

Homopterans and an Invasive Red Ant, *Myrmica rubra* (L.), in Maine

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Environ. Entomol. 41 (1): 59–71 (2012); DOI: <http://dx.doi.org/10.1603/EN11046>

ABSTRACT *Myrmica rubra* (L.), is an invasive ant that is spreading across eastern North America. It is presently found in over 40 communities in Maine and areas in Vermont, New Hampshire, Massachusetts, New York, and several provinces in the Canadian Maritimes and Ontario. In addition to disrupting native ant faunas, invasive ants also have been shown to influence homopteran abundance and species composition. We conducted surveys of Homoptera in infested and noninfested sites and conducted manipulative experiments to quantify the effects of *M. rubra* on homopteran abundance and composition in the summers of 2003, 2006, and 2007 on Mount Desert Island, ME. In 2003, Homoptera family-level richness was higher in infested sites compared with noninfested sites with two out of three sampling methods. Homopteran abundance in infested compared with noninfested sites depended upon the site. The sites with the highest population of *M. rubra* were associated with significant differences in Homoptera population abundance. In 2006 and 2007, two out of three host plants sampled had significantly higher abundances of the aphids, *Aphis spiraephila* Patch and *Prociphilus tessellatus* Fitch. An ant exclusion field experiment on the native plant, meadowsweet (*Spiraea alba* Du Roi), resulted in higher abundances of *A. spiraephila* with *M. rubra* tending compared with native ant tending. A predator exclusion field experiment was conducted on meadowsweet using adult ladybeetles, *Hippodamia convergens* Guérin-Méneville, larval green lacewings, *Chrysoperla carnea* Stephens, and no predators. Predator impacts on aphid populations were reduced in the presence of *M. rubra* with *C. carnea* and moderately reduced with *H. convergens*.

KEY WORDS invasive ant, *Myrmica rubra*, Homoptera, myrmecophily, aphid

Myrmica rubra (L.), is a homopteran-tending ant common to northern Europe (Groden et al. 2005, Wetterer and Radchenko 2010). Introduced into Massachusetts in the early 20th century, “*M. rubra*” has become invasive in several states and provinces in northeast North America and is now established in 42 communities along the coast of Maine (Groden et al. 2005, E. G., unpublished data). Some of the most heavily infested areas are on Mount Desert Island (MDI) where populations of these ants are particularly dense (1.4 nests/m²; Groden et al. 2005).

Invasive species are responsible for the loss of biodiversity and disruption of ecological stability in landscapes (Mack et al. 2000). Invasive ant ecology has been the focus of several studies (Holway et al. 2002, Morrison 2002, Groden et al. 2005, Mondor and Addicott 2007) investigating these phenomena. “Tramp” ants, distributed by human activity, often have significant direct and indirect impacts on the native flora and fauna in their invaded territories (Holway et al.

2002). Sanders et al. (2001) found that Argentine ants, *Linepithema humile* (Mayr), in northern California increased its range at the expense of native ant fauna. Wetterer (2007) observed that where the African big-headed ant, *Pheidole megacephala* (F.), became established on Pacific tropical islands, few native invertebrates remained. Likewise, Porter and Savignano (1990) determined that the red imported fire ant, *Solenopsis invicta* Buren, reduced native arthropod richness by 70%, as did Kaspari (2000) who found lower arthropod richness in tree canopies in areas invaded by *S. invicta* in Texas.

Myrmica rubra aggressively defends its territory and readily stings humans, small mammals, and birds that move through or rest within infested areas. In addition, similar to the invasive ants discussed above, *M. rubra* invasion in Maine results in a significant reduction in the native ant densities and a shift in community structure (Garnas 2005, Groden et al. 2005) and also reduces biodiversity of ground dwelling arthropods in general (Garnas 2005), although, an experimental approach, such as taken by King and Tschinkel (2006) is needed to confirm these conclusions.

Although the long-term effects of invasive ants on native ecosystems is still debated (Morrison 2002, King and Tschinkel 2006), short-term effects have been shown to be exhibited at many trophic levels. Detrimental effects of invasive ants include reduced seed

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dispersal (Zettler et al. 2001, Ness 2004); reduction or local extirpation of native arthropods (Porter and Savignano 1990, Daane et al. 2007); and vertebrate taxa (Holway et al. 2002, Orrock and Danielson 2004), including effects on behavior and evolution (Garnas 2005). In addition, invasive ants commonly impact honeydew-secreting insect populations (Beardsley et al. 1982, Wetterer 2003, Coppler et al. 2007).

Mutualistic relationships between ants and homopterans have received considerable research attention, particularly in agricultural systems where sap-feeding insects can be significant pests (Way 1963, Boucher et al. 1982, Buckley 1987, Bronstein 1994, Price 1997, Daane et al. 2007). Many homopterans excrete sugar-rich "honeydew" that is collected by ant workers and provides an important source of carbon (Skinner 1980, Tilles and Woods 1982, Helms and Vinson 2002). In turn, tending ants provide protection from predators and parasitoids (Way 1963, Yao et al. 2000, Coppler et al. 2007); improved hygienic conditions (Buckley 1987, Muller and Godfray 1999); shelter (Holldobler and Wilson 1994, Helms and Vinson 2002) and aid in dispersal to nutritionally superior plants (Vinson and Scarborough 1991). Homopteran population densities typically are higher in ant-invaded areas, owing to higher nest and worker densities relative to native ant communities and aggressive worker behavior (Michaud and Browning 1999, Wetterer 2003, Coppler et al. 2007, Daane et al. 2007). The provision of abundant, energy-rich honeydew from homopterans has been implicated in the success of invading ant (Helms and Vinson 2002, Holway et al. 2002, Helms and Vinson 2008).

Field observations in Maine suggested that homopterans apparently are more abundant in areas infested with *M. rubra* than in areas inhabited solely by native ants. The objectives of this multiyear study, conducted on Mount Desert Island, ME, were to: 1) assess the differential abundance of Homoptera in *M. rubra* infested areas compared with noninfested areas by field survey on a diversity of native and invasive plants; 2) experimentally determine the rate of population increase of aphid populations on meadow-sweet, *Spiraea alba* Du Roi, a native herbaceous plant species common in both *M. rubra* infested and noninfested areas; and 3) experimentally determine the impact of *M. rubra* on two aphid natural enemies (green lacewing, *Chrysoperla carnea* Stephens, and convergent lady beetle, *Hippodamia convergens* Guérin-Méneville) and subsequent aphid population increase. We hypothesized that 1) homopteran abundance would be greater in *M. rubra* infested areas compared with noninfested areas, and 2) aphid populations in infested areas would have higher intrinsic rates of growth linked to protection from natural enemies by *M. rubra*.

Materials and Methods

This study was conducted during the summers of 2003, 2006, and 2007. Two homopteran surveys and two manipulative field experiments were conducted

in and adjacent to Acadia National Park, Mount Desert Island in Hancock County, ME (44° 35' N, 68° 28' W). *Myrmica rubra* infestations are distributed irregularly over the island (Grodén et al. 2005). Acadia National Park is dominated by spruce-fir forest (Davis 1966), but also consists of regenerating Acadian deciduous forest (*Acer* spp., *Fagus grandifolia* Ehrh., *Quercus* spp.) as a result of a large forest fire in the 1940s (Patterson et al. 1983).

Homoptera Survey. Homopterans were surveyed in matched habitats on Mt. Desert Island, ME to determine if differences exist in homopteran communities in established *M. rubra* infested compared with adjacent noninfested sites.

Survey 1, 2003. In the summer of 2003 (31 July–4 August), vegetation was surveyed for Homoptera in three pairs of sites ($n = 6$) in or adjacent to Acadia National Park. Survey locations were randomly selected from areas of known *M. rubra* infestation on MDI and paired with nearby habitats, matched by major habitat type. Given the patchy distribution of *M. rubra* on the island, paired infested and noninfested sites were separated by a maximum of 400 m. Putative presence or absence of *M. rubra* was confirmed by visual observation and monitoring using sugar baited traps before each survey. Paired sites were located at: Bear Brook Pond (44° 21' N, 68° 11' W); Acadia National Park Hull's Cove Visitor's Center (44° 24' N, 68° 14' W); and a forested habitat and old wetland fields abutting a commercial greenhouse (44° 19' N, 68° 11' W). We employed three sampling methods at each site: sweepnet samples of herbaceous plants, visual inspection of herbaceous and woody plants in random quadrats, and visually searched woody shrub and tree branches. Sweepnet samples of herbaceous vegetation (36-cm-diameter canvas sweepnet, three sweeps per sample) were taken at each of 10 arbitrarily selected locations within each paired site. Fifteen quadrat samples also were taken at each paired site. At every 10 m along a line transect, a 1-m² PVC-pipe quadrat was placed on the ground and staked into place. All grasses and broad-leaf herbaceous vegetation within the designated quadrat were searched for Homoptera and ants, as were shrubs or trees that fell within an imaginary vertical column delimited by the quadrat frame, up to a height of 2 m. Traveling along the same line-transect and extending visually 5 m in each direction to form a 10-m band, 50 trees (identified in the field) were selected arbitrarily for sampling. A single branch from each selected tree was sampled within 1 m of the terminus. All ants and Homoptera from each sampling method were collected, placed in 70% ethanol, and brought to the laboratory for identification.

Analysis of the 2003 survey data first involved computation of Homoptera family-level richness for the dependent variable. A RCB (randomized complete block) analysis of variance (ANOVA) for the sweepnet samples with replication was used. This allowed a block \times treatment (*M. rubra* infested versus noninfested) interaction to be tested. A RCB MANOVA was used for the quadrat and branch samples derived from the linear transect sampling. Sweepnet sampling also

provided a quantitative measure of Homoptera abundance. Abundance of each Homopteran family was analyzed using a RCB MANOVA. No transformation of the data were necessary. SYSTAT (2004) was used for statistical analysis.

Survey 2, 2006 and 2007. The abundances of Homoptera and ants were visually sampled on specific homopteran host plants at paired infested and noninfested sites. Six pairs of sites ($n = 12$) were selected for the comparative plant survey. Paired sites were selected for similar habitat and vegetation among infested and noninfested areas. All sites were characterized by saturated soils and had populations of speckled alder [*A. incana* spp. *rugosa* (Du Roi) R.T. Clausen], meadowsweet (*Spirea alba* Du Roi), and gray birch (*Betula populifolia* Marshall). Paired sites were as follows: Sand Beach House (infested site), 44° 20' N, 68° 10' W and Bear Brook Road (noninfested site), 44° 21' N, 68° 11' W; Breakneck Road (infested site), 44° 22' N, 68° 15' W and Eagle Lake (noninfested site), 44° 22' N, 68° 15' W; Crooked Road (infested site), 44° 24' N, 68° 17' W and Duck Brook Road (noninfested site), 44° 22' N, 68° 14' W; Four Corners Road (infested site), 44° 24' N, 68° 17' W and Fresh Meadow (noninfested site), 44° 24' N, 68° 18' W; Millers Garden (infested site), 44° 19' N, 68° 11' W and Sieur de Mont (noninfested site), 44° 21' N, 68° 12' W; Hull's Cove Visitor Center (infested site), 44° 24' N, 68° 14' W and Hull's Cove Visitor Center (noninfested site), 44° 24' N, 68° 15' W. Characteristics of each of the sites are presented in McPhee (2008, Table 2.1, p. 35).

At each site in 2006, we assessed Homopteran diversity and abundance on gray birch (leaves), speckled alder (leaves and branches), and meadowsweet (leaves and stems). In 2007, only speckled alder and meadowsweet plants were surveyed. We visited each paired site on the same day and as close to the same time as possible. At each site, three distinct areas, or "patches," of each plant species were identified. These patches consisted of an aggregation of at least five plants. Each patch was surveyed for a 3-min interval (alder branches were surveyed for 5-min intervals) for the presence or absence of homopteran and ants by species and tending behavior. One species of aphid, *Aphis spiraeophila* Patch, was found in predominance on meadowsweet, whereas the woolly alder aphid, *Prociphilus tessellatus* Fitch, was found on alder. Dr. Gary Miller, Research Entomologist at the Systematics Entomology Laboratory in Beltsville, MD, confirmed the identification of both aphid species. In 2006, each paired site was visited twice throughout the season (21 June–19 July, and 9–21 August). In 2007, each paired site was visited five times (5–7 June, 25–29 June, 9–20 July, 30 July–15 August, and 31 August–8 September).

For aphids on alder only, we recorded aggregation size on an ordinal scale as sparse (1– two aphids observed), or by the length of branch covered by the aggregation (small aggregation, 1.3–2.5 cm; medium, 2.5–7.6 cm; large, 7.61–12.7 cm; extra large, >12.7 cm). The size of aphid aggregations on meadowsweet also was determined by branch coverage (sparse, 1–2 aphids; small, 1.3–2.5 cm; medium, 2.5–3.8 cm; large, 3.8–5.1 cm; extra large, >5.1 cm). This method was

chosen to provide an efficient means of estimating homopteran colony sizes. These aggregation sizes differed based on aphid species' morphology and respective plant morphology. *P. tessellatus* are larger aphids with a woolly appearance that cover more plant tissue than *A. spiraeophila*. On speckled alder, a colony of 30 *P. tessellatus* would cover more plant tissue than a colony of the same size of *A. spiraeophila*.

Analyses for the 2006 and 2007 surveys were conducted using the presence or absence of common homopteran families and *M. rubra* infestation. Within-site replicates were pooled to yield a site presence or absence per date and site. Data were analyzed using repeated measures nominal logistic regression with generalized estimating equations (GEE, Hanley et al. 2003, Hardin and Hilbe 2003); independent variables were treatment (infested versus noninfested), block (paired sites), and sampling date. We used ordinal logistic regression to assess the aphid density categories (four and five, respectively, on alder and meadowsweet) as a function of *M. rubra* presence or absence. All models were constructed in SPSS (2008).

Field Experiments. *Ant Exclusion Experiment, 2006.* A manipulative field experiment was conducted to investigate the effect of tending by native ants and *M. rubra* on the density and mortality of the aphid, *A. spiraeophila*, on potted meadowsweet plants. We employed a 2 by 2 factorial design (*M. rubra* infested versus noninfested sites and ant access to plants versus no access) with nine replicates per treatment. Thirty-six meadowsweet seedlings were collected from Blueberry Hill in Winterport, ME on 21–24 July, transferred to a 20.3-cm-diameter pot, and transported to Bar Harbor, ME (collecting plants in ANP is prohibited). On 24–25 July, each plant was inoculated with ≈ 30 nonalate *A. spiraeophila* collected the same day from meadowsweet growing on Mount Desert Island, ME. Plants were inoculated by pinning excised aphid-infested leaves collected from meadowsweet in Acadia National Park to experimental plants. Aphids moved of their own accord and began feeding on experimental plants within 24 h. Each plant was fertilized once with MiracleGro (1.5 mls/0.4 liter water/plant) to facilitate robust growth and allowed to acclimate in transplanted pots in a common garden represented by a partly shaded noninfested forest edge for 9–11 d.

Plastic blueberry "crates" were modified as follows to create containers for the plants in the field so that ants could be experimentally excluded (Fig. 1). Each crate (50.5 cm by 40.5 cm by 13.5 cm) is divided into two halves by a central plastic ridge. Eighteen blueberry crates were treated along their sides with Tanglefoot Pest Barrier (Tanglefoot, Grand Rapids, MI) and filled with soapy water, creating an ant-free space. We placed a gravel-filled 1-gallon nursery pot in each half of each crate; on which we placed a single potted aphid-inoculated meadowsweet seedling. Between 31 July and 2 August, crates were placed in three of the areas sampled for the homopteran survey (Bear Brook Road, Old Farm Road, and Hull's Cove Visitor Center) using three replicate crates in each of

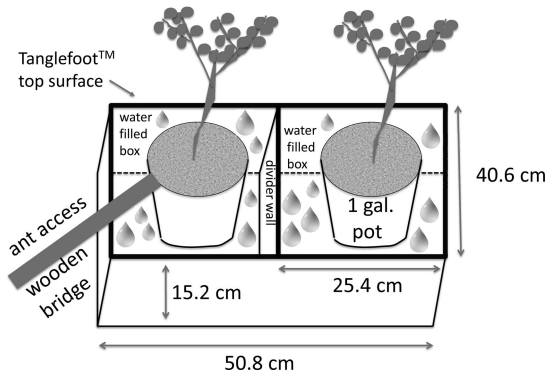


Fig. 1. Diagram of potted plant experimental unit design based upon a divided blueberry crate with Tanglefoot adhesive and water to prevent ant access and wooden bridges for the treatments where ant access was desired. Water drop icons denote water filled crate.

the three paired (infested or uninfested) sites. One plant per crate was randomly selected for ant access, and a 45.7-cm by 7.6-cm wooden bridge was extended from the ground outside of the blueberry crate to the top edge of the inner pot with the meadowsweet plant. Droplets of 25% (wt:vol) sugar water were placed on the bridges to encourage ants to climb to locate the aphid-infested plants. Plants were checked regularly to assure that ants were accessing plants with bridges and were successfully excluded for those without bridges. All plants were carefully examined five times on dates between 1 August and 7 September 2006, and the total number of aphids, ants, and predatory insects (coccinellids, reduviids, nabids, pentatomids, and chrysopids) were recorded per plant.

Aphid counts were analyzed as an RCB split-split plot ANOVA using Statistix 8.1 (Analytical Software, 2000). Main effects were *M. rubra* infestation (infested versus noninfested in paired sites), ant access (excluded versus encouraged), paired within sites as the split plot factor, and date was the split-split plot factor. Aphid counts were $\log(x + 1)$ transformed to reduce heteroscedasticity. In addition, log-transformed aphid alate density was analyzed at peak incidence (25 August) as a RCB split-plot ANOVA (no date effect). Intrinsic growth rate per tending ant and numbers of tending ants were additional measures that we used to test the significance of the main treatment effect (*M. rubra* infested sites versus noninfested sites) using an RCB ANOVA. The per capita rate of growth (R) was calculated as log aphids per plant at the final sampling date minus the log aphids per plant at the start of the experiment. We then calculated the per capita aphid growth rate per attendant ant as R divided by the mean number of tending ants per plant across sampling dates.

Predator Exclusion Experiment, 2007. To investigate the effect of tending by *M. rubra* ants on the density and colony growth rate of aphids in the presence of two predators native to Maine (the convergent ladybeetle adults, *Hippodamia convergens* Guérin-Méné-

ille, and green lacewing larvae, *Chrysoperla carnea* Stephens) we experimentally manipulated ant and predator access to aphid colonies established on potted plants in the field. The experimental design was a 2 by 2 by three factorial (factor A: *M. rubra* access versus no access; factor B: sampling date (early or late); and factor C: *H. convergens*, *C. carnea*, and a control of no predators) with three replicates per treatment combination. Approximately 70 meadowsweet seedlings were collected from Blueberry Hill in Winterport, ME in late July and early August. These plants were transferred to 20.3-cm-diameter pots and transported to a noninfested partly-shaded forest edge in Bar Harbor, ME. Each plant was fertilized with MiracleGro (1.5 mls/0.4 liter water/plant) and allowed to acclimate for 2 wk. The healthiest 36 meadowsweet seedlings were used for the experiment. Approximately 100 nonalate *A. spiraeophila*, collected from meadowsweet on Mount Desert Island, ME, were placed on each plant on 14 August; as for the ant exclusion experiment, a 51-cm by 37-cm-diameter wire frame was attached to each pot. After six days of acclimation, the pot was covered with a nylon mesh cage (1-mm² grid) and sealed with duct tape to exclude naturally colonizing aphids or predators and to maintain treatment integrity. Before caging we censused aphids and all aphid predators were removed. Ant access to half the plants was facilitated by placing a 26-cm piece of Nalgene (Thermo Fisher Scientific, Waltham, MA) 180 PVC plastic tubing (0.95 cm in diameter) running through a small hole in the lower side of the pots up through the soil in the pot, and emerging just above the soil surface inside the mesh cage. This tube was blocked until the start of the experiment. It was readily used to gain access by *M. rubra* and native ants to the experimental arena, while prohibiting aphid and predator escape.

On 21 August, caged, aphid-infested plants were transported to the *M. rubra*-infested Hull's Cove Visitor Center where pairs of plants were placed in 18 blueberry collection crates (Fig. 1) to exclude ant access and prevent contact between plants. Half of each crate was randomly assigned to an *M. rubra* access treatment; the other half served as a control (no access), respectively. Roughly 15 ml of a 25% concentration of sugar water (wt:vol) was dripped through the tubing before placement to encourage investigation by worker ants. Ants were given access to treatment plants for 24 h before predator release and for the duration of the experiment.

All predators were purchased from HydroGardens (Colorado Springs, CO). Convergent ladybeetles were delivered as adults and held for a week in a refrigerator at 5°C until release. Green lacewings were shipped as eggs, and when received were separated into 20 petri dishes (10 eggs per dish), held at room temperature (23°C), and monitored daily for hatch. Larvae were collected upon hatching, transferred to individual petri dishes, and held at room temperature with no food for ≈ 3 d until release. Each crate was randomly assigned a predator treatment (six crates per treatment). Three individuals per predator treatment

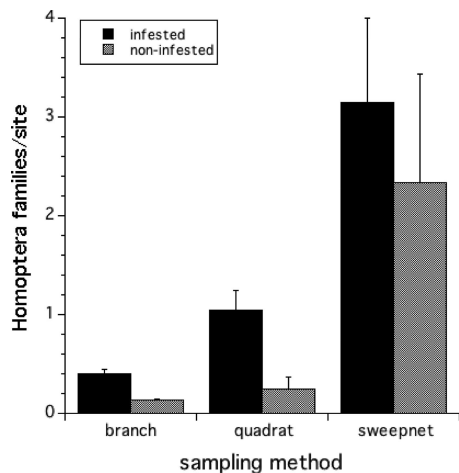


Fig. 2. Homoptera family-level richness at three paired sites (*M. rubra* infested versus noninfested) on Mt. Desert Island, ME, 2003. Error bars are standard errors of the means.

(ladybirds or lacewings) were placed on each plant, and the cages were securely sealed. Plants were checked daily throughout the experiment to ensure that cages remained sealed and water levels in the crates were maintained. Fifty percent of the plants ($n = 18$) were sampled and cages deconstructed 10 d post-predator release, on 31 August. The other 50% were sampled and deconstructed 20 d postrelease, on 9 September. At each time, the numbers of aphids, predators, and ants within each cage were recorded. Aphid counts were analyzed using an RCB ANOVA in a 2 by 2 by three factorial design using Statistix 8.1 (Analytical Software, USA). Aphid counts were $\log_{10}(x + 1)$ transformed.

Results

Homoptera Survey, Study 1, 2003. Family-level Homoptera richness captured from sweepnet samples was not significantly different between *M. rubra* infested and noninfested habitats ($F_{(1,2)} = 0.42, P = 0.58$). However, Homoptera richness captured with quadrat and terminal branch sampling was higher in habitats where *M. rubra* occurs (Wilks lambda: $\lambda_{2,1} = 6110.29, P = 0.009$, Fig. 2). The proportion of quadrats and terminal branches with Homoptera (calculated from samples within a site) was significantly higher in *M. rubra* infested sites ($\lambda_{2,1} = 6,088.2, P = 0.009$), and the proportion of homopterans tended by ants was marginally higher in *M. rubra* infested habitats ($\lambda_{2,1} = 115.4, P = 0.066$).

When the abundance of common Homoptera families estimated by sweepnet sampling was tested, a block \times *M. rubra* treatment (*M. rubra* infested versus noninfested habitat) effect was found ($\lambda_{8,102} = 2.98, P = 0.003$); thus the response in the Homoptera community because of *M. rubra* invasion depends on site. Only the commercial greenhouse site was found to have significantly higher Homopteran abundance in

M. rubra infested habitat ($\lambda_{4,15} = 10.51, P = 0.0003$), although similar trends were observed at the Acadia National Park Hull Cove Visitor's Center (Fig. 3).

Survey 2, 2006 and 2007. Gray birch leaf sampling in 2006 revealed no significant differences ($P > 0.05$) in homopteran communities, ant, spider, or caterpillar occurrences among *M. rubra* infested and noninfested habitats. However, we found that *M. rubra* infestation did affect homopteran communities on alder (Table 1) and meadowsweet (Table 2) in both 2006 and 2007. As expected, we observed a higher incidence of *M. rubra* on alder leaves and branches in infested sites compared with native ants in noninfested sites in both years (Table 1). In 2006, only leafhoppers on alder leaves and woolly alder aphids on branches were significantly more abundant in *M. rubra* infested sites compared with noninfested sites (Table 1). Contrary to our expectations, there was a higher incidence of homopteran taxa on alder leaves or branches in noninfested sites in 2006. In 2007, alder branches supported larger woolly alder aphid aggregations in *M. rubra* infested sites compared with noninfested sites (Table 1; $P < 0.0001$), with a significant ant treatment \times date interaction. There were consistently higher abundances of larger woolly alder aphid colonies in infested habitats and they grew larger throughout the summer. In addition, counts of woolly aphids initially were skewed toward larger aggregation classes and increased more throughout the summer of 2006 in infested sites than in noninfested sites ($\chi^2_1 = 271.752, P < 0.0001$). In 2007, there was a significant interaction between ant treatment and date for woolly alder aphid aggregation sizes ($\chi^2_4 = 16.711, P < 0.012$). Woolly alder aphids' incidence was consistently higher in *M. rubra* infested treatments but varied through the summer. The abundance of sparse aggregations tended to decline while abundance of larger aggregations increased throughout the season in *M. rubra* infested sites, whereas only the largest aphid aggregations persisted at the same or greater densities in noninfested sites.

Ant abundance on meadowsweet was similar among sites in 2006, but higher in *M. rubra* infested sites compared with noninfested sites in 2007 (Table 2). However, a higher proportion of homopterans were tended by ants in *M. rubra* infested sites than noninfested sites in both 2006 and 2007 (Table 2, 2006: [$\chi^2 = 5.244, P = 0.022, 2007: (\chi^2_4 = 10.26, P = 0.049)$]). In 2006, *A. spiraephila* was more abundant both as apterous and alate forms in infested sites compared with noninfested sites. In 2007, only apterous forms were more abundant in *M. rubra* infested sites, a similar (though nonsignificant) trend was seen for alates. There also was a significant difference in the presence of various *A. spiraephila* aggregations ($\chi^2_4 = 13.68, P = 0.008$), with higher densities of all aggregation sizes in *M. rubra* treatments relative to native ant treatments. Aggregation sizes of *A. spiraephila* also varied between sites. In 2007 there was a significant date \times treatment interaction; aggregation sizes started low in both treatments but grew to higher abundance in infested sites compared with noninfested sites (Table 2). All aggre-

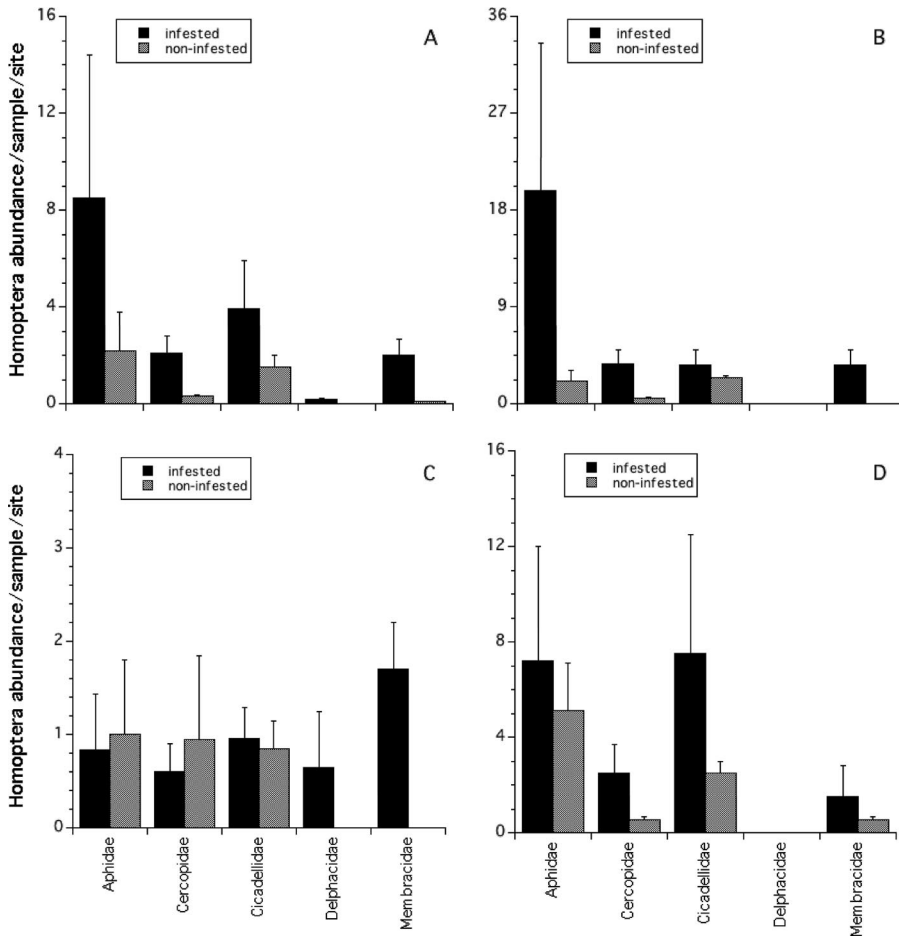


Fig. 3. Mean homopteran abundance collected in sweepnet samples across three paired sites (*M. rubra* infested versus noninfested) on Mt. Desert Island, ME, 2003 (A), commercial greenhouse site (B), Bear Brook Pond site (C), and Acadia Park Hull Cove Visitor's Center (D). Data plotted are only the five most abundant families. Error bars are standard errors of the means.

gation sizes peaked around the middle of July and began to decrease in both infested and noninfested sites thereafter. With the exception of the largest aggregations that were found in similar densities irrespective of infestation treatment, aphid aggregation densities were higher in infested sites than in noninfested at the end of the summer.

Field Experiments. Ant Exclusion Experiment, 2006. *M. rubra* had a significant impact on the growth and development of aphid populations on *S. alba* in the 2006 ant exclusion field experiment. Whether native or invasive, ant access significantly increased apterous aphid abundance on meadowsweet ($F_{(1,144)} = 12.493$, $P = 0.021$). There was a significant interaction between ant species (*M. rubra* invasive versus native), ant access, and time on the apterous aphid abundance ($F_{(5,144)} = 2.842$, $P = 0.032$; Fig. 4A). Apterous aphid abundance started out low in all treatments, but increased (13-fold) over time on plants for which *M. rubra* had access. Apterous aphid abundances also increased with time in the

native ant treatment with ant access, but final abundances were significantly lower than *M. rubra* access treatments (Fig. 4A). Aphid populations in the control treatment did not grow significantly in the duration of the experiment. Alate recruitment was marginally higher in the *M. rubra*-access treatment compared with native ant access (Fig. 4B). There was no significant difference between ant infestation treatments (*M. rubra* infested versus noninfested, native ant sites) on the intrinsic rates of growth for aphids per ant. However, there was a significant difference in the mean number of ants tending homopterans in infested compared with noninfested sites ($F_{(1,14)} = 4.961$, $P = 0.044$), with higher numbers in infested treatments (mean for infested sites = 14.60 ± 0.693 , noninfested sites = 1.11 ± 0.113). No significant differences were found between infestation treatments for the abundance of spiders, ladybeetles, parasitized aphid mummies, and diseased cadavers on the meadowsweet plants.

Table 1. Impact of *M. rubra* infestations on ant and Homoptera abundance associated with speckled alder (*A. incana* ssp. *rugosa*) leaves and branches on Mount Desert Island, ME, 2006 and 2007

Taxa sampled	Proportion of samples with presence of taxa ^a		Wald χ^2 for infested vs. noninfested	P value ^b
	<i>M. rubra</i> Infested	Noninfested		
2006:				
Alder leaves				
Alate Aphids	0.08	0.00	$\chi^2_1 = 5.07e-7$	$P = 0.999$
Apterous aphids	0.07	0.00	$\chi^2_1 = 4.90e-8$	$P = 0.999$
Cicadellidae	0.47 ^a	0.31	$\chi^2_1 = 4.834$	$P = 0.018^c$
Juvenile Cercopidae	0.18	0.18	$\chi^2_1 = 1.17e-6$	$P = 0.998$
Ants	0.67 ^a	0.36	$\chi^2_1 = 95.658$	$P < 0.0001$
Alder branches				
<i>P. tessellatus</i>	0.73 ^a	0.07	$\chi^2_1 = 271.752$	$P < 0.0001$
Cicadellidae	0.08	0.33	$\chi^2_1 = 2.720$	$P = 0.099$
Juvenile Cercopidae	0.08	0.08	$\chi^2_1 = 0.000$	$P = 1.000$
Membracidae	0.17	0.17	$\chi^2_1 = 0.000$	$P = 1.000$
Ants	0.92 ^a	0.32	$\chi^2_1 = 5.150$	$P = 0.023$
2007:				
Alder leaves				
Apterous Aphids	0.21	0.20	$\chi^2_1 = 2.795e-5$	$P = 0.996$
Cicadellidae	0.40	0.53	$\chi^2_1 = 193$	$P = 0.661$
Membracidae	0.06	0.05	$\chi^2_1 = 0.042$	$P = 0.838$
Ants	0.83 ^a	0.63	$\chi^2_1 = 16.259$	$P = 0.003^d$
Alder branches				
<i>P. tessellatus</i>	0.90 ^a	0.27	$\chi^2_4 = 271.503$	$P < 0.0001^e$
Aphid alates	0.17	0.13	$\chi^2_1 = 0.130$	$P = 0.718$
Cicadellidae	0.07	0.10	$\chi^2_1 = 0.233$	$P = 0.630$
Juvenile Cercopidae	0.13	0.03	$\chi^2_1 = 2.183$	$P = 0.140$
Membracidae	0.07	0.10	$\chi^2_1 = 0.233$	$P = 0.630$
Ants	0.93 ^a	0.40	$\chi^2_4 = 15.70$	$P = 0.003^f$

^a Indicates the significantly higher proportion of a taxa found in an infested or noninfested habitat.

^b P values listed are based upon a repeated measures over time logistic regression using generalized estimating equations (GEE). Significant ant infestation treatment effects are listed, date effects are not listed. If significant date \times ant infestation interactions were found, they are listed and demarcated by footnotes.

^c Significant ant treatment-by-date interaction with Cicadellidae presence consistently higher in *M. rubra* infested treatments but decreasing by the end of the summer, whereas Cicadellidae presence remained steady in noninfested native ant treatments.

^d Significant ant treatment-by-date interaction with ant presence consistently higher in *M. rubra* infested treatments and grew larger throughout the summer than in non-infested native ant treatments.

^e Significant ant treatment-by-date interaction with woolly alder aphid presence consistently higher in infested habitat and grew larger throughout the summer.

^f Significant ant treatment-by-date interaction with ant presence consistently higher in infested treatments than noninfested treatments; presence in infested treatments started out low in early summer, grew rapidly and peaked by late summer, and declined by summer's end.

Predator Exclusion Experiment, 2007. In the absence of *M. rubra*, both ladybirds and lacewings reduced aphid populations relative to the nonpredator control (Fig. 5). The presence of *M. rubra* had a significant positive effect on the per capita rate of aphid increase ($F_{(1,24)} = 7.981$, $P = 0.009$). Predator identity also had a significant effect on the rate of aphid increase ($F_{(2,24)} = 12.264$, $P < 0.001$; Fig. 5), but there was evidence of a trend toward an interaction of *M. rubra* access and predator type ($F_{(2,24)} = 2.693$, $P = 0.090$). Tukey's HSD all-pairwise comparisons test suggests that predator treatment effects only differed significantly between control and predators, but not between the predator species when there was no *M. rubra* access to the plants. Aphids did increase on plants with no *M. rubra* access and no predators, but in the absence of *M. rubra* with either lacewings or ladybeetles, aphid numbers declined. In the presence of *M. rubra*, aphid populations also were reduced by predators, but at a much reduced rate in lacewing treatments and only marginally with ladybeetles relative to predator exclusion controls. However, with *M. rubra* present and predators excluded, aphid per cap-

ita growth rate was higher than in the predator control where *M. rubra* was excluded. When sampled after 10 d, 11% of the released lacewing larvae and 61% of the released ladybeetle adults were found on the experimental plants. When sampled after 20 d, no lacewing larvae and 88% of the ladybeetle adults were found on the experimental plants. Sampling date had no detectable effect on aphid population increase.

Discussion

Our results demonstrate that non-native European red ants strongly impact the homopteran community on Mount Desert Island, ME. Comparative samples indicate that abundances of specific homopteran taxa are higher in areas infested with *M. rubra* relative to noninfested native ant sites. In 2003, 2006, and 2007, the attendant ants in the infested sites were 96.7% *M. rubra*. In the noninfested sites the species of attendant ants were divided nearly evenly among *Formica glacialis* Wheeler, *Lasius alienus* (Foerster), *Formica neogagates* (Viereck), and *Camponotus herculeanus* (L.).

Table 2. Impact of *M. rubra* infestations on ant and Homoptera abundance associated with meadowsweet (*S. alba*) on Mount Desert Island, ME, 2006 and 2007

Taxa sampled	Proportion of samples with presence of taxa ^a		Wald c ³ for infested vs. noninfested	P value
	<i>M. rubra</i> Infested	Noninfested		
2006:				
Apterous <i>A. spiraephila</i>	0.82 ^a	0.25	$\chi^2_{(1)} = 17.913$	$P < 0.001$
Alate <i>A. spiraephila</i>	0.38 ^a	0.11	$\chi^2_{(1)} = 16.417$	$P < 0.001$
Cicadellidae	0.08	0.0	$\chi^2_{(1)} < 0.001$	$P = 0.998^b$
Juvenile Cercopidae	0.13	0.08	$\chi^2_{(1)} = 0.001$	$P = 0.979$
Fulgoroidea	0.03	0.00	$\chi^2_{(1)} < 0.001$	$P = 0.998^b$
Ant tended aphid colonies	0.33 ^a	0.11	$\chi^2_{(1)} = 5.244$	$P = 0.022$
Ants	0.48	0.31	$\chi^2_{(1)} = 0.915$	$P = 0.339$
2007:				
Apterous <i>A. spiraephila</i>	0.95 ^a	0.15	$\chi^2_{(4)} = 9.453$	$P = 0.053^c$
Alate <i>A. spiraephila</i>	0.70	0.22	$\chi^2_{(1)} = 0.806$	$P = 0.369$
Cicadellidae	0.08	0.10	$\chi^2_{(1)} = 0.582$	$P = 0.445$
Juvenile Cercopidae	0.41	0.11	$\chi^2_{(1)} = 1.136$	$P = 0.286$
Ant tended aphid colonies	0.83 ^a	0.23	$\chi^2_{(4)} = 10.26$	$P = 0.049^d$
Ants	0.90 ^a	0.40	$\chi^2_{(4)} = 16.946$	$P = 0.002^e$

^a Indicates the significantly higher value based on repeated measures logistic regression (GEE).

^b P value based on logistic regression of presence and absence data with dates pooled due to rarity of occurrence.

^c Ant treatment by date interaction with presence consistently higher in infested treatments and not climbing or falling as rapidly as presence in noninfested treatments.

^d Ant treatment by date interaction with presence of tending ants consistently higher in infested treatments and initially rising in both treatments. Presence of tending ants fell by July in noninfested treatments but did not drop off in *M. rubra* treatments until late August.

^e Ant treatment by date interaction with presence consistently higher in *M. rubra* treatments. Both treatments saw a fall in presence in the middle of July, however in noninfested treatments, presence continued to fall after that while presence continued to rise in infested treatments until the end of the summer.

In 2003, mean homopteran richness was greater in *M. rubra* infested sites than nearby noninfested sites in two out of three sampling approaches. Families of Homoptera that were found in higher abundance in infested sites included Aphidae, Cicadellidae, Cercopidae, Delphacidae, and Membracidae, though magnitude of these differences varied by site. Sampling of homopteran taxa on specific common herbaceous and woody plant species in 2006–2007 showed

that *A. spiraephila* and *P. tessellates* are at higher densities in infested sites. *M. rubra* also influenced seasonal progressions in homopteran colony growth, resulting in larger aggregations over time. Aggregation size and density for two common aphid species were higher in infested sites, suggesting that *M. rubra* tending encourages colony establishment and growth. In fact, a higher proportion of branch and quadrat samples in 2003 and meadowsweet samples in 2006 and

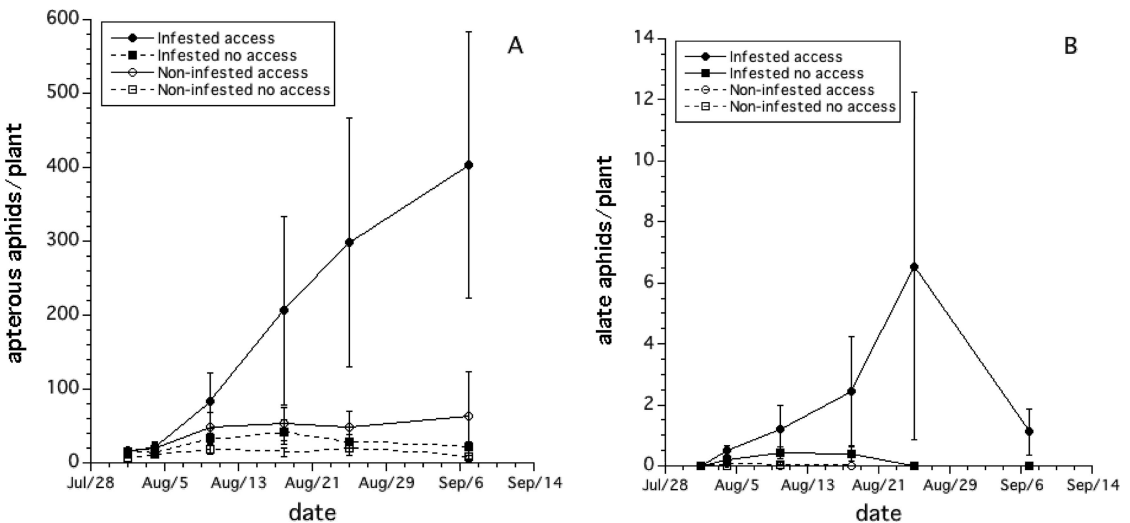


Fig. 4. Impact of *M. rubra* and native ant tending on apterous aphid abundance (A) and on alate aphid abundance (B) on meadowsweet in ant exclusion field experiment on Mount Desert Island, ME, 2006. (Error bars are SE).

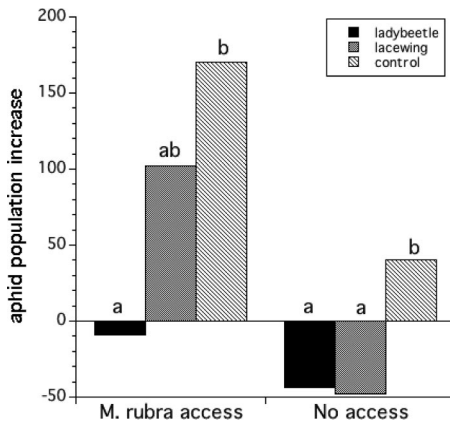


Fig. 5. The influence of *M. rubra* and predator treatments on the mean rate of increase of *A. spiraephila* on caged meadowsweet plants, summer 2007. Predator treatments included *H. convergens* adults, *C. carnea* larvae, and no predator for control. Pairwise comparisons were made between predator treatments within no *M. rubra* access and within *M. rubra* access treatments separately. Treatments labeled with different letters were significantly different according to Tukey HSD.

2007 showed ant tending to be higher by *M. rubra* in infested sites than by native ant species in noninfested sites. The large proportion of untended Homoptera in 2003 (72% in noninfested sites versus 9% in *M. rubra* infested sites), 2006 (89% in noninfested sites versus 67% in *M. rubra* infested sites), and 2007 (77% in noninfested sites versus 17% in *M. rubra* infested sites) suggests a dearth of native ant attendants under natural (noninfested conditions) and that *M. rubra* may be filling a semivacant or unsaturated niche.

To assess the direct effect of ant densities on homopteran abundance, we used proportion samples observed with ant or homopteran presence as a proxy for abundance. Then we regressed (nominal and ordinal logistic regressions) ant abundance on homopteran abundance in 2003, 2006, and 2007. We found a significant positive relationship between proportion of samples with ants and proportion of samples of overall homoptera in 2003 for both branch ($P = 0.031$) and quadrat samples ($P < 0.0001$). In 2006 and 2007 on alder, ants were not positively related to overall homopteran density ($P = 0.342$, $P = 0.711$, $P = 0.416$). However, when only *P. tessellatus* (the only homopteran shown to have significantly higher abundance in infested areas) was considered on alder branches in 2006 and 2007, there was a positive relationship between ant abundance across all sites and *P. tessellatus* abundance ($P = 0.017$). This is reflected in Table 1 by a four- to 10-fold increase in *P. tessellatus* abundance in infested areas compared with noninfested areas and a two- to three-fold increase in ants on these branches in infested areas compared with noninfested areas. In 2006 and 2007 on meadowsweet, ants were again not related to overall homopteran abundance ($P = 0.676$, $P = 0.475$). In 2007, however, ant abundance did explain the abundance of *A. spi-*

raephila ($P = 0.001$) on meadowsweet. This is reflected in Table 2 by a 4.5-fold increase in aphid abundance in infested areas compared with noninfested areas and a 2.3-fold increase in ants on these plants in infested areas compared with noninfested areas.

As discussed above, the interaction strength and positive effects of *M. rubra* are not general to all Homoptera, even among those producing honeydew. A preliminary survey by McPhee (2008) showed that Diaspididae, Coccidae, and Cercopidae nymphs were in higher abundance in *M. rubra* infested sites, whereas Pseudococcidae, Membracidae, and Hemiptera were significantly more abundant in noninfested sites. The differential colonization among homopteran species remains unexplained, but could be related to behavior, phenology, honeydew quality, or microhabitat preference among potential homopteran associates. Only some homopteran species are myrmecophilous (McPhee et al. 2008). Many myrmecophilous insects share a suite of behaviors and morphologies including the propensity to form large aggregations (for aphid), have conspicuous coloration, reduced cauda, and tend to excrete honeydew relatively slowly in semipersistent droplets (Dixon 1973, Holldobler and Wilson 1990). In contrast, nonmyrmecophilous aphids usually form diffuse colonies, show cryptic coloration, and excrete honeydew by kicking droplets away with hind legs or forcefully expelling it (Way 1963, Dixon 1973, Holldobler and Wilson 1990). It is possible that nonmyrmecophilous homopterans are attacked by *M. rubra* (Novgorodova 2005), and the increased Homoptera abundances found in *M. rubra* sites represent myrmecophilous homopterans.

We have observed nontended aphid species in *M. rubra* infested sites, especially on goldenrods (*Solidago* spp). The absence of tending by a generalist ant such as *M. rubra* (Brian and Brian 1951, Brian and Abbott 1977) may suggest these aphids were nonmyrmecophilous. In contrast, the woolly alder aphid, *P. tessellatus*, is myrmecophilous (Milbrath et al. 1993) and was tended actively by *M. rubra*. This may explain the apparently strong responses observed in this species to *M. rubra* invasion. *Prociphilus tessellatus* migrate to alder by midsummer from their perennial host, silver maple (*Acer saccharum* L.). *Prociphilus tessellatus* is commonly associated with several species of homopteran tending formicine ants, such as the species *Camponotus noveboracensis*, *C. pennsylvanicus*, and *F. subsericea* (Milbrath et al. 1993). Our study suggests that *A. spiraephila* is also myrmecophilous. In our field experiments, the aphid *A. spiraephila* was tended by both *M. rubra* and native ants. Thus, myrmecophily may represent powerful preadaptations conferring benefits to myrmecophilous Homoptera in the presence of ant invaders, which are growing worldwide.

Is there a concomitant (or disproportionate) propensity among invasive ants to tend aphids (Reilly and Sterling 1983, Helms and Vinson 2002, Wetterer 2003, Coppler et al. 2007, Daane et al. 2007, Gaigher et al. 2011)? Certainly in the case of *M. rubra* there is. This may be solely to the densities that they attain (Grodén et al. 2005). This means that human land use changes

that tend to benefit invasive ants (or tramp ants at least) are likely to carry at least one additional trophic level with them (Helms and Vinson 2002). In some cases, increases in homopteran abundance and unpredictable changes in species composition may be more detrimental to human endeavors (e.g., agriculture) than the ants themselves. The effects of ant invasion on co-evolved mutualists could turn out to be at least as strong an effect on biodiversity and ecosystem structure, and suggest the possibility for important indirect effects on plant diversity and primary productivity (Holway et al. 2002).

The quantity and quality of honeydew has been shown to affect the intensity of ant tending. Fischer et al. (2001) found *Lasius niger* (L.) preferentially tended the aphids, *Metopeurum fuscoviride* Stroyan, which produced four times more honeydew, over *Brachycaudus cardui* L. and *Aphis fabae* Scop. Ants also have been found to preferentially tend homopterans that produce honeydew with a higher concentration of melezitose (Fischer and Shingleton 2001, Woodring et al. 2004). Further research is necessary to clarify why some homopterans increase differentially in *M. rubra* infested areas and not others, but we hypothesize that the homopterans that increase in abundance in *M. rubra* infested sites have a superior quantity or quality of the honeydew compared with those that are not increased.

Several invasive ant species have been shown to increase homopteran populations at invaded sites (Reilly and Sterling 1983, Helms and Vinson 2002, Wetterer 2003, Coppler et al. 2007, Daane et al. 2007, Gaigher et al. 2011). A very likely mechanism supported in our research is that of increased protection against natural enemies. In our surveys, the proportion of aphids tended was higher in *M. rubra* infested sites than noninfested sites. Based on the analysis of the population growth rate for *A. spiraeophila* per ant in the ant exclusion experiment, there is no difference between per ant tending by *M. rubra* or native ants. When ants had access to meadow-sweet, both *M. rubra* and native ants (most commonly *Formica glacialis*, *F. neogagates*, *Lasius alienus*, or *Camponotus hurculeanus*) increased the abundance of *A. spiraeophila*. However, there were significantly more apterous aphids present on plants in infested sites compared with plants in noninfested sites. The higher density of *M. rubra* workers, as opposed to greater per ant efficiency, appears to be responsible for the increases in *A. spiraeophila*. Our predator experiments confirm that *M. rubra* does defend aphid colonies, but to varying degrees depending on the predator—aphid colony growth was higher in the presence of lacewings when tended by *M. rubra*, but not in the presence of ladybeetles in no-choice caging experiments. This supports findings from Finlayson et al. (2009) who reported *M. rubra* exhibiting differential aggression toward ladybeetle species with a tendency to be more aggressive toward native Maine species. Whether *M. rubra* deters predators, parasitoids, or both under natural conditions remains an open question, but appears quite likely.

The foraging pattern of tending ant species can have a significant impact on the quality of predator protection provided to the aphid. Katayama and Suzuki

(2003) found that *Tetramorium caespitum* L. was less effective in protecting *Aphis craccivora* Koch from predacious ladybeetle larvae (*Coccinella septempunctata* L.) than *L. niger*. Although similarly aggressive ant species, the difference in protection abilities was attributed to their different foraging behaviors. *Lasius niger* foragers frequent all parts of the plant, whereas *T. caespitum* foragers concentrate on the stem of plants. This leads to an increased encounter rate between *L. niger* and ladybeetle larvae, which ultimately led to lower residence time by ladybeetle larvae and fewer predated aphids. Similar to *L. niger*, *M. rubra* is often observed climbing and spreading throughout the plant architecture when foraging. This wide coverage in the foraging area may increase their chances of encountering a potential homopteran predator and thus increase their protective abilities.

Differential levels of aggression also have been linked to differences in homopteran protection by ants. When testing the homopteran defense of four ant species, Buckley and Gullan (1991) found a positive correlation between the aggressive nature of the ants and lower numbers of parasitized Homoptera. Likewise, when comparing *Lasius niger* (L.) and the ant, *Pristomyrmex pungens* Mayr, Itioka and Inoue (1999) found increased citrus mealybug, *Pseudococcus citriculus*, populations when tended by *L. niger*. The higher abundance of *P. citriculus* was attributed to the higher aggressiveness of *L. niger* and increased protective abilities. *M. rubra* is more aggressive than many native ant species (Garnas 2005). However, as mentioned previously, our ant exclusion study suggests that at least when tending *A. spiraeophila*, *M. rubra* is not more efficient in tending on a per ant basis. The higher densities of *M. rubra* foragers compared with native ant foragers (Grodén et al. 2005) likely contribute to increased populations of tended Homoptera.

Based on our predator exclusion experiment, *M. rubra* tending clearly benefits aphid populations beyond simply reducing predation rates, because *A. spiraeophila* colonies tended by *M. rubra* increased in the control (no predators) treatments. Previous studies have shown tended aphids produce more offspring than untended aphids (Flatt and Weisser 2000, Fischer et al. 2001) likely because of increased feeding rates (Bristow 1984, Katayama and Suzuki 2002). Removal of honeydew by ants can also prevent fungal overgrowth or infection (Bartlett 1961, Muller and Godfray 1999, Flatt and Weisser 2000).

The tending of Homoptera could be an important factor contributing to the dominance of invasive ant species (Helms and Vinson 2002). There is a concomitant (or disproportionate) propensity among invasive ants for use of plant exudates, honeydew, or both, which likely contributes to their ability to attain such large populations (Helms and Vinson 2002, Holway et al. 2002). Helms and Vinson (2003) estimated that $\approx 50\%$ of an *S. invicta* colony's daily energy requirements derive from various species of Homoptera, and that these ants are widely associated with an invasive mealybug, *Atonina graminus* (Maskell), whose colo-

nies comprise nearly 70% of insects tended by this ant. These authors demonstrated that access to the honeydew food resources produced by the mealybug resulted in significantly greater *S. invicta* colony growth than when fed on unlimited insect prey (Helms and Vinson 2008). Further surveys and experiments should be conducted to determine if a similar positive feedback between *M. rubra* and some species of Homoptera in the Northeast that may contribute to the high population densities achieved by each.

Few studies have directly addressed actual changes in the prevalence, abundance, or community composition of homopteran associates and other arthropods in an ant invaded habitat (Helms and Vinson 2003). Kaplan and Eubanks (2002) found the relationship between *S. invicta* and aphids was a key interaction that altered the structure of arthropod communities in cotton fields. Through tending of the aphids, *S. invicta* foraged higher in cotton plants and significantly decreased populations of herbivores and aphid-predators in cotton plants. In some cases, increases in homopteran abundance and unpredictable changes in species composition may be more detrimental to human endeavors (e.g., agriculture) than the ants themselves. The effects of ant invasion on co-evolved mutualists could turn out to be at least as strong an effect on biodiversity and ecosystem structure, and suggest the possibility for important indirect effects on plant diversity and primary productivity (Holway et al. 2002). Our surveys and experiments suggest that *M. rubra* selectively tend some species of Homoptera and negatively impact some predator species in the Northeast, indicating the potential for cascading effects on community composition and ecosystem function (Grodén et al. 2005). We speculate that this might suggest a selective advantage for more damaging or virulent homopteran, or select for greater rates of feeding within species. It could also favor particular plant hosts or habitats. By extension, ant invasion success could be influenced by the plant and homopteran communities that in turn could influence their distribution.

Acknowledgments

We thank Bruce Hazen-Connery and David Manski, biologists with the National Park Service at Acadia National Park, for their support and assistance with the logistics of conducting research in Acadia National Park. In addition, we want to thank two anonymous reviewers for their invaluable comments. This research was supported by several entities: the Maine Agriculture and Forestry Experiment Station, the University of Maine Graduate School, the National Park Service at Acadia National Park, and the L.L. Bean Acadia Research Fellowship Program run by the Friends of Acadia. This is Maine Agricultural and Forestry Experiment Station journal article no. 3245.

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Received 18 February 2011; accepted 17 October 2011.
