The Impacts of the Invasive Argentine Ant and Native Ant Species on the Insect Community on Willow (*Salix lasiolepis*)

Julie P. Nygard*

Nathan J. Sanders+

and

Edward F. Connor**

***Department of Biology**
San Francisco State University
1600 Holloway Avenue
San Francisco, CA 94132

+Department of Ecology and Evolutionary Biology
569 Dabney Hall
University of Tennessee
Knoxville, TN 37996

**corresponding author: efc@sfsu.edu, fax 415-405-0306

Abstract

1. We examined the effects of the invasive Argentine ant, *Linepithema humile*, and native ants on the community of herbivorous insects occurring on willow trees, *Salix lasiolepis* in Northern California, USA.

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 native ants. Argentine and native ants suppressed the damage by skeletonizing insects by 50%, but had little effect on most other external-feeding or internal-feeding guilds.

3. Argentine ants also increased the abundance of aphids by 100% while native ants did not. Late season aphid numbers were substantially higher in the presence of Argentine ants, but not native ants.

4. The effects of Argentine ants on skeletonizing 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, invasive ants, native ants, herbivores, willow, *Salix*.

Introduction

Invasive ant species threaten natural systems because of their potential to disrupt mutualisms, displace native organisms, and alter community structure (Holway et al. 2002a). For example, the invasive Argentine ant (*Linepithema humile* Mayr, Hymenoptera: Formicidae) can displace native ants and may have community-wide impacts on a wide variety of ground-dwelling arthropods (Ward 1987, Human and Gordon 1996, 1997). The direct effects of Argentine ants on native ants and other ground-dwelling arthropods can indirectly alter plant community structure (Bond and Slingsby 1984, Christian 2001, Carney et al. 2003) and affect vertebrate predators of native ant species (Suarez et al. 2000).

Few studies have examined the extent to which Argentine ants, or for that matter, any invasive ant species, affect herbivorous insect species (Kaplan and Eubanks 2005, Altfield and Stiling 2006), though native ant species can dramatically affect herbivorous insects (Finnegan 1974, Skinner and Whittaker 1981, Fowler and MacGarvin 1985, Warrington and Whittaker 1985, Whittaker 1991, Wimp and Whitham 2001, Sipura 2002). The invasive fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), alters the structure of herbivore communities on cotton plants, but its effects are context dependent and temporally variable (Kaplan and Eubanks 2005). Argentine ants on *Baccharis halimifolia* L. (Asteraceae) plants increased the densities of aphids and aphid predators, but did not affect leaf miner density (Altfeld and Stiling 2006).

Most studies show that the effects of ants on the composition of arthropod communities are taxon dependent (Bentley 1976, Heads and Lawton 1984, Fowler and MacGarvin 1985, Rashbrook *et al*. 1992). For example Skinner and Whittaker (1981) found that ants reduced the number of lepidopteran larvae but had no effect on other herbivore guilds. Fowler and MacGarvin (1985) showed that ants reduced the number of species of exposed herbivores on birch trees; but concealed feeders, like leaf miners, increased in numbers in the presence of ants. Therefore, a better understanding of the effects of ants, especially invasive ant species, on other arthropods will require examining multiple guilds.

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*) across several guilds of willow-feeding herbivores.

Methods

The Argentine ant - Argentine ants were introduced to California around 1907 (Newell and 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 (Holway 1995, Human *et al*. 1998, Holway 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 and 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.

Experimental System - To determine if Argentine ants affect herbivorous insects, we studied the community of herbivorous insects on the willow tree *Salix lasiolepis* in Owl Canyon on San Bruno Mountain in San Mateo County, California. Argentine ants have invaded the S. *lasiolepis*-dominated lower reaches of the riparian corridor in Owl Canyon (invaded region), but are absent from the upper reaches of the watershed oak which transitions from willow to oak woodland (*Quercus agrifolia* Née, Fagaceae) (un-invaded region). 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 omnivores, seed-harvesters, and predators (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 were randomly selected and one branch was assigned to receive the exclusion treatment. On April 8, 2003, Tanglefoot© (Grand Rapids, MI, USA) 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 between 0.4 – 0.6 (Low and 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-skeletonizing insects, and aphids). We quantified the effects of leaf-chewing and skeletonizing insects by measuring the percent surface area damaged on each leaf. To estimate the total area of the leaf and the leaf area damaged, we measured leaf surface area damaged by using 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 sex (SEX). Because individual willow trees received both levels of the exclusion treatment and were observed monthly, the exclusion and season effects are within-subjects factors. We report adjusted univariate *F*-tests to account for non-sphericity of the variance-covariance matrix (O'Brien and Kaiser 1985).

Because of the complex experimental design, we identified four broad categories of effects and assigned each of the statistical effects (15 effects from the four-factor ANOVA) into one of the four categories: (1) direct suppression or enhancement of herbivores by Argentine ants, (2) generalized predator effects, (3) effects consistent with suppression or enhancement by Argentine ants, but confounded with differences between the invaded and un-invaded regions (confounded effects), and (4) effects unrelated to ants or other predators (Table 1).

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, Figure 1, Appendix 1). The only native ant observed foraging on willow, *Prenolepis 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 an un-invaded areas (TIME × INVASION: $F_{1.93, 52.15} = 7.64$, p = 0.001; Figure 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 × INVASION: $F_{1.59, 43.04} = 4.64$, p = 0.021; Figure 2, Appendix 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 (Figure 2).

Skeletonizing Insects - Skeletonizing damage was 50% lower in the presence of ants (EXCLUSION: $F_{1, 27} = 10.60$, p = 0.003; Appendix 3). While the degree of suppression of skeletonizers by predators did not differ between un-invaded and invaded areas (EXCLUSION × INVASION: $F_{1, 27} = 2.74$, p = 0.110), native ants apparently suppressed skeletonizing damage more than did Argentine ants since willow branches without ants in the un-invaded area suffered twice as much damage over the entire season compared to branches with ants (Figure 2). Skeletonizing damage was greater in the un-invaded region (INVASION: $F_{1, 27} = 24.88$; p <0.001), but mostly early in the study (SEASON × 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 in the season (Figure 2). But by the end of the season, aphids were detected only in the invaded area. Moreover, aphids were twice as abundant on branches with ants as on branches without ants, but only in the invaded region (Figure 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 × SEASON: $F_{2.3, 65.05} = 23.17$, p <0.001: Appendix 4). The absence of aphids from the un-invaded region, and the higher abundance of aphids on branches with ants in the invaded region suggests that late in the season Argentine ants increase aphid numbers.

Internal Feeding Guilds

Gall-forming Insects – The abundance of gall-forming insects increased as the study progressed (TIME: $F_{2.42, 67.79} = 8.675$, $p < 0.001$; Figure 3, Appendix 5). The average abundance of galls was 30% higher in the invaded area than the un-invaded area (Invasion: $F_{1, 28} = 3.161$, $p = 0.086$). Furthermore, in the invaded area, gall-forming insects were more abundant in the presence of ants, while in the un-invaded area galls were more abundant in the absence of ants (Figure 3). However, because 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 (EXCLUSION: $F_{1, 28} = 0.692$, $p = 0.413$) or an interaction effect with the invasion treatment (EXCLUSION × 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 (Figure 3). The highest abundance of leaf-mining insects was on branches with ants excluded in the invaded region (Figure 3). Overall, leaf-mining insects tended to be more abundant on branches with ants excluded (EXCLUSION: $F_{1, 28} = 3.877$, $p = 0.059$; Appendix 6), although not to a greater extent in the invaded area than the un-invaded area (EXCLUSION × 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 beginning in late spring and early summer (Figure 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 (Figure 3). However, no differences in the abundance of leaf tiers and rollers between excluded and unexcluded branches were detected throughout the study (EXCLUSION: $F_{1, 27} = 0.499$, $p = 0.486$; EXCLUSION × INVASION: $F_{1, 27} = 0.301$, $p = 0.588$; Appendix 7).

Other Effects

Sex Effects – We detected no statistically significant differences in the abundances of any feeding guild of herbivores between male and female trees (Appendix 8). However, female willow trees had almost twice the number of galls and mines relative to male trees. The INVASION × SEX interaction was significant for the leaf-tiers and leaf-rollers (INVASION × SEX: $F_{1,\,27} = 10.481$, p = 0.003), although this difference is likely caused by the high abundance of leaf-tiers and leaf-rollers found on male trees early 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 any EXCLUSION × INVASION effect (p = 0.093).

Discussion

Our results suggest that the effect of ants on herbivore communities varies both temporally and among herbivore feeding guilds. Overall, the effects of ants on the herbivorous insects on *Salix lasiolepis* appear to be largely limited to the external-feeding guilds. Furthermore, the effects of Argentine ants on most guilds of herbivorous insects are similar to the effects of *Prenolepis impairs* (Say) (Hymenoptera: Formicidae), the most common native ant in this riparian system. However, Argentine ants increased the abundance of aphids late in the season which was not detected for *P. imparis*.

Of the six feeding guilds we examined, only aphids showed effects due to 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 skeletonizing insects was reduced by 50%, but there was no significant difference in the extent of suppression by native and Argentine ants. Furthermore, although not statistically significant leaf-mining insects were almost twice as abundant on branches without native or Argentine ants.

Studies with other ant species have also shown that ants, both native and invasive, can directly affect the amount of damage by leaf-chewing insects. *Forelius pruinosus* (Roger) (Hymenoptera: Formicidae) has a larger effect on reducing chewing damage on wild cotton plants than on reducing the abundance of the herbivore, *Bucculatrix thurberiella* Busck (Lepidoptera: Lyonetiidae) (Rudgers *et al*. 2003). 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. Although not invasive ants, these studies demonstrate that ants can affect the amount of damage plants experience.

The presence of invasive ants also can lead to differing amounts of leaf damage. Koptur (1979) found that herbivory on vetch was lower in the presence of Argentine ants. Argentine ants prey on larvae of *Thaumetopoea pityocampa* Schiffermuller (Lepidoptera: Notodontidae) reducing chewing damage to needles of *Pinus pinaster* Aiton (Pinaceae), but native ants ignore the larvae, so trees with native ants are more heavily damaged (Way *et al*. 1999).

Ant suppression of leaf-mining insects has not previously been reported (Fowler and MacGarvin 1985, Altfield and 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.

Argentine ants also directly led to increased aphid densities. When aphid abundance peaked late in the study in the invaded area, so did Argentine ant abundance. 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 increase aphid numbers. These observations are supported by other studies that have demonstrated that Argentine ants can affect aphid abundance (Way 1963). For example, the abundance of aphids increased in the presence Argentine ants on walnut trees in California (Frazer and Van Den Bosch 1973). 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 have been shown to disrupt parasitoid activity while defending aphids and are successful in capturing parasitoids (Heimpel *et al*.1997). Thus, Argentine ants may enhance aphid populations by reducing attack from parasitoids or predators. Similar effects on predators and parasitoids have been demonstrated with other species of ants (Way 1963, Messina 1981, Buckley 1987, Bach 1991).

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*. *S. invicta* is a voracious predator that can significantly reduce the number of beneficial arthropods on cotton (Eubanks *et al*. 2002). *S. invicta* also preferentially forages on plants with aphids, releasing the plants from predation by other insects (Kaplan and Eubanks 2002). Like Argentine ants, fire ants may protect aphid populations from predators, but unlike Argentine ants, fire ants generally prey on other herbivores or predators of aphids (Kaplan and Eubanks 2002). *S. 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 and Eubanks 2005). In the lab, 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 and Eubanks 2005). Similarly, the aggressiveness of Argentine ants may depend on the herbivore, the season, or the abundance of ants or aphids.

Other effects we detected are unlikely to have been caused by *P. imparis* or Argentine ants. The TIME main effect may simply reflect temporal patterns in the abundance of herbivores unrelated to the ants or other predators. All guilds showed strong seasonal patterns of abundance or feeding damage (Figure 2 and 3). However, none of the seasonal patterns of abundance of the herbivore guilds are likely to be caused by the seasonal activity levels of Argentine ants. Some guilds are most prevalent early in the season when Argentine ants are rare (chewing insects, skeletonizers, leaf-tiers and leaf-rollers), so they may escape from strong effects of Argentine ants because of this temporal mismatch. However, other concealed-feeding guilds increase in abundance over the season in spite of the late season increase in the abundance of Argentine ants (gall formers and leaf miners). But, concealed feeders often escape the effects of ants and other predators (Connor and Taverner 1997). Only aphids showed seasonal changes in abundance that is concordant with seasonal changes in Argentine ant activity.

On the other hand, the INVASION main effect and the INVASION × TIME interaction may be caused by Argentine ants. Native ants were never abundant in the un-invaded region, so the INVASION main effect implies Argentine ants have more impact on herbivores than 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 cause an effect of INVASION × TIME 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.

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.

Acknowledgements

We would like to thank Phil Ward for assistance in ant identification, George Argus for verifying our willow identifications, John Fawkes, Ryan Abel, and Jeff Rutter for assistance in the field, and Gretchen LeBuhn and John Hafernik for their comments on an earlier version of the manuscript. We thank the San Mateo County Parks Department for permission to conduct this study at San Bruno Mountain State and County Park. This research was supported in part by at ARCS Scholarship to J.P. Nygard and by NSF UMEB Grant DBI-0207090.

References

Altfield, L., and P. Stiling. 2006. Argentine ants strongly affect some but not all common insects on *Baccharis halimifolia*. Environmental Entomology **35**:31-36.

Bach, C.E. 1991. Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). Oecologia **87**:233-239.

Bentley, B.L. 1976. Plants bearing extrafloral nectaries and the associated ant community: Interhabitat differences in the reduction of herbivore damage. Ecology **57**:815-820.

Boecklen, W.J., P.W. Price, and S. Mopper. 1990. Sex and drugs and herbivores: Sex-biased herbivory in arroyo willow (*Salix lasiolepis*). Ecology **71**:581-588.

Bond, W., and P. Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology **65**:1031-1037.

Buckley, R.C. 1987. Interactions involving plants, Homoptera, and ants. Annual Review of Ecology & Systematics **18**:111-135.

Carney, S.E., M.B. Byerley, and D.A. Holway. 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

Connor, E.F. and M.P. Taverner. 1997. The evolution and adaptive significance of the leaf-mining habit. Oikos **79**:6-25.

Crutsinger, G.M. and N.J. Sanders. 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.

Eubanks, M.D., S.A. Blackwell, C.J. Parrish, Z.D. Delamar, and H. Hull-Sanders. 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.

Finnegan, R.J. 1974. Ants as predators of forest pests. Entomophaga **7**:53-59.

Fowler, S.V., and M. MacGarvin. 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., and R. Van Den Bosch. 1973. Biological control of the walnut aphid in California: the interrelationship of the aphid and its parasite. Environmental Entomology **2**:561-568.

Heads, P.A., and J.H. Lawton. 1984. Bracken, ants and extrafloral nectaries. II. The effect of ants on the insect herbivores of bracken. Journal of Animal Ecology **53**:1015-1031.

Heimpel, G.E., J.A. Rosenheim, M. Mangel. 1997. Predation on adult *Aphytis* parasitoids in the field. Oecologia **110**:346 - 352.

Hölldobler, B., and E.O. Wilson. 1990. The Ants. - Harvard University Press, Cambridge.

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., L. Lach, A.V. Suarez, N.D. Tsutsui, and T.J. Case. 2002. The causes and consequences of ant invasions. Annual Review of Ecology & Systematics **33**:181-233.

Holway, D.A., A.V. Suarez, and T.J. Case. 2002. The role of abiotic factors in governing susceptibility to invasion: a test with a widespread invasive social insect. Ecology **83**:1610-1619.

Human, K.G., and D.M. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia **105**:405-412.

Human, K.G., S. Weiss, A. Weiss, B. Sandler and D.M. Gordon. 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., and M.D. Eubanks. 2002. Disruption of cotton aphid (Homoptera: Aphididae) - Natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). Environmental Entomology **31**:1175-1183.

Kaplan, I., and M. D. Eubanks. 2005. Aphids alter the community-wide impact of fire ants. Ecology **86**:1640-1649.

Koptur, S. 1979. Facultative mutualism between weedy vetches bearing extrafloral nectaries and weedy ants in California. American Journal of Botany **66**:1016-1020.

Low, C., and E.F. Connor. 2003. Birds have no impact on folivorous insect guilds on a montane willow. Oikos **103**:579-589.

Messina, F.J. 1981. Plant protection as a consequence of an ant-membracid mutualism: interactions on Goldenrod (*Solidago* sp.). Ecology **62**:1433-1440.

Newell, W., and T.C. Barber. 1913. The Argentine Ant. USDA, Washington, D.C.

O'Brien, R.G., and M.K. Kaiser. 1985. MANOVA Method for analyzing repeated measures designs: An extensive primer. Psych. Bull. **97**:316-333.

Passera, L. 1994. Characteristics of tramp species. – In: Exotic Ants: Biology, Impact and Control of Introduced Species. Westview Press, Boulder, CO.., pp. 23-43.

Radeghieri, P. 2004. *Cameraria ohridella* (Lepidoptera: Gracillariidae) predation by *Crematogaster scutellaris* (Hymenoptera Formicidae) in northern Italy (preliminary note). Journal of Insectology **57**: 63-64.

Rashbrook, V. K., S. G. Compton, and J. H. Lawton. 1992. Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. Ecology **73**:2167-2174.

Rudgers, J.A., J.G. Hodgen, and J.W. White. 2003. Behavioral mechanisms underlie an ant-plant mutualism. Oecologia **135**:51-59.

Sanders, N. J., K. E. Barton, and D. M. Gordon. 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.

Skinner, G.J., and J.B. Whittaker. 1981. An experimental investigation of inter-relationships between the wood ant (*Formica rufa*) and some tree-canopy herbivores. Journal of Animal Ecology **50**:313-326.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology **79**:2041-2056.

Suarez, A. V., J.Q. Richmond, and T.J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine ants in Southern California. Ecological Applications **10**:711-725.

Suarez, A.V., D.A. Holway, and T.J. Case. 2001. Patterns of spread in biological Invasions dominated by long-distance jump dispersal: Insights from Argentine ants. - Proceedings of the National Academy of Sciences **98**:1095-1100.

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., and J.B. Whittaker. 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., M.R. Paiva, and M.E. Cammell. 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.

Whittaker, J.B. 1991. Effects of ants on temperate woodland trees. – In: C. R. Huxley and D. F. Cutler, (ed.). Ant-Plant Interactions. Oxford University Press, Oxford, UK., pp. 67-79.

Wimp, G.M., and T.G. Whitham. 2001. Biodiversity consequences of predation and host plant hybridization on an aphid-ant mutualism. Ecology **82**:440-452.

Table 1. Assignment of ANOVA effects into broad categories of ecological effects

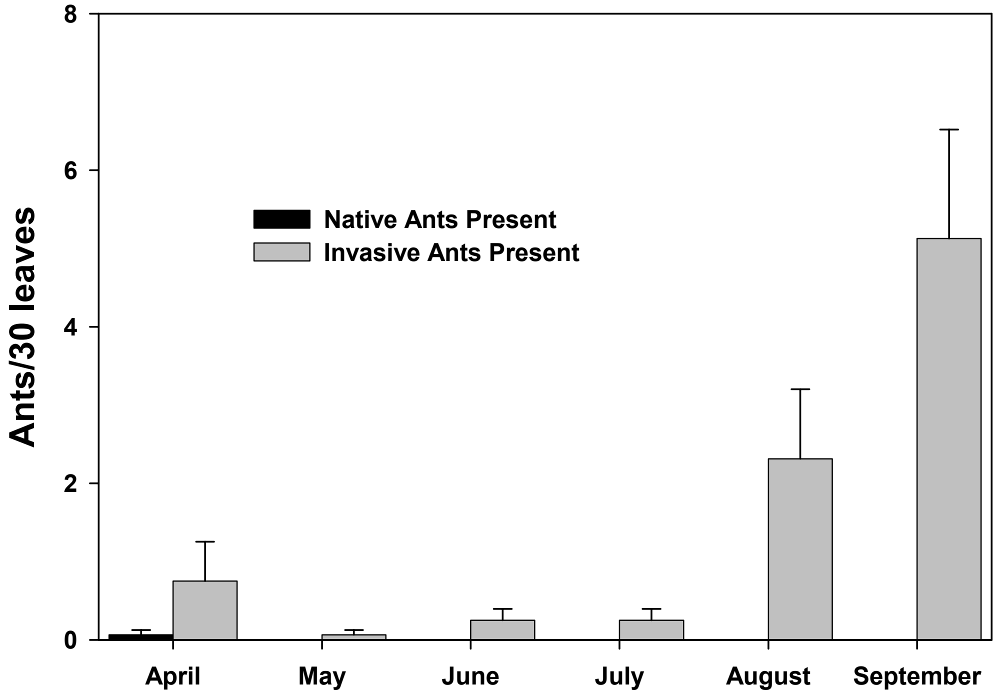
Category of Effect	**Main Effects and Interactions from ANOVA**
Direct suppression or enhancement of herbivores by Argentine Ants	Exclusion by Invasion Exclusion by Season Exclusion by Invasion by Season
Generalized predator effects (Direct suppression or enhancement of herbivores by ants or other non-volant predators)	Exclusion
Confounded Effects (Effects consistent with suppression or enhancement by Argentine ants, but confounded with differences between the invaded and un-invaded regions)	Invasion by Season Invasion
Effects unrelated to ants or other predators	Season Sex Sex by Season Sex by Exclusion Sex by Invasion Sex by Season by Exclusion Sex by Season by Invasion Sex by Exclusion by Invasion Sex by Exclusion by Invasion by Season

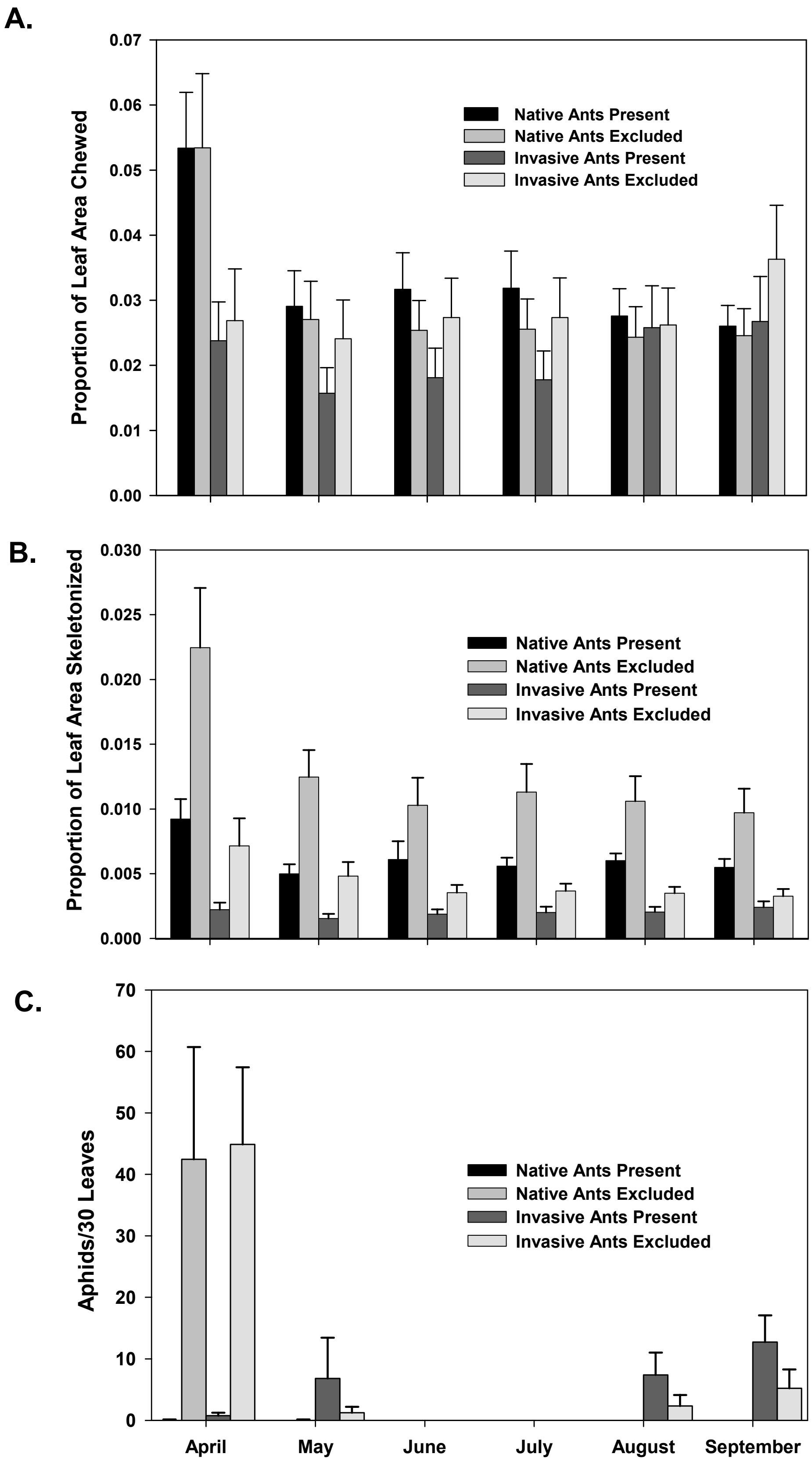
Figure Legends

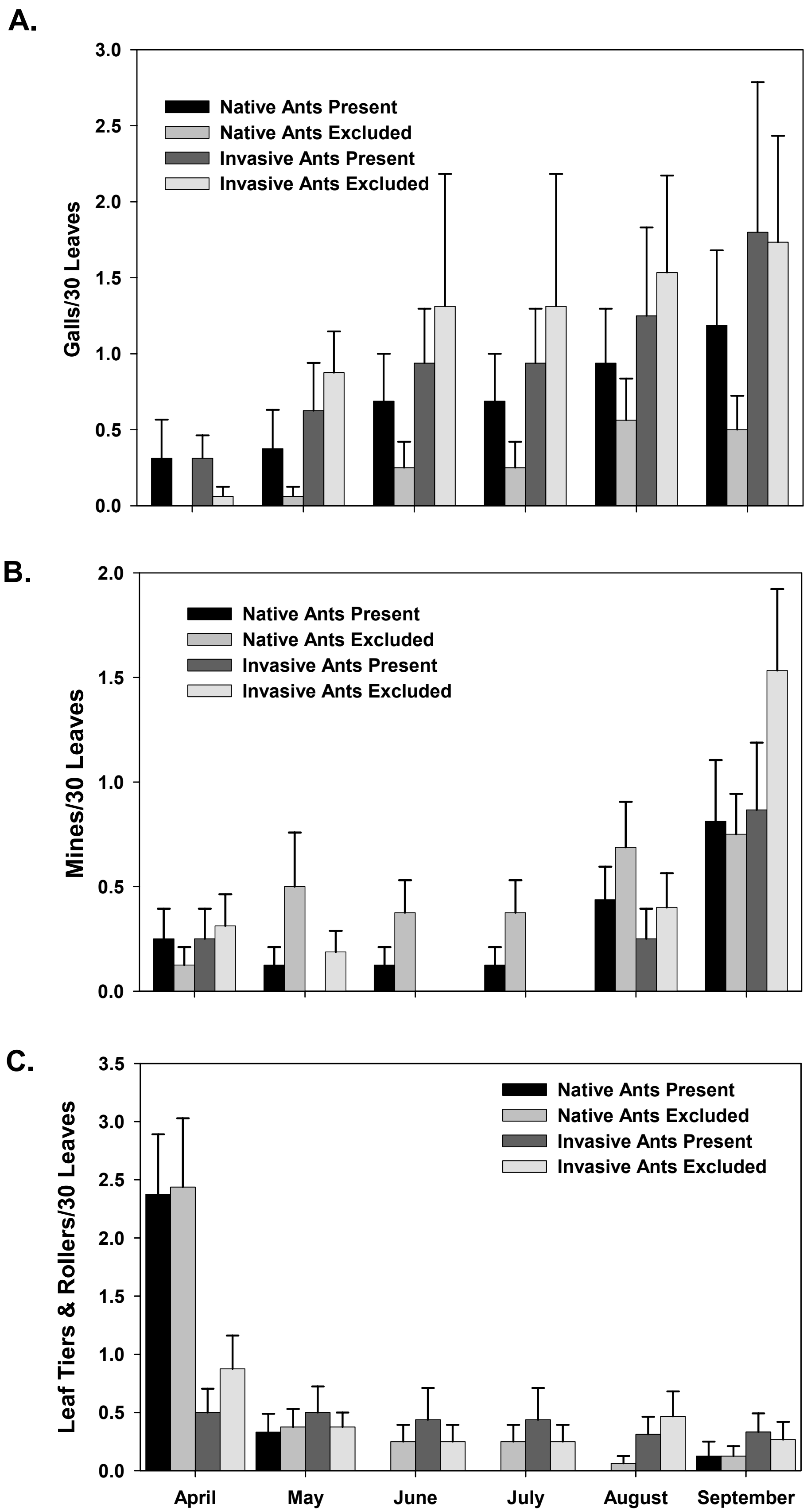
Figure 1. Number of ant workers/30 leaves on control branches (ants not excluded) in invaded and un-invaded areas. Broad bars are means and narrow bars indicate ± 1 standard error.

Figure 2. Foliar damage or abundance of external feeding guilds in invaded and un-invaded areas on branches with ants present and ants excluded. A. leaf-chewing insects, B. skeletonizing, C. aphids. Broad bars are means and narrow bars indicate ±1 standard error.

Figure 3. Abundance of internal feeding guilds in invaded and un-invaded areas on branches with ants present, and branches with ants excluded. A. gall forming insects, B. leaf-mining insects, and C. leaf-tying and leaf-rolling insects. Broad bars are means and narrow bars indicate ±1 standard error.


8
6
4
2
0
Ants/30 leaves
Native Ants Present
Invasive Ants Present
April
May
June
July
August
September


A.
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Proportion of Leaf Area Chewed
Native Ants Present
Native Ants Excluded
Invasive Ants Present
Invasive Ants Excluded
B.
0.030
0.025
0.020
0.015
0.010
0.005
0.000
Proportion of Leaf Area Skeletonized
Native Ants Present
Native Ants Excluded
Invasive Ants Present
Invasive Ants Excluded
C.
70
60
50
40
30
20
10
0
Aphids/30 Leaves
Native Ants Present
Native Ants Excluded
Invasive Ants Present
Invasive Ants Excluded
April
May
June
July
August
September


A.
Galls/30 Leaves
Native Ants Present
Native Ants Excluded
Invasive Ants Present
Invasive Ants Excluded
3.0
2.5
2.0
1.5
1.0
0.5
0.0
B.
Mines/30 Leaves
Native Ants Present
Native Ants Excluded
Invasive Ants Present
Invasive Ants Excluded
2.0
1.5
1.0
0.5
0.0
C.
Leaf Tiers & Rollers/30 Leaves
Native Ants Present
Native Ants Excluded
Invasive Ants Present
Invasive Ants Excluded
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
April
May
June
July
August
September