *et al.*, 2000).

Numerous studies have shown how native ant species can affect herbivorous insect communities (Fowler & MacGarvin,

1985; Mahdi & Whittaker, 1993; Wimp & Whitham, 2001; Oliveira & Del-Claro, 2005). The effects of native ants on herbivore communities are largely mediated by ant–hemipteran mutualisms such that the ants protect the hemipterans from their predators and parasitoids and in return receive honeydew – a carbohydrate and amino acid rich resource – from the hemipterans (Way, 1963). Because hemipteran-tending native ant species can vary in the degree of mutualism, their aggressiveness, and territoriality, they can also vary in their effects on herbivorous insect communities. In addition, particular herbivore guilds might be more or less vulnerable to ant predation. For example, aphid abundance usually increases in the presence of ants, but other guilds of herbivorous insects usually decrease in abundance and richness (Fowler & MacGarvin, 1985; Mahdi & Whittaker, 1993; Wimp & Whitham, 2001; Crutsinger & Sanders, 2005).

Despite the widespread appreciation that hemipteran-tending native ant species can alter herbivore community structure, and that invasive ant species dramatically alter ground-foraging insect

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communities, few studies have examined the extent to which invasive ant species might alter herbivorous insect communities (Kaplan & Eubanks, 2005; Altfield & Stiling, 2006; Styrsky & Eubanks, 2007). Argentine ants, in particular, have long been associated with high densities of honeydew-producing hemipterans and displacement of the natural enemies of the hemiptera, especially in agricultural and riparian systems (Newell & Barber, 1913; Way, 1963; Frazer & van den Bosch, 1973; Ward, 1987; Holway, 2005; Daane *et al.*, 2007). However, little is known about the extent to which Argentine ants alter entire communities of herbivores (Styrsky & Eubanks, 2007).

In this study, we examine the impacts of Argentine ants on the herbivore community associated with Arroyo Willow (*Salix lasiolepis* Benth., Salicaceae) in northern California. Using manipulative experiments, we contrast the effect of Argentine ants and a common native ant species [*Prenolepis imparis* (Say), Hymenoptera: Formicidae] across several guilds of willow-feeding herbivores.

Methods

The Argentine ant

Argentine ants were introduced to California around 1907 (Newell & Barber, 1913; Holway *et al.*, 2002a). Now, they are widely distributed at lower elevations in California with most of their spread occurring from human-mediated jump dispersal rather than by colony fission and budding (Holway, 1995, 1998; Human *et al.*, 1998; Suarez *et al.*, 2001). Argentine ants are found in a variety of habitats characterized by warm, moist Mediterranean climates, often along riparian corridors (Hölldobler & Wilson, 1990; Passera, 1994; Holway, 1995; Human *et al.*, 1998; Suarez *et al.*, 2001; Holway *et al.*, 2002b). As with other tramp ants, they often occur in disturbed areas and may not move into natural areas unless suitable habitat is available. Human and Gordon (1997) reported that the diet of Argentine ants is dominated by secretions from phloem-feeding insects and the body fluids of dead organisms. However, Argentine ants will occasionally prey on small, slow moving arthropods and their eggs.

Experimental system

To compare the effects of the invasive Argentine ant and the most common native ant species (*Prenolepis imparis*) on herbivorous insect communities, we studied the community of herbivorous insects on the willow tree *S. lasiolepis* in Owl Canyon on San Bruno Mountain in San Mateo County, California (37°40'15"N, 122°23'56"W). Argentine ants have invaded the *S. lasiolepis*-dominated lower reaches of the riparian corridor in Owl Canyon (invaded region, 30 m above sea level), but had not yet invaded the upper reaches of the watershed which transitions from willow to oak woodland (*Quercus agrifolia* Née, Fagaceae) (un-invaded region, 68 m above sea level). The average annual low temperature at the nearest recording station (Brisbane, California, U.S.A.) is 9 °C and the average high temperature is 18 °C. Outside the riparian corridor, the vegetation consists

of coastal scrub and grassland. Besides Argentine ants, the ant fauna of San Bruno Mountain consists of 25 native ant species including the genera *Camponotus*, *Crematogaster*, *Formica*, *Temnothorax*, *Monomorium*, and *Pheidole*, among others (P. S. Ward, pers. comm.).

In March 2003, 32 willow trees were randomly chosen, half from the lower reaches of Owl Canyon, which has been invaded by Argentine ants, and half from the upper reaches of Owl Canyon where Argentine ants were absent. Because herbivore abundance and levels of herbivory may depend on tree gender (Boecklen *et al.*, 1990), equal numbers of male and female trees were chosen. On each tree, two branches of similar rank and height were randomly selected and one branch was assigned to receive the exclusion treatment. All experimental branches were easily accessible from the ground without the use of ladders. On 8 April 2003, Tanglefoot® (Grand Rapids, MI) Pest Barrier was applied to the base of each exclusion branch to prevent ants from climbing onto branches. Nearby branches were trimmed to prevent ants from dropping onto treatment and control branches. Tanglefoot was reapplied as needed.

To determine an appropriate sample size, we used data from Sipura (2002) for a preliminary estimate of variance, and assumed that correlations among the levels of the within-subjects factors ranged from 0.4 to 0.6 (Low & Connor, 2003). We estimated the effect size based on Sipura (2002) in which ant exclusion caused a 100% increase in the level of herbivory on willow. To achieve 80% power with a 100% effect size, we estimated that a minimum of 12 replicates was needed.

Estimating insect abundance

We examined the 30 most distal leaves on each experimental branch monthly from April to September. We grouped herbivores into internal-feeding guilds (leaf-mining, gall-forming, leaf-tying, and leaf-rolling insects) and external-feeding guilds (leaf-chewing, leaf-skeletonising insects, and aphids). We quantified the effects of leaf-chewing and skeletonising insects by measuring the percentage of surface area damaged on each leaf. To estimate the total area of the leaf and the leaf area damaged, we used a 1 × 1 cm transparent grid placed over each leaf. In addition, for each branch, we counted the number of aphids, frequencies of leaf galls, leaf mines, leaf-ties, and leaf-rolls. Individual insects were counted when present. In addition to each feeding guild, the total number of ants of each species was tallied during each sampling period. To determine if premature leaf abscission distorted our estimates of herbivory by external-feeding insects or the frequency of internal-feeding insects, we estimated leaf abscission by counting abscised and attached leaf nodes.

Statistical analysis

To test for effects of ants on herbivore communities on willow, we used a four-factor experimental design with an exclusion treatment (EXCLUSION), an invasion treatment (INVASION), a season treatment (TIME), and host-plant gender (GENDER).

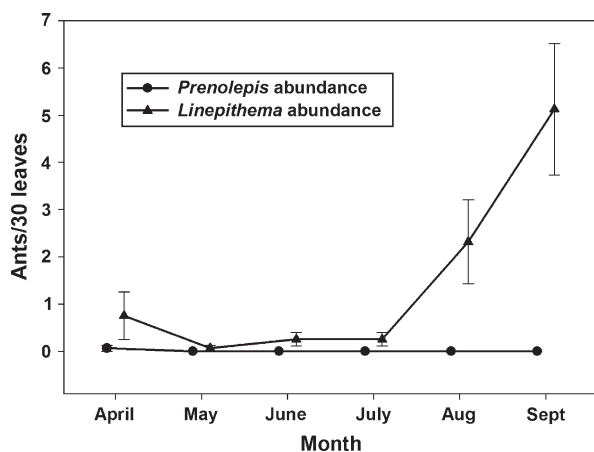


Fig. 1. Number of *Linepithema humile* or *Prenolepis imparis* workers per 30 leaves on control branches (ants not excluded) in invaded and un-invaded areas, respectively. Symbols are means and narrow bars indicate ± 1 standard error.

Because individual willow trees received both levels of the exclusion treatment and were observed monthly, the exclusion and season effects are within-subjects factors (repeated-measures factors). We report Greenhouse–Geisser adjusted univariate *F*-tests to account for non-sphericity of the variance-covariance matrix (O'Brien & Kaiser, 1985).

Results

Ants

Argentine ants were abundant on willows early in the spring, virtually absent during the early summer, and increased in abundance five-fold in late summer and early fall (TIME: $F_{1,93,52.15} = 7.48$, $P = 0.002$; Fig. 1). Argentine ants were much more abundant than native ants and spent most of their time tending aphids (INVASION: $F_{1,27} = 35.244$, $P < 0.001$). The only native ant observed foraging on willow, *P. imparis*, was present early in the study, but was never as abundant as the Argentine ant, which caused a temporal difference in ant abundance between the invaded and un-invaded areas (TIME \times INVASION: $F_{1,93,52.15} = 7.64$, $P = 0.001$; Fig. 1).

External feeding guilds

Leaf-chewing insects. Early in the study, willows in the un-invaded region suffered more damage from chewers than willows in the invaded area (TIME \times INVASION: $F_{1,59,43.04} = 4.64$, $P = 0.021$; Fig. 2). However, as the study progressed, leaf damage decreased on willows in the un-invaded area and increased on willows with ants excluded in the invaded area (Fig. 2).

Skeletonising insects. Skeletonising damage was 50% lower in the presence of ants (EXCLUSION: $F_{1,27} = 10.60$,

$P = 0.003$). While the degree of suppression of skeletonisers by predators did not differ between un-invaded and invaded areas (EXCLUSION \times INVASION: $F_{1,27} = 2.74$, $P = 0.110$), native ants apparently suppressed skeletonising damage more than Argentine ants. Willow branches without ants in the un-invaded area suffered twice as much damage over the entire season compared with branches with ants (Fig. 2). Skeletonising damage was greater in the un-invaded region (INVASION: $F_{1,27} = 24.88$; $P < 0.001$), but mostly early on in the study (SEASON \times INVASION: $F_{1,42,38.19} = 6.30$, $P = 0.009$).

Aphids. Aphids were abundant on branches with ants excluded in the invaded and the un-invaded areas early on in the season (Fig. 2). By the end of the season, however, aphids were detected only in the invaded area, where they were twice as abundant on branches with ants present, as on branches devoid of ants (Fig. 2). These results suggest a change in the effect of ant exclusion from suppression early in the season to enhancement late in the study (EXCLUSION \times SEASON: $F_{2,3,65.05} = 23.17$, $P < 0.001$).

Internal feeding guilds

Gall-forming insects. The abundance of gall-forming insects increased as the study progressed (TIME: $F_{2,42,67.79} = 8.675$, $P < 0.001$; Fig. 3). The average abundance of galls was 30% higher in the invaded area than in the un-invaded area (Invasion: $F_{1,28} = 3.161$, $P = 0.086$). In the invaded area, gall-forming insects were slightly more abundant in the absence of ants, while in the un-invaded area, galls were 2.5 times more abundant in the presence of ants (Fig. 3). However, as the directional effects of ant exclusion were opposite in the invaded and un-invaded areas, there was no statistically significant effect of the exclusion treatment. That is, increased abundances of galls on branches with ants present in the un-invaded area cancel out decreased abundance of galls on branches without ants in the invaded area (EXCLUSION: $F_{1,28} = 0.692$, $P = 0.413$). Furthermore, no interaction effect between exclusion and invasion was detected, because of high variation among replicates (EXCLUSION \times INVASION: $F_{1,28} = 0.726$, $P = 0.401$).

Leaf-mining insects. Leaf miners were not common in either the invaded or un-invaded areas until late in the season, when they almost doubled in abundance relative to early season numbers (Fig. 3). The highest abundance of leaf-mining insects were on branches with ants excluded in the invaded region (Fig. 3). Overall, leaf-mining insects tended to be more abundant on branches with ants excluded (EXCLUSION: $F_{1,28} = 3.877$, $P = 0.059$), although not to a greater extent in the invaded area than the un-invaded area (EXCLUSION \times INVASION $F_{1,28} = 0.005$, $P = 0.946$).

Leaf-tying and Leaf-rolling insects. Leaf-tiers and leaf-rollers were abundant early in the season in the un-invaded region, but their numbers declined and remained low from late spring and early summer (Fig. 3). Leaf-tiers and leaf-rollers were approximately four times more abundant in the un-invaded area than in the invaded area early in the season, but this difference vanished by late spring (Fig. 3). However, no differences in the abundance of leaf tiers and rollers between excluded and unexcluded branches were detected throughout

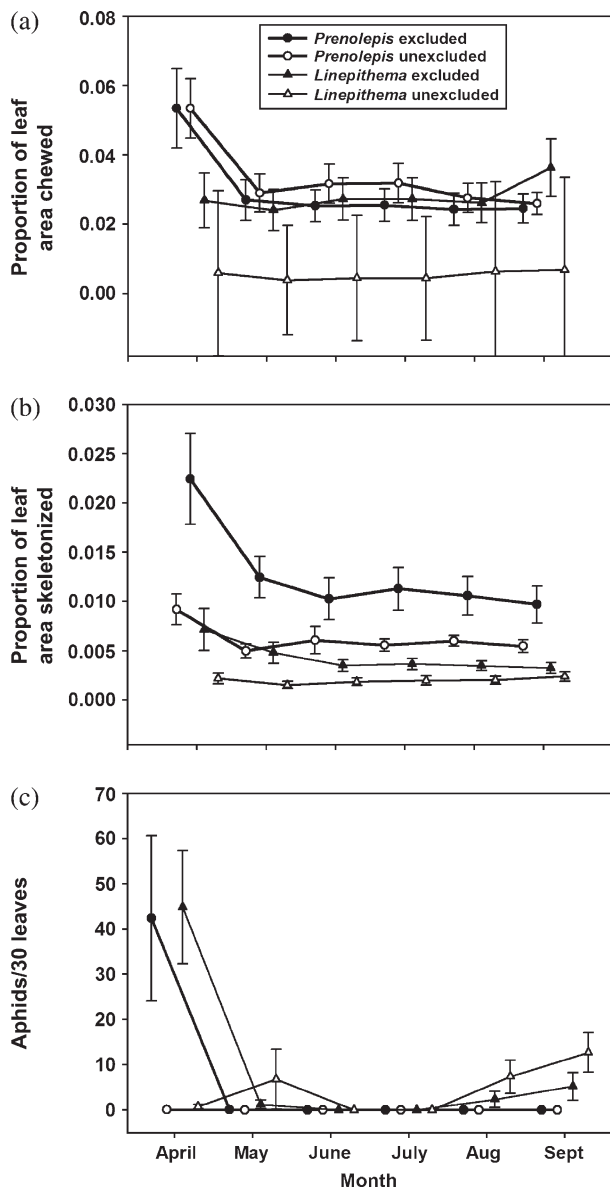


Fig. 2. Foliar damage or abundance of external feeding guilds in invaded and un-invaded areas on branches with *Linepithema humile* or *Prenolepis imparis* present or excluded. (a) leaf-chewing insects, (b) skeletonising, (c) aphids. Symbols are means and narrow bars indicate ± 1 standard error.

the study (EXCLUSION: $F_{1,27} = 0.499$, $P = 0.486$; EXCLUSION \times INVASION: $F_{1,27} = 0.301$, $P = 0.588$).

Other effects

Gender effects. We detected no statistically significant differences in the abundances of any feeding guild of herbivores between male and female trees. However, female willow trees had almost twice the number of galls and mines relative to male trees. The INVASION \times GENDER interaction was significant

for the leaf-tiers and leaf-rollers (INVASION \times GENDER: $F_{1,27} = 10.481$, $P = 0.003$), although this difference is likely to be caused by the high abundance of leaf-tiers and leaf-rollers found on male trees early on in the study.

Leaf abscission. Leaves did not start dropping until August, the penultimate month of sampling, and did not drop in substantial amounts until after the final sampling date. There was no significant difference between the numbers of leaves abscised in the invaded area and the un-invaded area ($P = 0.636$) nor was there any EXCLUSION \times INVASION effect ($P = 0.093$).

Discussion

The effects of the invasive Argentine ants on most guilds of herbivorous insects were similar to the effects of *P. imparis*, the most common native ant in this riparian system. The effects of ants, however, varied among herbivore feeding guilds and over time. However, Argentine ants increased the abundance of aphids late in the season, which was not detected for *P. imparis*. This suggests that the degree of protection provided by Argentine ants is greater than that provided by the most common native ant species in this system. It is also conceivable that the presence of aphids in the invaded region increased the perceived abundance of Argentine ants. It was observed that when foraging on willows, they focused their food collecting activity on honey-dew producing aphids.

Variable effects of ants among feeding guilds

Of the six feeding guilds we examined, only aphids demonstrated effects due to the Argentine ants, and that effect was an increase in abundance. Two additional guilds showed evidence of suppression by both native and Argentine ants: leaf damage by skeletonising insects was reduced by 50%, but there was no significant difference in the extent of suppression by native and Argentine ants. Additionally, leaf-mining insects were almost twice as abundant on branches without native or Argentine ants, although this pattern was not statistically significant.

Aphid densities were highest in the presence of the invasive Argentine ant. When aphid abundance peaked late on in the study in the invaded area, so did the number of Argentine ant foragers on willow. The virtual absence of aphids from the un-invaded region and the more than doubling of the abundance of aphids on branches with Argentine ants, suggests that Argentine ants increased aphid numbers. These observations are supported by other studies (Way, 1963; Altfield & Stiling, 2006). Altfield and Stiling (2006) found that aphid populations increased in density and persisted longer on *Baccharis halimifolia* in the presence of Argentine ants. Argentine ants likely enhance aphid populations by reducing attack from parasitoids or predators (Heimpel *et al.*, 1997; Grover *et al.*, 2007). For example, Grover *et al.* (2007) found that the number of Argentine ants and aphids on *Solanum nigrum* was positively correlated, which led to an increased probability that natural enemies of the aphid would be removed by Argentine ants.

The effects of Argentine ants on the rest of the arboreal herbivore community are likely to be mediated by Argentine ant–aphid

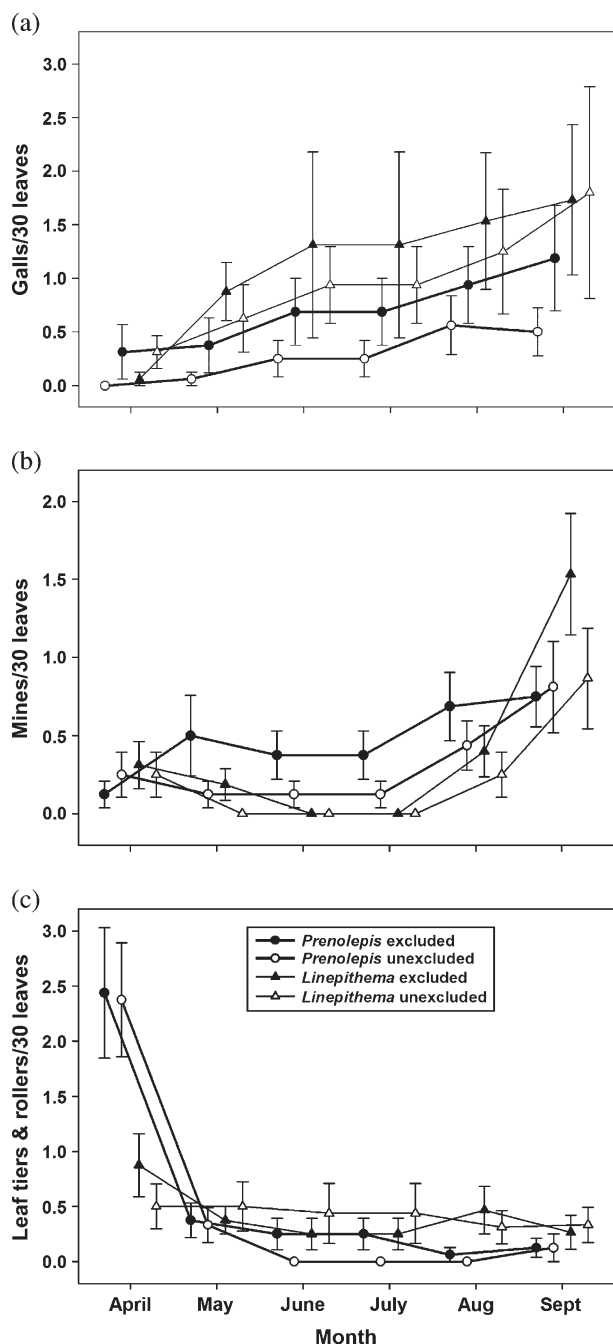


Fig. 3. Abundance of internal feeding guilds in invaded and un-invaded areas on branches with *Linepithema humile* or *Prenolepis imparis* present or excluded. (a) Gall forming insects, (b) leaf-mining insects, and (c) leaf-tying and leaf-rolling insects. Symbols indicate means and narrow bars indicate ± 1 standard error.

interactions, especially late on in the season (see below). It has been hypothesised that the extent to which Argentine ants tend hemipterans, contributes to the ecological dominance and negative effects of Argentine ants in many systems (Holway *et al.*, 2002; Grover *et al.*, 2007). Argentine ant foraging activity on

willows was increased in the presence of aphids in this study, and on other plants in other studies (Altfield & Stiling, 2006; Grover *et al.*, 2007). Taken together, this suggests that the mutualism between Argentine ants and aphids might exacerbate their impacts on native arboreal herbivores.

Ant suppression of leaf-mining insects has not previously been shown (Fowler & MacGarvin, 1985; Altfield & Stiling, 2006), although some ants have been reported to prey on some leaf-mining species (Faeth, 1980; Radeghieri, 2004). The fact that we detected a difference in the number of leaf-mines initiated, suggests that both native and Argentine ants inhibit oviposition of leaf-mining insects, which would account for the higher number of leaf mines on branches with ants excluded.

Damage by external feeding herbivores was generally lowest in the invaded region of our study site. In the invaded region, when we excluded Argentine ants, damage by external feeding herbivores tended to increase. Together, these results suggest that Argentine ants might have positive effects on willow by reducing damage by leaf-chewing insects. However, aphid densities were also highest in the presence of Argentine ants, which could have negative effects on willow. Although we did not measure growth rates or fitness of willows as part of this study, other studies have indicated that aggressive hemipteran-tending native ant species can have positive effects on the growth rates of willows in other systems (Sipura, 2002).

It is important to note that the presence of ants, regardless of whether they are tending honeydew-producing aphids, can lead to reductions in herbivore densities and damage by herbivores. For example, Warrington and Whittaker (1985) found that sycamore trees with wood ants, *Formica rufa* L. (Hymenoptera: Formicidae), had less leaf damage than those without wood ants. Similarly, Crutsinger and Sanders (2005) showed that herbivory on willow branches with *Formica obscuripes* Forel (Hymenoptera: Formicidae) workers was two times lower than on branches without *F. obscuripes* workers. Future work in this system should experimentally manipulate the presence of ants and aphids, in a full factorial design, and assess the combined and relative effects of ants and the aphids they tend, on the rest of the herbivore community and on the growth rate of the willows.

Linepithema humile versus other ant species

The effects of the Argentine ant and *P. imparis* on the herbivore community were generally similar, except for the positive effects of *L. humile* on aphid densities. Only one study to our knowledge, has directly compared the effects of an invasive ant on herbivore damage with the effects of native ants. In the presence of Argentine ants, needle damage on *Pinus pinaster* by the pine processionary moth [*Thaumetopoea pityocampa* Schiffermuller (Lepidoptera: Notodontidae)] was reduced, but not in the presence of several native ant species (Way *et al.*, 1999). It is surprising that so few studies have explicitly compared the effects of hemipteran-tending native and non-native ants on plants and the damage plants receive by herbivores.

Argentine ants may prey on herbivorous insects on willow, or may inhibit them by aggressive behaviour. Behavioural inhibition includes aggressive behaviour such as biting, stinging,

lunging, or chasing herbivores (Bentley, 1977b). Furthermore, high numbers of ants alone may deter herbivorous insects, and ants may be more likely to be aggressive when in large numbers (Way, 1963). Argentine ants may be efficient predators (Cole *et al.*, 1992), but others have noted that they may only occasionally act as predators, selectively preying on slow moving, dying, or small insects (Human & Gordon, 1997). While we did not observe Argentine ants preying upon caterpillar larvae, we suggest that both predation and behavioural inhibition by Argentine ants affects herbivorous insects on willows. De la Fuente and Marquis (1999) found that the reduced plant damage in the presence of ants was a result of molestation of herbivores by ants, not predation. Similarly, Human and Gordon (1997) noted that Argentine ants often interfere with the foraging activity of arthropods, which can ultimately lead to the migration of these organisms. Other studies have shown that the mere presence of ants on the same leaf can initiate anti-predatory behaviours, such as silking in caterpillars, and can deter oviposition by butterflies (Freitas & Oliveira, 1996; Ruggers *et al.*, 2003). Finally, ant pheromones could contribute to herbivore deterrence (Offenberg *et al.*, 2004).

The mechanisms used by Argentine ants to influence herbivore communities differ with those of another invasive ant species; the red imported fire ant, *Solenopsis invicta*. *Solenopsis invicta* is a voracious predator that can significantly reduce the number of beneficial arthropods on cotton (Eubanks *et al.*, 2002). *Solenopsis invicta* also preferentially forages on plants with aphids, releasing the plants from predation by other insects (Kaplan & Eubanks, 2002). Similar to Argentine ants, fire ants may protect aphid populations from predators and may prey on other herbivores or predators of aphids (Bolger *et al.*, 2000; Kaplan & Eubanks, 2002; Grover *et al.*, 2007). *Solenopsis invicta* may influence the amount of herbivore damage on plants more quickly than Argentine ants, by reducing the number of herbivores and predators of aphids in a relatively short time period. Despite being efficient predators, the effects of *S. invicta* can vary depending on season, taxa, or size (Kaplan & Eubanks, 2005). In the laboratory, Kaplan and Eubanks (2005) found consistent effects of *S. invicta* on the arthropod community on cotton in the presence of aphids. However, in the field, when aphids were present, the effects of ants varied. They suggest that interactions between *S. invicta* and aphids vary within and among seasons, which can affect interactions with other arthropods (Kaplan & Eubanks, 2005). Similarly, the aggressiveness of Argentine ants may depend on the herbivore, the season, or the abundance of ants or aphids.

We observed significant effects of the invasion treatment for both aphids and skeletonising insects, which we suggest are likely to be caused by the much greater foraging activity of Argentine ants on willow than that of *P. imparis*. Native ants were never abundant in the un-invaded region, so the INVASION main effect implies Argentine ants have more impact on herbivores than do native ants. However, the invasion effect is confounded with differences between the lower and upper reaches of Owl Canyon. If host-plant quality or other factors differ between these regions, these differences could account for any invasion effect. Argentine ants could also account for the INVASION \times TIME effect we observed for aphids, because they are much more abundant late in the season. However, once again, effects could also be explained by seasonal differences in host-plant quality

between the upper and lower reaches of Owl Canyon. In addition, *P. imparis* tends to be most active in the winter months in this region (Suarez *et al.*, 1998; Sanders *et al.*, 2001), so seasonal differences in the relative effects of Argentine ants and *P. imparis* are also likely.

Conclusions

In conclusion, a growing number of studies highlight the negative impacts of invasive Argentine ants on native insects. However, our work suggests that the impact of the invasive Argentine ant on native herbivore communities on arroyo willow arises largely through the enhancement of aphid abundance, which may have indirect effects on other predator and herbivore guilds.

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References

- Altfield, L. & Stiling, P. (2006) Argentine ants strongly affect some but not all common insects on *Baccharis halimifolia*. *Environmental Entomology*, **35**, 31–36.
- Bentley, B.L. (1977) The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). *Journal of Ecology*, **65**, 27–38.
- Boecklen, W.J., Price, P.W. & Mopper, S. (1990) Sex and drugs and herbivores: sex-biased herbivory in arroyo willow (*Salix lasiolepis*). *Ecology*, **71**, 581–588.
- Bolger, D.T., Suarez, A.V., Crooks, K.R., Morrison, S.A. & Case, T.J. (2000) Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecological Applications*, **10**, 1230–1248.
- Bond, W. & Slingsby, P. (1984) Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology*, **65**, 1031–1037.
- Carney, S.E., Byerley, M.B. & Holway, D.A. (2003) Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. *Oecologia*, **135**, 576–582.
- Christian, C.E. (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature*, **413**, 635–639.
- Cole, F.R., Medeiros, A.C., Loope, L.L. & Zuehlke, W.W. (1992) Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology*, **73**, 1313–1322.
- Crutsinger, G.M. & Sanders, N.J. (2005) Aphid-tending ants affect secondary users in leaf shelters and rates of herbivory on *Salix*

- hookeriana in a coastal dune habitat. *American Midland Naturalist*, **152**, 296–304.
- Daane, K.M., Sime, K.R., Fallon, J. & Cooper, M.L. (2007) Impacts of Argentine ants on mealybugs and their natural enemies in California's coastal vineyards. *Ecological Entomology*, **32**, 583–596.
- De la Fuente, M.S. & Marquis, R.J. (1999) The role of ant-tended extrafloral nectaries in the protection and benefit of a Neotropical rainforest tree. *Oecologia*, **118**, 192–202.
- Eubanks, M.D., Blackwell, S.A., Parrish, C.J., Delamar, Z.D. & Hull-Sanders, H. (2002) Intraguild predation of beneficial arthropods by red imported fire ants in cotton. *Environmental Entomology*, **31**, 1168–1174.
- Faeth, S.H. (1980) Invertebrate predation on leaf-miners at low densities. *Ecological Entomology*, **5**, 111–114.
- Fowler, S.V. & MacGarvin, M. (1985) The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *Journal of Animal Ecology*, **54**, 847–855.
- Frazer, B.D. & Van Den Bosch, R. (1973) Biological control of the walnut aphid in California: the interrelationship of the aphid and its parasite. *Environmental Entomology*, **2**, 561–568.
- Freitas, A.V.L. & Oliveira, P.S. (1996) Ants as selective agents on herbivore biology: effects on the behavior of a non-mymecophilous butterfly. *Journal of Animal Ecology*, **65**, 205–210.
- Grover, C.D., Dayton, K.C., Menke, S.B. & Holway, D.A. (2008) Effects of aphids on foliar foraging by Argentine ants and the resulting effects on other arthropods. *Ecological Entomology*, **33**, 101–106.
- Heimpel, G.E., Rosenheim, J.A. & Mangel, M. (1997) Predation on adult *Aphytis* parasitoids in the field. *Oecologia*, **110**, 346–352.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Harvard University Press, Cambridge, Massachusetts.
- Holway, D.A. (1995) Distribution of the Argentine ant (*Linepithema humile*) in Northern California. *Conservation Biology*, **9**, 1634–1637.
- Holway, D.A. (1998) Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia*, **116**, 252–258.
- Holway, D.A. (2005) Edge effects of an invasive species across a natural ecological boundary. *Biological Conservation*, **121**, 561–567.
- Holway, D.A., Lach, L., Suarez, A.V., Tsutsui, N.D. & Case, T.J. (2002a) The causes and consequences of ant invasions. *Annual Review of Ecology & Systematics*, **33**, 181–233.
- Holway, D.A., Suarez, A.V. & Case, T.J. (2002b) The role of abiotic factors in governing susceptibility to invasion: a test with a wide-spread invasive social insect. *Ecology*, **83**, 1610–1619.
- Human, K.G. & Gordon, D.M. (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia*, **105**, 405–412.
- Human, K.G. & Gordon, D.M. (1997) Effects of Argentine ants on invertebrate biodiversity in Northern California. *Conservation Biology*, **11**, 1242–1248.
- Human, K.G., Weiss, S., Weiss, A., Sandler, B. & Gordon, D.M. (1998) The effect of abiotic factors on the local distribution of the invasive Argentine ant (*Linepithema humile*) and native ant species. *Environmental Entomology*, **27**, 822–833.
- Kaplan, I. & Eubanks, M.D. (2002) Disruption of cotton aphid (Homoptera: Aphididae) – Natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). *Environmental Entomology*, **31**, 1175–1183.
- Kaplan, I. & Eubanks, M.D. (2005) Aphids alter the community-wide impact of fire ants. *Ecology*, **86**, 1640–1649.
- Low, C. & Connor, E.F. (2003) Birds have no impact on folivorous insect guilds on a montane willow. *Oikos*, **103**, 579–589.
- Mahdi, T. & Whittaker, J.B. (1993) Do birch trees (*Betula pendula*) grow better if foraged by wood ants? *Journal of Animal Ecology*, **62**, 101–116.
- Newell, W. & Barber, T.C. (1913) *The Argentine Ant*. USDA, Washington, District of Columbia.
- O'Brien, R.G. & Kaiser, M.K. (1985) MANOVA method for analyzing repeated measures designs: an extensive primer. *Psychological Bulletin*, **97**, 316–333.
- Offenberg, J., Nielsen, M.G., MacIntosh, D.J., Havanon, S. & Aksornkoae, S. (2004) Evidence that insect herbivores are deterred by ant pheromones. *Proceedings of the Royal Society of London Series B*, **271**, S433–S435.
- Oliveira, P.S. & Del-Claro, K. (2005) Multitrophic interactions in a neotropical savanna: ant-hemipteran systems, associated insect herbivores and a host plant. *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity* (ed. by D. Burslem, M. Pinar and S. Hartley), pp. 414–438. Cambridge University Press, New York.
- Passera, L. (1994) Characteristics of tramp species. *Exotic Ants: Biology, Impact and Control of Introduced Species* (ed. by D. F. Williams), pp. 23–43. Westview Press, Boulder, Colorado.
- Radeghieri, P. (2004) *Cameraria ohridella* (Lepidoptera: Gracillariidae) predation by *Crematogaster scutellaris* (Hymenoptera Formicidae) in northern Italy (preliminary note). *Journal of Insectology*, **57**, 63–64.
- Rudgers, J.A., Hodgen, J.G. & White, J.W. (2003) Behavioral mechanisms underlie an ant-plant mutualism. *Oecologia*, **135**, 51–59.
- Sanders, N.J., Barton, K.E. & Gordon, D.M. (2001) Long-term dynamics of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia*, **127**, 123–130.
- Sipura, M. (2002) Contrasting effects of ants on the herbivory and growth of two willow species. *Ecology*, **83**, 2680–2690.
- Styrsky, J.D. & Eubanks, M.D. (2007) Ecological consequences of interactions between ants and honey-dew producing insects. *Proceedings of the Royal Society of London Series B*, **274**, 151–164.
- Suarez, A.V., Bolger, D.T. & Case, T.J. (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology*, **79**, 2041–2056.
- Suarez, A.V., Holway, D.A. & Case, T.J. (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 1095–1100.
- Suarez, A.V., Richmond, J.Q. & Case, T.J. (2000) Prey selection in horned lizards following the invasion of Argentine ants in Southern California. *Ecological Applications*, **10**, 711–725.
- Ward, P. (1987) Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia*, **55**, 1–16.
- Warrington, S. & Whittaker, J.B. (1985) An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) I. Lepidopteran larvae. *Journal of Applied Ecology*, **22**, 775–785.
- Way, M.J. (1963) Mutualism between ants and honeydew producing Homoptera. *Annual Review of Entomology*, **8**, 307–344.
- Way, M.J., Paiva, M.R. & Cammell, M.E. (1999) Natural biological control of the pine processionary moth *Thaumetopoea pityocampa* (Den. & Schiff.) by the Argentine ant *Linepithema humile* (Mayr) in Portugal. *Agricultural and Forest Entomology*, **1**, 27–31.
- Wimp, G.M. & Whitham, T.G. (2001) Biodiversity consequences of predation and host plant hybridization on an aphid-ant mutualism. *Ecology*, **82**, 440–452.

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