

# Effect of an Invasive and Native Ant on a Field Population of the Black Citrus Aphid (Hemiptera: Aphididae)

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**ABSTRACT** Invasive ants often enter into facultative mutualisms that frequently lead to outbreaks of the hemipteran partner. Native ants may also enter into similar mutualisms but often these do not lead to outbreaks. However, field studies comparing the impact of an invasive and native ant on a honeydew-producing hemipteran are lacking. We monitored numerical changes of the black citrus aphid, *Toxoptera aurantii*, tended by adjacent colonies of the invasive Argentine ant, *Linepithema humile*, and the endemic odorous house ant, *Tapinoma sessile*, during 2005, 2006, and 2007. Ant-tended aphid numbers were higher than those of untended aphids, with *L. humile*-tended and *T. sessile*-tended *T. aurantii* populations being comparable in 2005 and 2007. However, in 2006, a severe storm, with heavy rainfall, reduced *T. sessile* and aphid populations in areas occupied by *T. sessile*, whereas *L. humile* and aphids tended by *L. humile* were not reduced. This suggested that *T. sessile* foraging activity and hemipteran-tending was negatively impacted by severe weather. A laboratory experiment simulating rainfall striking the surface of a leaf showed that *T. sessile* foraging activity declined sharply under severe simulated rainfall conditions, whereas foraging activity of *L. humile* did not. Maintaining populations of honeydew-producing Hemiptera across broad climatic conditions may be one mechanism by which *L. humile* gains a competitive advantage over native ants occupying overlapping niches.

**KEY WORDS** ant-aphid interaction, precipitation, foraging

Invasive species are among the most influential factors in reshaping ecological systems (Elton 1958). In some cases, invasive species have provided benefits to areas of introduction, i.e., increased biodiversity (Brown 2003, Sax and Gaines 2008). However, invasive species usually have negative, and occasionally devastating, impacts on native flora and fauna, e.g., *Phragmites* and other plants (Franklin et al. 1999, Gratton and Denno 2005) and zebra mussels (Ludyanskiy and McDonald 1993). Among the most destructive invasive taxa are ants, which are capable of displacing local organisms including arthropods (Holway 1998a), reptiles (Suarez and Case 2002), birds (Plentovich et al. 2009), and mammals (Allen et al. 2004). Invasive ants, such as the Argentine ant, *Linepithema humile* (Mayr) (Formicidae: Dolichoderinae), can disrupt entire communities by displacing local ants (e.g., Erickson 1971, Bond and Slingsby 1984, Carpintero et al. 2005), in large part because of their aggressive nature and ability to recruit overwhelming numbers of workers (Holway et al. 2002a). The success of *L. humile* is best shown through their massive supercolonies, in some cases spanning thousands of kilometers (Tsutsui et al. 2000, Giraud et al. 2002).

Although there is good support for abiotic factors affecting *L. humile* spread (e.g., soil moisture, Menke and Holway 2006; high temperatures, Holway et al. 2002b, Walters and Mackay 2005; winter temperatures, Krushelnycky et al. 2005; humidity, Holway 1998b; rainfall, Krushelnycky et al. 2005, Heller et al. 2008), there is limited evidence for biotic resistance against *L. humile* establishment within areas of introduction (Walters and Mackay 2005, Sagata and Lester 2009). *L. humile* outcompetes native ants, both through exploitative and interference competition, at artificial bait stations (Holway 1999, Human and Gordon 1999, Rowles and O'Dowd 2007) and at natural resources (Nygard et al. 2008, Rowles and O'Dowd 2009). By comparing honeydew resource utilization between *L. humile* and sympatric native ants, we may gain insights into one possible mechanism (a more effective mutualist) underlying the invasion success of the Argentine ant. The Argentine ant has often been implicated in explosive outbreaks of honeydew-producing Hemiptera (reviewed in Ness and Bronstein 2004, Holway et al. 2002a), and it is thought that a plentiful carbohydrate resource, such as honeydew, can fuel the high worker densities required to dominate an ant community (Holway et al. 2002a, Ness and Bronstein 2004, Davidson et al. 2004).

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We discovered a unique site in Raleigh, NC, supporting both *L. humile* and *Tapinoma sessile* (Say) (Formicidae: Dolichoderinae), an ant native to North America (Smith 1928). *T. sessile*, like *L. humile*, is polydomous and polygynous (Smith 1928; Passera 1994; Barbani 2003; Buczkowski and Bennett 2006, 2008a, b) and consumes hemipteran honeydew (B.P., personal observation). Both ants at our site were observed tending the black citrus aphid, *Toxoptera aurantii* (Boyer de Fonscolombe) (Hemiptera: Aphididae), on Chinese holly, *Ilex cornuta*. *T. aurantii* is a facultative myrmecophile that excretes large volumes of honeydew (Dartigues 1992).

Herein, we compare the survival and growth of a field population of *T. aurantii* when tended by *L. humile* or *T. sessile*. During our study, we noted a significant reduction in *T. sessile* and *T. sessile*-tended aphids after a severe rain event in 2006. We suspected that significant rainfall affected *L. humile* and *T. sessile* foraging activity differently, leading to different consequences for *T. aurantii*. Therefore, we simulated the effect of a rainfall disturbance on *L. humile* and *T. sessile* foraging activity in a laboratory experiment and predicted that *L. humile* foragers would be less disturbed by heavy rainfall than *T. sessile*.

### Methods and Materials

We conducted our experiment in a commercial park ( $\approx 100$  ha) in North Carolina from 2005 to 2007. The park has extensive *I. cornuta* plantings, which are periodically colonized by *T. aurantii* from June through September. *L. humile* is the most abundant ant in the park and was frequently observed tending *T. aurantii* on *I. cornuta*. *T. sessile* was restricted to one small ( $<1$  ha) section of the park containing a single *I. cornuta* hedge (30 m in length). Both *L. humile* and *T. sessile* tended *T. aurantii* on this hedge, although the foraging territories of *L. humile* and *T. sessile* were discrete, and interactions between the ant species were not observed. Aphid aggregations occurred only on the new growth ( $\approx 20$ – $30$  cm) of *I. cornuta*, with the leaf habitable for 10–20 d before *T. aurantii* dispersed.

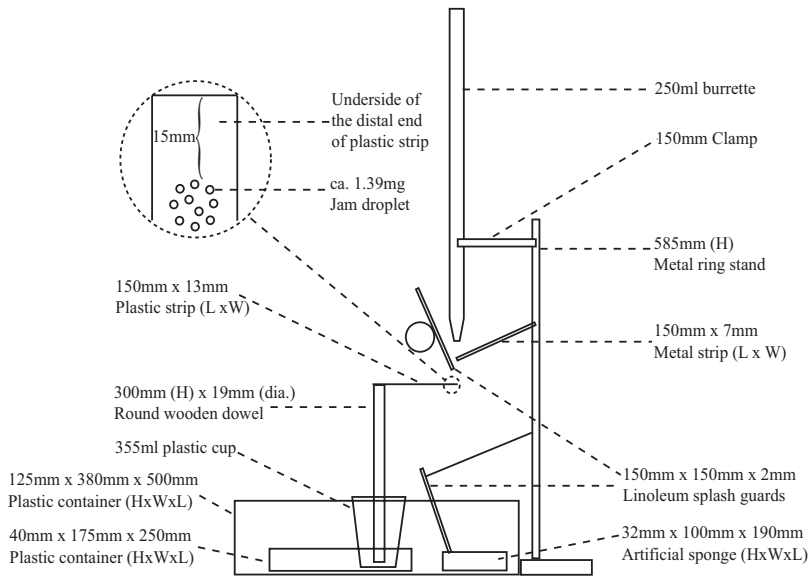
We randomly selected 30–40 *I. cornuta* tips of new growth with *T. aurantii* within each area occupied by *L. humile* or *T. sessile* during the period of each year that *T. aurantii* were detected. We selected plant tips with at least one ant tending *T. aurantii*. Tips were identified with flagging tape (ENVC, Sherman, TX). We saw no evidence that the flagging tape affected ant foraging. We randomly selected one half of the *Ilex* stems and applied an  $\approx 50$ -mm-wide Tanglefoot barrier (The Tanglefoot Company, Grand Rapids, MI) below the new growth. These served as ant-exclusion controls. We examined the barrier each day and re-applied Tanglefoot when needed.

We counted aphids on the experimental tips each day, noted the presence of ants (2005 and 2006), and counted the number of ants tending aphids in 2007. We also counted and identified predators of *T. aurantii* on tips to the family level. The most common

predators were larvae of Coccinellidae and Syrphidae; however, their numbers were too low to analyze statistically. Our discovery of this unique site with both *L. humile* and *T. sessile* in 2005 was quite fortuitous and, consequently, we were not prepared to record numbers of ants tending *T. aurantii* on the plants. In 2006, few *T. sessile* occurred on the plant after heavy rainfall (NOAA 2008) 4 d after our experiment began, thereby precluding a comparison of ant forager numbers.

After the 3 yr of field recordings, we tested our hypothesis that heavy rainfall was responsible for the decline of foraging *T. sessile* in 2006. We developed a laboratory assay to simulate the responses of *L. humile* and *T. sessile* to a rainfall event while feeding. We used a 250-ml burette combined with various flow regulating devices (Fig. 1) to provide low (0.175 ml/s), medium (0.283 ml/s), and high (0.55 ml/s) water release with a mean droplet size of 0.10 ml at all flow rates. Strawberry jam dabbed onto the underside of a flexible strip of plastic simulated honeydew from *T. aurantii* attached to the underside of a leaf (Fig. 1). Prior laboratory work (B.E.P. and J.S., unpublished data) showed that *L. humile* recruited proportionally more workers per colony than *T. sessile* to *Aphis gossypii* (Hemiptera: Aphididae), ( $F_{1,36} = 18.57$ ,  $P = 0.0001$ ). Therefore, a larger number of *T. sessile* workers (300 plus three queens) were used per replicate than *L. humile* (200 plus two queens) to ensure comparable numbers of foraging ants of each species. Colonies of both ants were taken from laboratory cultures (originating from wild populations in Wake Co., NC) that were maintained on 20% sucrose solution and freshly killed female German cockroaches (*Blattella germanica*) weekly. Ants were placed in a 355-ml plastic cup containing moistened soil and a vertical wooden dowel (300 [height] by 19 mm [diameter]) with the jam-dabbed flexible plastic strip (150 by 13 mm) stapled to the end of the dowel. The cup was housed within a Fluon-coated plastic container (40 by 175 by 250 mm). Each replicate was supplemented with two to three freshly killed female German cockroaches and deprived of sugar for 72 h.

To ensure consistent vibration across the plastic strip when struck by a water droplet, wooden shims were used to make certain the plastic strips were horizontal after positioning under the burette. Care was taken to ensure that only the distal 10 mm of the plastic strip was exposed to the water droplets; otherwise, the water would displace the ants and jam from the plastic strip. Jam (0.39 mg) was placed in a circular pattern  $\approx 15$  mm away from the distal end of the plastic strip. The time to discover the jam and initial recruitment were highly variable between replicates regardless of ant species, so we waited until there was no further recruitment to the jam for 30 s before releasing water droplets. Ten replicates were performed for each of the three flow rates. We counted ants on the jam just before and immediately after ( $<10$  s) droplets were released, followed by counts each minute for 10 min of continued water disturbance. We recorded



**Fig. 1.** Schematic of the simulated rainfall apparatus drawn to scale except for the underside of the plastic strip insert. The linoleum splash guards were held at an  $\approx 65.4^\circ$  angle, and the metal strip was held at an  $\approx 23.6^\circ$  angle. The lower splash guard was fixed to the ring stand using flexible tape on one side so that it could be moved out of the larger container to wring out the sponge between replicates. The tip of the water exit (i.e., burette or pipette tip) was positioned 15 mm above the metal strip. The metal strip standardized droplet size, and the splash guards kept water from physically removing the jam and or ants (upper) and water from entering the smaller container (lower). The flow adjustment knob on the burette was sufficient control for the high and medium rates but a pipette tip was affixed to the end of the burette to slow the flow for the lower rate.

only those ants on the jam. Control replicates were identical to the treatments except water was not applied.

We analyzed both aphid population growth rate (2005–2007) and ant numbers (2007) among treatments and controls using a repeated-measures models (PROC MIXED), with appropriate contrasts (SAS Institute 2004). The presence of ants (2005 and 2006) was analyzed using a logistic data, repeated-measures model under PROC GENMOD with appropriate contrasts. The change in the number of ants during the simulated rainfall trials was analyzed with a repeated-measures model (PROC MIXED) after log transformations of the proportional difference from the original recruited ant numbers.

## Results

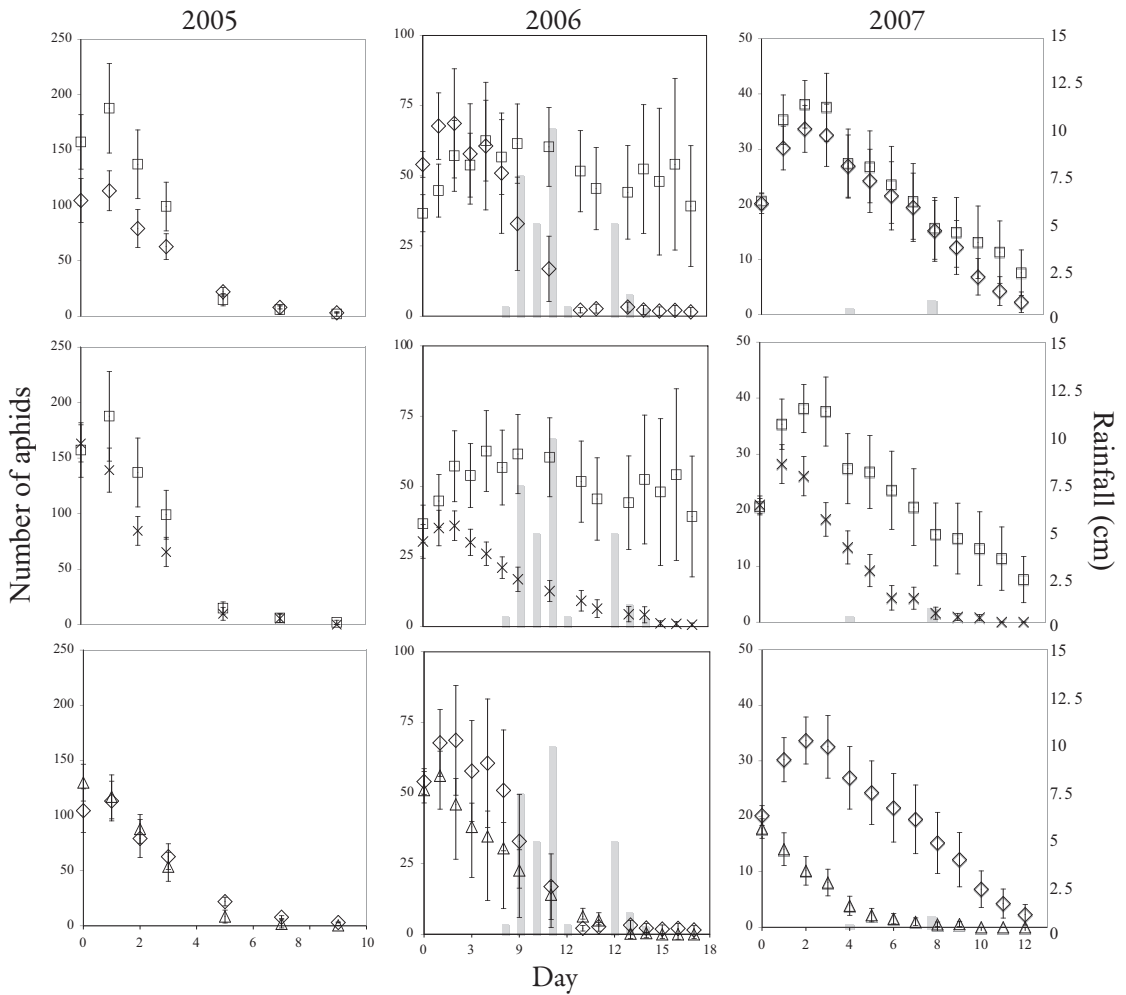
In 2005, there was no difference in the population curves between *L. humile* and *T. sessile*-tended aphids ( $F_{1,472} = 1.27$ ,  $P = 0.26$ ; Fig. 2). Aphid populations tended by *T. sessile* and *L. humile* were no different from ant-excluded controls ( $F_{1,472} = 1.61$ ,  $P = 0.21$  and  $F_{1,472} = 1.27$ ,  $P = 0.17$ , respectively; Fig. 2). There was no difference between *L. humile* and *T. sessile* worker presence on treatment tips in 2005 ( $\chi^2 < 0.01$ ,  $P = 0.96$ ; Fig. 3).

In 2006, *L. humile*-tended aphid populations remained higher through time than *T. sessile*-tended aphid populations ( $F_{1,832} = 11.55$ ,  $P < 0.001$ ; Fig. 2), which declined precipitously (Fig. 2). Aphid popula-

tions excluded from *L. humile* remained significantly lower through time than *L. humile*-tended populations ( $F_{1,832} = 7.11$ ,  $P = 0.0078$ ; Fig. 2). In contrast, aphid numbers declined both on tips with foraging *T. sessile* and *T. sessile*-excluded tips ( $F_{1,832} = 0.31$ ,  $P = 0.58$ ; Fig. 2). There was a large amount of rain in 2006 that began  $\approx 4$  d into the experiment and continued to the end of counting, with several inches recorded (NOAA 2008; Fig. 2). The presence of *T. sessile* workers was lower than *L. humile* workers on treatment tips this year ( $\chi^2 = 3.96$ ,  $P < 0.05$ ; Fig. 3).

In 2007, the decline in *T. aurantii* numbers through time was less when tended by either *L. humile* or *T. sessile* than when ants were excluded ( $F_{1,712} = 15.72$ ,  $P < 0.0001$  and  $F_{1,712} = 22.71$ ,  $P < 0.0001$ , respectively; Fig. 2). The population curves for *L. humile*-tended and *T. sessile*-tended aphids were similar to each other ( $F_{1,712} = 0.12$ ,  $P = 0.73$ ; Fig. 2). There were no differences in the numbers of foraging ants on treatment tips in 2007 between the two species ( $F_{1,28} = 0.01$ ,  $P = 0.92$ ; Fig. 3), mirroring our results from 2005.

Aphid numbers in 2005 were higher than in 2006 ( $F_{1,82} = 3.77$ ,  $P = 0.05$ ) and 2007 ( $F_{1,82} = 13.17$ ,  $P = 0.0005$ ), and aphid numbers between 2006 and 2007 were not different ( $F_{1,82} = 0.01$ ,  $P = 0.90$ ). We previously noted that we saw no difference in aphid numbers when ant foragers were excluded or not in 2005 but recorded lower aphid numbers in the exclusion treatments in 2007.



**Fig. 2.** Mean ( $\pm$ SE) *T. aurantii* numbers per tip through time for 2005–2007:  $\square$ , *L. humile* present;  $\diamond$ , *T. sessile* present;  $\times$ , *L. humile* exclusion;  $\triangle$ , *T. sessile* exclusion. Columns represent years of data, left to right, for 2005, 2006, and 2007, respectively. The top row represents aphid populations in the presence of *T. sessile* and *L. humile*. The middle row represents aphid populations in the presence of *L. humile* and respective ant-exclusion controls. The bottom row represents aphid populations in the presence of *T. sessile* and respective ant-exclusion controls. Daily rainfall histogram has been superimposed on the 2006 graphs.

The response to the simulated rainfall was different between the two ants at low ( $F_{1,784} = 5.01, P < 0.05$ ; Fig. 4), medium ( $F_{1,784} = 31.90, P < 0.0001$ ; Fig. 4), and high ( $F_{1,784} = 38.25, P < 0.0001$ ; Fig. 4) flow rates. For *L. humile*, there was a constant rapid retreat from the carbohydrate resource followed by recruitment to the carbohydrate resource over the next several minutes. *L. humile* workers differed from undisturbed controls at medium ( $F_{1,784} = 19.02, P < 0.0001$ ; Fig. 4) and high ( $F_{1,784} = 7.19, P = 0.0075$ ; Fig. 4) flow rates. This contrasted with the gradual decline of *T. sessile* at the carbohydrate resource for the medium ( $F_{1,784} = 3.98, P = 0.046$ ; Fig. 4) and high ( $F_{1,784} = 9.46, P = 0.0022$ ; Fig. 4) rates. The numbers of *T. sessile* at the resource remained constant during the low flow rate ( $F_{1,784} = 0.03, P = 0.86$ ; Fig. 4).

**Discussion**

Contrary to evidence that *L. humile* is more dominant than most co-occurring native ants, including *T. sessile* (Human and Gordon 1999, Holway 1999) and has been implicated in outbreaks of honeydew-producing Hemiptera (Ness and Bronstein 2004), we observed higher *T. aurantii* numbers on plant stems visited by *L. humile* compared with *T. sessile* in just 1 of the 3 yr of our study. We surveyed the common border on *I. cornuta* between *L. humile* and *T. sessile* over 3 yr and were somewhat surprised that this ant boundary remained static given that *L. humile* displaces many other ant species including *T. sessile* (Holway 1999, Human and Gordon 1999, Rowles and O’Dowd 2007). Intensive scouting within our field site showed only one instance of a

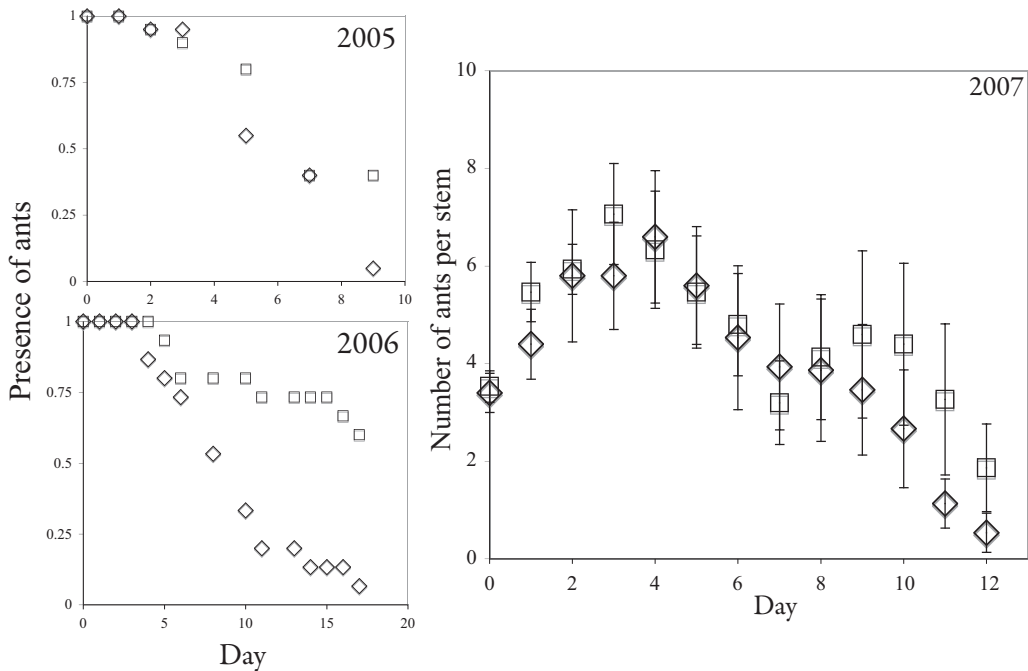


Fig. 3. Ant activity during 2005–2007. Years 2005 and 2006 show presence of ants. Year 2007 represents the mean ( $\pm$ SE) number of ants per stem over time.  $\square$ , *L. humile*;  $\diamond$ , *T. sessile*.

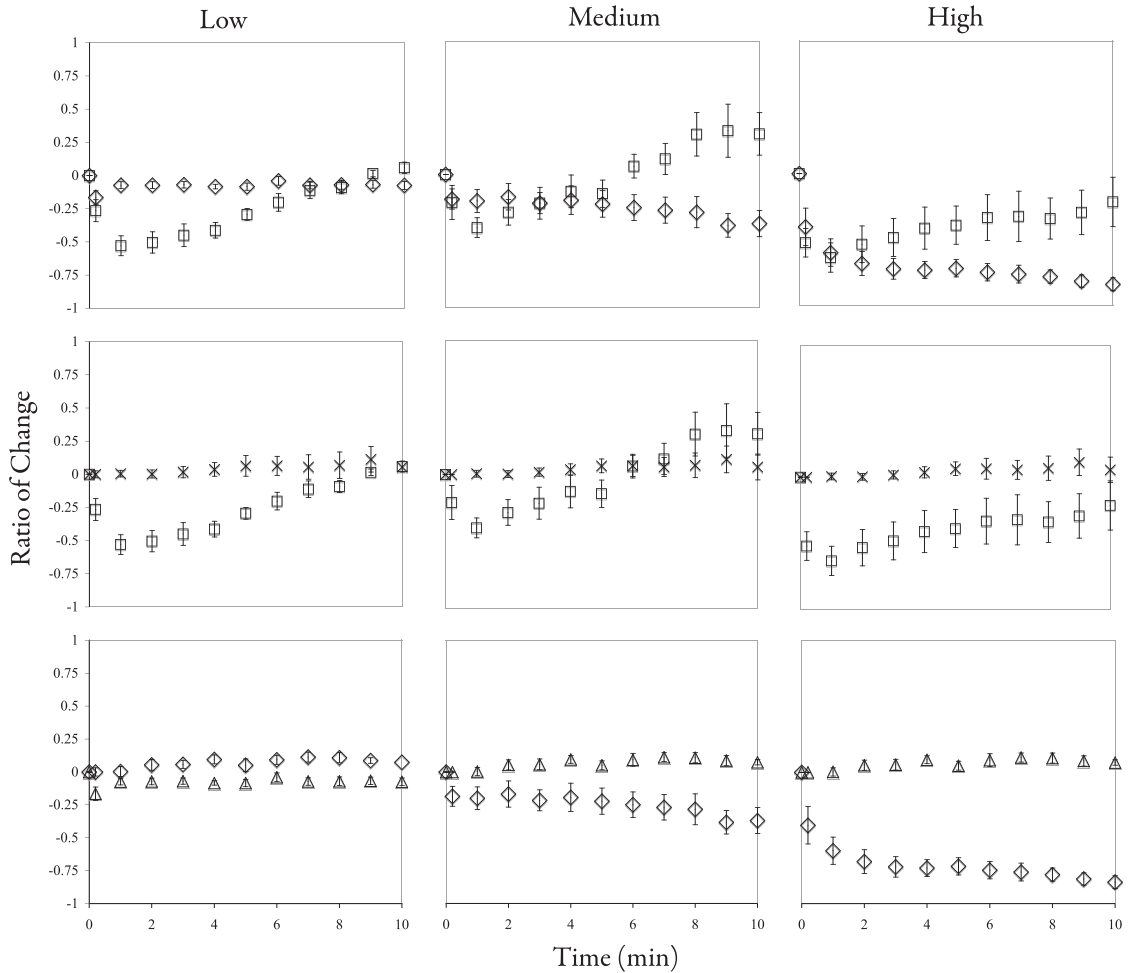
common border between *L. humile* and *T. sessile*. This particular *T. sessile* colony may have been of sufficient size to resist *L. humile* colony expansion. We saw no difference in 2005 in numbers of untended and tended aphids, nor did we record a difference between *L. humile*-tended and *T. sessile*-tended *T. aurantii* populations. Our discovery of this native ant/invasive ant/hemipteran system in 2005 was indeed fortuitous, and it is quite possible that our data in this first year were collected during a natural population decline of *T. aurantii* as *I. cornuta* tips hardened. This may, in part, explain the lack of difference in numbers of tended and untended aphids.

In 2007, untended aphid populations were smaller than ant-tended populations, yet no differences in aphid numbers tended by either *L. humile* or *T. sessile* were evident. We considered that both ant species afforded *T. aurantii* greater protection from their natural enemies at lower aphid densities (2007 versus 2005). Breton and Addicott (1992) and Harmon and Andow (2007) reported that higher ratios of tending ants to aphids in small versus large aphid populations positively impact aphid survival, possibly because of greater harassment of aphid natural enemies. Suzuki and Ide (2008) showed that, in the absence of *Lasius japonicus*, there was an increase in the number of *Aphis craccivora* consumed by the coccinellid, *Coccinella septempunctata*. Harassment by *L. japonicus* increased *C. septempunctata* prey handling time, thereby reducing aphid mortality.

In 2006, a persistent heavy rain appeared to cause a dramatic decline in foraging *T. sessile*, with a compa-

table decline in *T. sessile*-tended aphids. The steep decline in *T. sessile*-tended aphids in 2006 suggests that the rain-induced absence of foraging *T. sessile* caused many *T. aurantii* to drop from the plant, whereas the continued presence of *L. humile* may have prevented this. This is a common response to disturbance for many aphid species (Dixon 1986), including a close relative of *T. aurantii*, the brown citrus aphid, *T. citricida* (Michaud and Belliure 2001). Ant-aphid mutualisms impose costs on aphids, which include restricted dispersal (Stadler and Dixon 1998, 1999). *L. humile* is native to flood prone areas of the Paraná River drainage in northern Argentina (Wild 2004) and thus is adapted to extreme climatic events. By preventing aphid dispersal during a disturbance event such as heavy rainfall, *L. humile* retains a reliable carbohydrate resource. Our laboratory experiment showed that *L. humile* recruited to food at a higher rate than *T. sessile* during a water-induced disturbance, which may largely explain the ant and aphid field distribution in 2006. A direct test of the aphid/ant interaction under simulated rainfall would provide more definitive support for this explanation.

Growth of invasive ant colonies is often fueled by hemipteran honeydew (Ness and Bronstein 2004). *Solenopsis invicta* colonies that had access to mealybug honeydew grew  $\approx$ 50% larger than access-restricted colonies (Helms and Vinson 2008). Incipient colonies of invasive ants may provide no better services to their partner hemipterans (e.g., natural enemy defense) than native ants under optimal conditions (Ness and Bronstein 2004). However, by remaining with *T. aurantii*, and likely other hemipterans, on feeding sur-



**Fig. 4.** Mean ( $\pm$ SE) ratio of change of ant numbers in response to low, medium, and high rates of simulated rainfall.  $\square$ , *L. humile* present;  $\diamond$ , *T. sessile* present;  $\times$ , *L. humile*, no rainfall;  $\triangle$ , *T. sessile*, no rainfall. Columns represent different flow rates, from left to right: low (0.175 ml/s), medium (0.283 ml/s), and high (0.55 ml/s), respectively. The top row represents response of *T. sessile* and *L. humile*. The middle row represents response of *L. humile* and respective waterless controls. The bottom row represents response of *T. sessile* and respective waterless controls.

faces during climatic events severe enough to deter native ants, *L. humile* may have prevented the hemipterans from dropping to the ground and being lost, thereby usurping hemipteran resources from native ants forced to retreat.

A climatic event such as rainfall may deter attendance of aphids by native ant species, but not invasive ant species like *L. humile*, which may have profound consequences for myrmecophilic hemipteran populations. Conversely, *L. humile* may, in part, dominate native ants by fueling colony growth through maintaining high numbers of honeydew-producing hemipterans during adverse climatic conditions.

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