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ORIGINAL PAPER

Invasive Argentine ants reduce fitness of red maple via a mutualism with an endemic coccid

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Abstract Many invasive ant species form mutualisms with honeydew-producing Hemiptera and their aggressive presence deters the natural enemies of the Hemiptera. Invasive ant species like the Argentine ant have often been associated with hemipteran outbreaks in urban, agricultural and natural ecosystems. We investigated the effects of a mutualism between the invasive Argentine ant and the endemic terrapin scale on coccid density and the fitness of the host of this mutualism, the endemic red maple, situated in a commercial park. The terrapin scale has numerous natural enemies and we predicted that the high terrapin scale numbers associated with tending Argentine ants would collapse once Argentine ants were excluded from the host tree canopy. We predicted that excluding the Argentine ant from the tree canopy would result in an indirect net fitness benefit to the host. Terrapin scale numbers collapsed when Argentine ants were excluded from the host tree canopy. Red maples with Argentine ants excluded from their canopy had higher seed mass and larger early leaves indicating that this invasive ant-endemic scale mutualism imposed a net fitness cost to the host tree. The Argentine ant has yet to invade closed-canopy forest within its introduced range. The red maple is common in adjacent closed-canopy forest fragments and recent work has shown that invasion of these forest fragments by the Argentine ant is limited by a steady carbohydrate resource. We discuss the implications to forest invasion posed by a mutualism involving the Argentine ant and an endemic coccid.

Keywords Coccidae · Host fitness · Invasion · *Linepithema humile* · *Mesolecanium nigrofasciatum* · Mutualism

Introduction

The role of mutualisms in structuring ecosystems has received growing recognition in recent decades (Bronstein 1994; Bruno et al. 2003). Mutualisms involving ants and Hemiptera have been described as keystone interactions due to their extraordinary influence over the structure of a community (Eubanks and Strysky 2006). Ants provide their hemipteran partners protection from natural enemies in exchange for the carbohydrate resource honeydew, often resulting in significant increases in hemipteran abundance (Buckley 1987; Way 1963). Ant-hemipteran mutualisms exert detrimental influence on the host plant through sap removal, tissue damage and increased risk from a variety of pathogens (Buckley 1987). In some instances, however, they may confer an indirect benefit to the host plant through deterrence of non-sapsucking herbivores (Strysky and Eubanks 2007).

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Tending of honeydew-producing Hemiptera by invasive ant species usually results in an increase in hemipteran densities (Abbott and Green 2007; Altfield and Stiling 2006; Coppler et al. 2007; Daane et al. 2007; Ness and Bronstein 2004). This small suite of invasive ants has affected the abundances and species diversity of vertebrates, invertebrates and plants and are capable of disrupting whole ecosystems (reviewed in Holway et al. 2002). Invasive ant-hemipteran mutualisms have been shown to exert both positive and negative fitness effects on the host. Studies demonstrating indirect benefits center on the suppression of a particularly destructive herbivore by the aggressive invasive ant (e.g. Altfield and Stiling 2009; Kaplan and Eubanks 2005). Negative effects to the host include pollination disruption (e.g. Blancafort and Gomez 2005; Lach 2007), seed dispersal disruption (e.g. Bond and Slingsby 1984; Rowles and O'Dowd 2009b), and forest canopy die-back (Hill et al. 2003; O'Dowd et al. 2003).

The Argentine ant, *Linepithema humile*, is among the most widespread of invasive ants and is now found on six continents and many oceanic islands (Suarez et al. 2001). *Linepithema humile* has been consistently linked to outbreaks in honeydew-producing Hemiptera (Bartlett 1961; Buckley 1987; Daane et al. 2007; Lach 2003; Ness and Bronstein 2004; Way 1963) This ant is capable of invading open canopy woodland habitat in many parts of the world (Bond and Slingsby 1984; Espadaler and Gomez 2003; Rowles and O'Dowd 2007; Ward 1987), the degree of penetration usually limited by proximity to water (Menke and Holway 2006; Ward 1987). *Linepithema humile* have been unable to penetrate closed canopy forests in its introduced range (Ward and Harris 2005), possibly because these forests lack a readily available stable carbohydrate resource (Rowles and Silverman 2009).

We examined the effects on the hemipteran partner, and host tree, of an invasive ant-endemic coccid mutualism involving *L. humile*. This study was conducted in a commercial business park located outside Raleigh, North Carolina, USA with *L. humile* tending infestations of the endemic terrapin scale, *Mesolecanium nigrofasciatum*, on the endemic red maple host, *Acer rubrum*. *Mesolecanium nigrofasciatum* is widely distributed in eastern North America with an immature crawling stage that is readily transported by ballooning or avian mediated transport (Simanton 1916). *Acer rubrum* is one of the most abundant trees in eastern North America, (Walters and Yawney 1990). Most published studies investigating indirect effects of ant mutualisms on woody hosts have concluded net benefits, perhaps because these were considered more noteworthy (Strysky and Eubanks 2007). However, *A. rubrum* typically experience low levels of foliar herbivory (Seastedt et al. 1983). We hypothesized, therefore, that the presence of *L. humile* in the canopy of *A. rubrum* contributed to the high numbers of *M. nigrofasciatum* seen in infested *A. rubrum* and that this interaction negatively affected host fitness.

The extensive range and ready portability of *M. nigrofasciatum* makes its presence or eventual arrival likely in forest fragments bounding *L. humile* infestations along the southeastern United States. Pine-hardwood forest fragments surround this commercial park, as is common in North Carolina urban environments, with *A. rubrum* well represented in these forest fragments (Rowles and Silverman 2009). This invasive ant-endemic hemipteran mutualism has the potential to provide a mechanism for *L. humile* to expand its range to include closed canopy forest fragments in North Carolina.

Methods

The commercial park contains a contiguous infestation of *L. humile*, present for the last 10–20 years, and now covers approximately 42 Ha. The site has extensive ornamental plantings including a considerable number of mature *A. rubrum* planted at the development of the park. All of the ornamental plantings within the commercial park were subjected to the same management regime, which included pine needle mulching, yearly fertilizing and a regular irrigation regime. All ornamental plantings were subjected to a standard watering regime through an underground irrigation system.

Effect of Argentine ant presence on terrapin scale numbers

We had observed that many of the *A. rubrum* located within the *L. humile* infestation were infested with *M. nigrofasciatum*. However, those *A. rubrum* located outside of the *L. humile* infestation showed no sign of *M. nigrofasciatum*. We undertook a survey of the 18 *A. rubrum* that were situated outside of the *L. humile* infestation within the commercial park. On these 18 trees, we carried out an extensive search for *M. nigrofasciatum* in mid-July 2005 when females had settled on new growth stems (Simanton 1916) and we noted any ant species observed foraging on the tree.

Within the *L. humile* infestation, ten *M. nigrofasciatum*-infested *A. rubrum* trees were selected to determine the effect of *L. humile* presence on *M. nigrofasciatum* numbers. An initial count of *M. nigrofasciatum* and foraging *L. humile* was undertaken in late July 2005 on four selected branches on the 10 trees. This count was recorded as week one. Two of the branches were randomly allocated as treatment branches, treatment being a wide band of duct tape covered with Tanglefoot® (Tanglefoot Company, Grand Rapids, Michigan, USA) applied as close to the trunk of the tree as practicable to exclude *L. humile* from the *M. nigrofasciatum*. These branches were three to four meters in length with the coccids settling approximately 500 mm from the stem tip. Initial coccid counts per branch ranged from 35 to 444 individuals. Weekly counts of *M. nigrofasciatum* and *L. humile* were conducted on these trees until week 10 and then fortnightly to week 18. Counts of *L. humile* were taken just trunk side of the *M. nigrofasciatum* infestation with workers travelling both to and from the infestation included. Ant excluded branches were checked weekly for barrier failure and Tanglefoot® reapplied as necessary. Data was tested using PROC MIXED repeated measures ANOVA, with barrier treatment as the between-subjects variable and time as the within-subjects variable, and was performed using SAS v.9.1.3 (SAS 2002).

Effect of Argentine ant canopy foraging on red maple fitness

Nineteen *A. rubrum* trees were selected for *L. humile* exclusion with nineteen more *A. rubrum* allocated as controls. Treatment consisted of an ant exclusion band on the treatment trees at breast height with Tanglefoot® over the summer for two consecutive years. Ant exclusion banding began in early August 2006 and maintained until leaf drop in November with Tanglefoot® banding reapplied twice weekly to prevent *L. humile* from gaining access to the treatment tree canopy. Ant exclusion on the treatment trees were repeated over the same months in 2007 with a similar maintenance schedule (Brightwell and Silverman 2009). Seeds were collected in mid-April shortly before seed drop (Walters and Yawney 1990). Samaras (winged fruit) were collected by running a closed fist down samara-bearing branches reachable from the ground. The samaras from each tree were placed in a paper bag and dried in an oven (60°C) for 7 days. Only those trees from which 100 or more seeds were collected were included in the analysis to control for any unanticipated local abiotic effects on individual *A. rubrum* fitness. We randomly selected nine ant excluded and nine control trees bags. From each bag, 40 samaras were randomly selected and the dried seed excised from the samara. Each seed was weighed on a Cahn C27 Electrobalance (Cahn Instruments Inc. Cerritos California, U.S.A.).

Early leaves were collected in late April when the first leaves emerge. Early leaf growth in *A. rubrum* consists of two to three early, or preformed, pairs of leaves emerging from the dormant budscale formed the previous autumn (Critchfield 1971). Larger early leaves the following spring indicate more resources allocated to the dormant buds (Critchfield 1971). The two or three pairs of early leaves were collected from the individual twigs of reachable branches; ensuring leaves were collected from all points of the tree. In all, 1494 leaves from the 18 selected *A. rubrum* trees were measured. A proximate measure of leaf size was determined by measuring the distance between the tips of the outer lobes of the leaf. Some of the smallest leaves were not sufficiently developed to distinguish the outer lobes and in this case all leaves from the twig were discarded. Gottschalk (1994) demonstrated that shading could significantly decrease average *A. rubrum* leaf size. The trees selected for this experiment were all situated so that they received full sun. Leaf width and seed weight data were tested using PROC GLM ANOVA, and was performed using SAS v 9.1.3 (SAS 2002).

Results

Our survey of 18 *A. rubrum* trees outside of the *L. humile* infestation found no evidence of *M. nigrofasciatum*. We observed a number of ant species on these trees. These were the native *Tapinoma sessile* along with *Formica*, *Forelius* and *Crematogaster* species. The invasive *Solenopsis invicta* was also observed on two of the 18 trees.

There was a reduction in *M. nigrofasciatum* abundance on the treatment branches compared to the control branches once *L. humile* was excluded with *M. nigrofasciatum* numbers being reduced to virtually zero on the treated branches ($F_{1,38} = 29.25$, $P < 0.0001$; Fig. 1). The exclusion treatment was effective in reducing *L. humile* foraging with *L. humile* presence on exclusion treatment branches reduced to near zero once the banding was applied ($F_{1,18} = 32.42$, $P < 0.0001$; Fig. 1).

The mean dried seed mass from the exclusion treatment trees was heavier than the mean dried seed mass from the unbanded control trees ($F_{5,12} = 6.03$, $P = 0.0051$; Fig. 2) as would be expected where more resources allocated to each seed produced on those *A. rubrum* where *L. humile* was excluded from the canopy than in the control trees. Likewise, leaves from the exclusion treatment trees were wider than those from the unbanded control trees ($F_{5,12} = 5.48$, $P = 0.0075$; Fig. 2). This indicates that *A. rubrum* leaf bud was earlier and/or leaf growth was stronger in those trees where *L. hum*ile was denied access to the canopy.

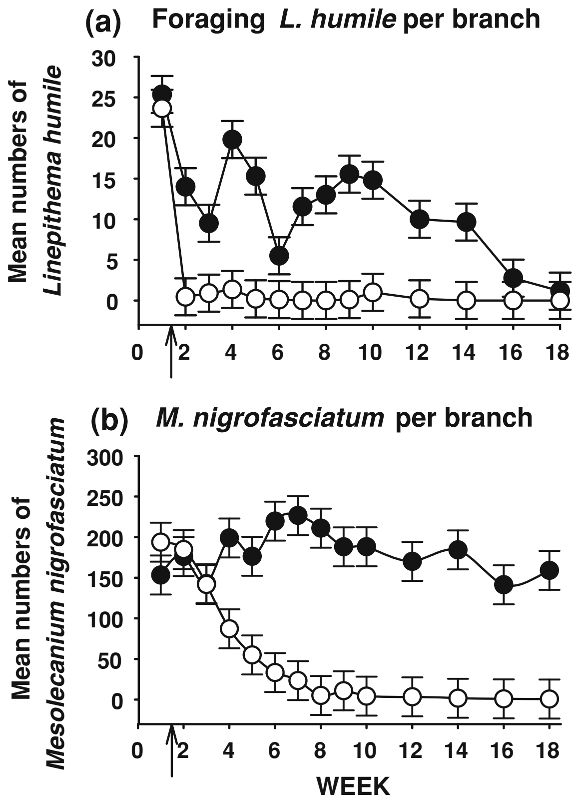

Fig. 1 Mean (± SE) numbers of **a** *L. humile* foraging per branch and **b** *M. nigrofasciatum* per branch of *A. rubrum* trees with branch access permitted or denied to foraging *L. humile*. *Filled circle* indicates *L. humile* permitted to forage on branches. *Open circle* indicates *L. humile* excluded from branches. *Arrow* indicates day when Tanglefoot® banding was applied to treatment

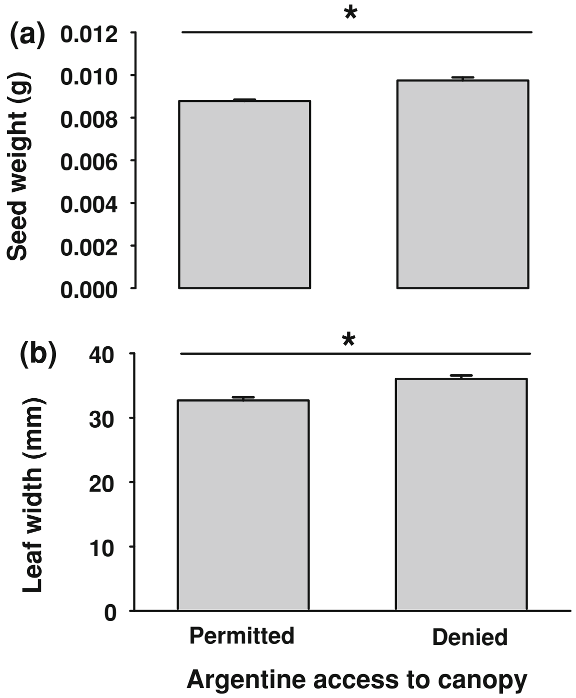

Fig. 2 Effects on *A. rubrum* fitness the following spring when *L. humile* canopy foraging was permitted or denied. **a** Mean (± SE) dried seed weight. **b** Mean (± SE) leaf width. Wider leaf width infers earlier leaf bud and/or faster leaf growth. *Asterisk* indicates significant difference between treatments by general linear model: * < 0.05

Discussion

Mesolecanium nigrofasciatum was only found on those *A. rubrum* trees with *L. humile* foraging in the canopy. The presence of *L. humile* encouraged high densities of *M. nigrofasciatum* on *A. rubrum*, with *M. nigrofasciatum* populations collapsing when *L. humile* was excluded. Our two proximate measures of host fitness increased when *L. humile* was excluded from tree canopies, with heavier dried seed mass seen in the following spring along with larger early leaves indicating more resources stored in the dormant buds.

To date, *L. humile* has been confined to small patches in urban settings in North Carolina (Buczkowski et al. 2004). As previously mentioned, many urban areas within this region have forest fragments abutting their boundaries with *A. rubrum* a common trees species within these natural habitats. The wide distribution of *M. nigrofasciatum* suggests that the successful establishment of *L. humile* within these natural habitats, facilitated by a mutualism with *M. nigrofasciatum*, increases with the length of time an urban *L. humile* infestation abuts the forest fragment. The presence of *L. humile* can alter non-ant arthropod abundances and diversity (Bolger et al. 2000; Cole et al. 1992; Human and Gordon 1997; Walters 2006), although this is not universal (Holway 1998; Rowles and O'Dowd 2009a). The presence of *L. humile* almost always negatively affects local ant diversity and abundance in its introduced range (Holway et al. 2002; Lach 2007; Oliveras et al. 2005; Rowles and O'Dowd 2007; Sanders et al. 2003). Rowles and Silverman (2009) found over 20 species of ants when they surveyed these forest fragments. If *L. humile* does establish in forest fragments the inevitable loss of native ant species will lead to changes in ecosystem processes including seed dispersal and soil turnover.

We found that the mutualism between *L. humile* and *M. nigrofasciatum* resulted in an indirect fitness cost to the host *A. rubrum*. The positive effects on seed mass and early leaf size seen when *L. humile* was excluded from the tree canopy were small but quantifiable with just 2 years exclusion. *Acer rubrum* can live to 150 years (Walters and Yawney 1990). A mutualism such as we describe could exert considerable injury over the lifetime of the host. *Mesolecanium nigrofasciatum* has more than 30 known host plants including *Acer, Betula, Plantanus, Prunus* and *Quercus* species amongst others (Simanton 1916; Williams and Kosztarab 1972). Invasive ant-invasive hemipteran mutualisms have led to negative effects on forest systems including reduced foliage cover, smaller leaf size in the Seychelles and canopy dieback on Christmas Island (Hill et al. 2003; O'Dowd et al. 2003). An invasive ant-endemic hemipteran mutualism such as ours may lead to potential long-term detrimental fitness effects similar to those listed above.

We chose to measure dried seed weight and early leaf width as proximate measures of tree fitness. Dried seed mass minus any dispersal structures has been recommended as the best and easiest method of seed measurement (Westoby 1998), with larger seeds producing seedlings better able to survive a variety of seedling hazards (Westoby et al. 1996). We chose leaf width as a proxy for leaf area as leaf width has proven a good indirect measurement for leaf area (Tsialtas and Maslaris 2005; Williams and Martinson 2003). We believe early leaf size reflects plant fitness as early leaves are formed in the dormant buds the previous autumn (Critchfield 1971; Kikuzawa 1983). Larger early leaves the following spring indicate more resources allocated to the dormant buds. Foliar herbivory can induce a compensatory response from plants (reviewed in Trumble et al. 1993). It is possible that host *A. rubrum* allocated more resources to dormant buds and seed production in response to a possible decrease in fitness after the exclusion of *L. humile* from their canopies. We did not quantify defoliating herbivore abundance and, therefore, cannot rule out this possibility. *Acer rubrum* usually experiences low levels of foliar herbivory as it invests heavily in chemical defenses to deter defoliating arthropod and mammalian herbivores (Abou-Zaid et al. 2001; Loughrin et al. 1997; Müller-Schwarze et al. 1994).

Our 2005 survey of *A. rubrum* outside of the *L. humile* infestation found no *M. nigrofasciatum* even though these trees were within crawler ballooning distance. This prevented any comparison of indirect host plant effects from mutualisms between *M. nigrofasciatum* and *L. humile* and native ants. *Mesolecanium nigrofasciatum* is subject to predation from a multitude of natural enemies (Simanton 1916; Williams and Kosztarab 1972) with very high rates of parasitism reported in North Carolina (Devorshak 1994; Meyer et al. 2001). *Mesolecanium nigrofasciatum* is known to produce copious quantities of honeydew which it can expel to a distance of 200 mm (Simanton 1916). This method of honeydew excretion and the results of our survey of *A. rubrum* outside of the *L. humile* infestation suggest that *M. nigrofasciatum* does not reach high densities in association with native ant mutualisms. However, *M. nigrofasciatum* is capable of reaching high densities in association with *L. humile*.

Linepithema humile has had great difficulty in penetrating closed canopy forests within its introduced range. As previously mentioned, invasion by *L. humile* of forest fragments in the southeastern United States is limited by the absence of a stable carbohydrate resource. An invasive ant mutualism situated at the forest edge, involving an endemic coccid partner on a host already abundant within the forest fragments, may provide the limiting resource and a potential mechanism for invasion. Such an invasion poses a dual threat to the forest habitat. The presence of *L humile* will lead to the exclusion of native ants and consequent disruption of ecosystem processes. The associated coccid outbreak may lead to a significant increase in stress on a number of tree species and a decline in the health of these natural habitats.

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