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Host Utilization of Chinese Privet (Lamiales: Oleaceae) and Host Choice by *Leptoypha mutica* (Hemiptera: Tingidae)[1]

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Abstract Exotic lace bugs (Hemiptera: Tingidae) have previously been evaluated for potential biocontrol of pervasive, exotic Chinese privet, *Ligustrum sinense* Lour. This study was conducted to determine if a native lace bug, *Leptoypha mutica* Say, could utilize Chinese privet and to determine the lace bug's preferred host plant. A no-choice test determined the lace bug's acceptance and utilization of three plant hosts: fringe tree (*Chionanthus virginicus* L.), swamp privet (*Foresteria acuminata* Michx), and Chinese privet, based on frass production, oviposition, and survival of lace bugs. Choice tests in the laboratory and the field evaluated lace bug preference among swamp privet, Chinese privet, and green ash (*Fraxinus pennsylvanica* Marsh). All plant hosts supported the lace bugs in laboratory assays, but fewer eggs were produced on Chinese privet. Green ash was the most preferred while Chinese and swamp privet were equally preferred. These laboratory results were consistent with a field choice test and field observations. Chinese privet is a suitable host for *Le. mutica*, but not an optimal host, suggesting that host switching to *Li. sinense* by this lace bug is unlikely.

Key Words *Leptoypha mutica*, *Ligustrum sinense*, Chinese privet, biological control, host study

Chinese privet *Ligustrum sinense* Lour (Oleaceae), has become widespread in the southeastern United States and is now found on approximately 7.1 million ha and densely covering approximately 1 million ha of that area (Miller et al. 2008, Rudis et al. 2006). Chinese privet's success can be attributed to its aggressive adaptability to a range of environments and habitats (Brown and Pezeshki 2000). In addition, Chinese privet is characterized by a high growth rate, vegetative reproduction, and prolific seed production (Langeland and Burkes 1998). Once it is established, privet becomes very difficult to remove, and large-scale control requires extensive labor and the use of herbicides (Hanula et al. 2009). Chinese privet depletes native plant biodiversity, decreasing invertebrate communities and causing toxicosis in animals (Biesmeijer et al. 2006, Crisp et al. 1998, Kerr et al. 1999; Morris et al. 2002). Chinese privet is a major concern for forest ecosystems in Georgia (The Nature Conservancy 2004), and the Florida Exotic Pest Plant Council Invasive Plant Lists (1996) listed it as a Category 1 invasive species.

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The spread of Chinese privet has impending consequences, and it is evident that control needs to be implemented. One method may be through using lace bugs (Hemiptera: Tingidae) as a classical biological control agent (Zhang et al. 2011, 2013, 2016). Although biocontrol is favored because it is considered to be environmentally safe and economically favorable, safety regulations have become increasingly stringent for prerelease of organisms because of risks associated with introduced biocontrol agents on nontarget organisms and biodiversity (Simberloff and Stiling 1996). Tingids are useful for biological control because of their typical host specificity (Drake and Ruhoff 1965). However, lace bug host specificity sometimes extends to other members of a genus or plant family. For example, the azalea lace bug, *Stephanitis pyrioides* Scott, primarily feeds on plants in the family Ericaceae, but there are limited reports of *S. pyrioides* extending feeding to different plant families (Nair and Braman 2012). To insure relative host specificity and evaluate risks on nontarget organisims, host-specificity tests are performed on candidates for biocontrol (Schroeder and Goeden 1986).

One candidate is *Leptoypha hospita* Drake et Poor (Hemiptera: Tingidae), found in China feeding on Chinese privet and causing plant dieback (Zhang et al. 2008). The potential of *Le. hospita* prompted our study of a native, congeneric lace bug species that currently utilizes swamp privet (Oleaceae), *Foresteria acuminata* Michx, but does not use Chinese privet as a host (Mead 1975). Swamp privet is similar to Chinese privet in size, growth habit, and habitat but differs in that it is deciduous (Johnson and Hoagland 1999; Krüssmann 1986). Much like Chinese privet, it is found in swamps, wetlands, riparian forests, and around ponds and lakes in the southeastern United States (Johnson and Hoagland 1999). Lace bug species *Leptoypha ilicis* Drake, *Leptoypha elliptica* Mcatee (Wheeler 2002), and *Le. mutica* Say (Mead 1975) all utilize swamp privet as a host. *Leptoypha mutica* was the most-commonly collected species in our area and became the focus of our studies. The fringe tree, *Chionanthus virginicus* L., and green ash, *Fraxinus pennsylvanica* Marsh, both in the family Oleaceae, tribe Oleeae, are also reported hosts of *Le. mutica* (Drake 1918). The similarities between these Oleaceae plant species suggest potential for the native *Leptoypha* spp. to utilize the nonnative Chinese privet. Response of native insects to invasive plants varies greatly (Bezemer et al. 2014, Castells et al. 2014). A better understanding of *Leptoypha* spp. and their plant host selection will aid in understanding how exotic plants interact with native herbivores and in selection of future candidates for biocontrol of invasive weeds.

Materials and Methods

Collection and rearing methods. A population of lace bugs was collected on 13 July and 19 August 2011 from the Montezuma Bluff Wildlife Management Area, Montezuma, GA (Macon Co., N 32°20.274′, W 084°1.2245′) from native swamp privet and green ash using beat sheets and aspirators. Dense forest bounded by a river characterizes this sometimes swampy area. A second population of lace bugs was collected in July 2011 from an established fringe tree in Spalding Co., GA (N 33°11.6638′, W 084°8.7993′).

Lace bugs were reared at the University of Georgia Griffin Campus in Griffin, GA (Spalding Co., N 33°15.6353′, W 084°16.8139′) with the two lace bug populations being kept separate. They were placed in plastic friction-fitting petri dishes (17.8 cm diameter × 7.6 cm height) on small branches of swamp privet with the cut ends wrapped in moist paper towels. The lace bugs were maintained on a 14:10 (L:D) photoperiod at approximately 23°C.

Lace bugs were also continuously reared on Chinese privet in a greenhouse in 1-m^3 cages constructed of PVC pipe frames and covered in 32-mesh screen. Containerized privet was added as needed to the cages. Initiated with five male and five female lace bugs per cage on 14 December 2011, the populations were assessed on 29 March 2012.

No-choice test. A no-choice study was conducted between 21 October and 15 November 2011 to determine acceptance and utilization of Chinese privet by the two lace bug populations. Lace bugs were added to 30 containers consisting of plastic Petri dishes with friction-fitting lids (17.8 cm diameter × 7.6 cm height) to which four lace bugs were added per container (five male and five female). Each container had either a fringe tree leaf, a 10-cm clipping of new growth from swamp privet, or a 10-cm clipping from Chinese privet. Each clipping or leaf had moist paper towels placed around their stems to maintain moisture. There were 10 containers of each of the three plant species. There were five replications of Population 1 lace bugs, collected from fringe tree (Spalding Co.) and five replications of Population 2 lace bugs collected from swamp privet (Macon Co). Experiments were conducted in a Percival growth chamber (Model: I-36VL, Percival Scientific, INC., Perry, IA) at the University of Georgia Griffin campus set at a temperature of 27°C (±0.5°) and a 14:10 (L:D) photoperiod. Containers were then placed randomly within the growth chambers.

Water was added to the paper towel as needed every 2 to 3 days to keep the plants hydrated. Plant material that turned brown or desiccated was replaced with fresh cuttings or leaves. The old plant material was placed in a small Petri dish and labeled accordingly. At the end of the 25 d, each dish was examined and the frass spots (upper leaf/lower leaf), eggs, and live bugs were recorded.

Laboratory choice tests. Lace bug preference and the extent of damage to Chinese privet and swamp privet were evaluated in two separate laboratory choice trials (combined in analysis) consisting of 24 replications each. Three additional trials (combined in analysis) comparing their choice among three plant species: Chinese privet, swamp privet, and green ash, were conducted and also replicated 24 times each. All trials were conducted in Percival growth chambers at 24 ± 0.5°C and 14:10 (L:D) photoperiod from 19 June to 2 August 2012. Plant species were arranged like spokes of a wheel in the same type of containers previously described. A single lace bug was placed in the middle of each petri dish (not on plants) containing the plant species of interest. Twenty-four total lace bugs were used in each trial with 12 (6 female and 6 male) being from Population 1 lace bugs and 12 (6 female and 6 male) being from Population 2 lace bugs.

The containers were then randomly placed in growth chambers. The stems of each cutting were wrapped in paper towels and kept moist daily. Data were collected daily and included the location of the lace bug and damage to plants on a scale of 1–10 (1 being least damaged). Trials 1 and 2 were 3-d evaluations and trials 3, 4 and 5 were 7-d evaluations.

Field choice test. This experiment took place at the University of Georgia Griffin Campus in May 2013. Five (6 × 6 × 6 ft, 20 × 20 mesh) Bioquip mesh Lumite portable field cages (Model 1406B, Bioquip Products Inc., Rancho Dominguez, CA) were set up in a shaded area under a pecan grove in a randomized block design. Three different potted host plants were used as treatments: Chinese privet, swamp privet, and green ash. One of each host plant was randomly placed inside each cage. Fourteen male and 14 female *L. mutica* that had been reared on fringe tree leaves were added to each cage by placing them in small Petri dishes on top of ≈0.3-m-tall boxes to discourage predation by any ground predators. Test plants were arranged so they were equidistant from the release point and each other. For 7 d at approx. 3:30 p.m., plants were examined to determine the location of the lace bugs, and the extent of feeding damage was estimated on each using a scale of 1–10 (1 = least damaged).

Statistical analysis. *No-choice test*. Data from the no-choice test were subjected to analysis of variance (ANOVA) using the general linear model (GLM) procedure, and means were separated with Fisher's protected least significant difference (LSD) (SAS Institute 2010). Data from the laboratory choice tests were also subjected to ANOVA using the GLM procedure, and means were separated with Fisher's protected LSD test. Effects of gender and population were compared for plant choice and damage with Trials 1 and 2 and Trials 3, 4, and 5 combined for analysis (SAS Institute 2010). Data from the field choice test were also subjected to ANOVA using the GLM procedure and means were separated with Fisher's protected LSD test (SAS Institute 2010).

Results

Collection and rearing methods. Lace bugs collected from the Montezuma Bluff Wildlife Management Area (Macon Co.) were more abundant and higher in the canopy in July than in August. The lace bugs were found primarily feeding on the upper surface of swamp privet and green ash. When lace bugs were reared only on Chinese privet, from 14 December 2011 to 29 March 2012 there were over 100 adults per cage, a 10-fold increase (J.K. unpubl.). The lace bugs have the potential to utilize Chinese privet and can be kept in continuous colony on privet, but we did not observe significant infestations in the field on Chinese privet.

No-choice test. Frass, an indication of feeding, on the upper ($F_{1,22} = 0.00$, $P = 0.957$) and lower ($F_{1,22} = 0.24$, $P = 0.628$) surfaces of the leaves and combined surfaces ($F_{1,22} = 0.13$, $P = 0.71$), was similar for both populations (Table 1). Lace bugs collected from fringe tree (Population 1) produced 4 times as many eggs as those collected from swamp privet (Population 2) ($F_{1,22} = 6.32$, $P = 0.02$, Table 1). Lace bugs collected from fringe tree (Population 1) had a higher survival rate than lace bugs collected from swamp privet (Population 2), living over 1.5 weeks longer, which could have contributed to the increased egg production ($F_{1,22} = 4.95$, $P = 0.037$).

Frass abundance was highest on the upper leaf surface of Chinese privet followed by swamp privet then fringe tree ($F_{2,22} = 17.31$, $P < 0.0001$; Table 2). In contrast, frass on the lower leaf surface did not differ among plant hosts ($F_{2,22} = 0.65$, $P = 0.530$). When surfaces were combined there was no difference in amount of frass among plant hosts ($F_{2,22} = 1.33$, $P = 0.285$). *Leptoypha mutica* laid more eggs on swamp privet than on Chinese privet but not on fringe tree ($F_{2,22} = 3.92$, $P =$

Table 1. Mean (±SE) number of *Le. mutica* frass spots on upper, lower, and combined leaf surfaces, eggs laid, and survival of lace bug from two populations during no-choice laboratory assays in which they were limited to one of three hosts.*

Population	Frass (upper)	Frass (lower)	Frass (combo)	Eggs	Survival
1**	100.13 ± 16.9 A	122.27 ± 26.0 A	222.40 ± 27.2 A	8.87 ± 2.8 A	3.53 ± 0.2 A
2**	101.00 ± 15.9 A	107.07 ± 14.9 A	208.07 ± 26.5 A	2.20 ± 0.8 B	2.87 ± 0.3 B

* Means in the in the same column bearing the same letters are not significantly different ($\alpha = 0.05$); Numbers are the means for all three hosts combined.
** Population 1 = fringe tree lace bug, Population 2 = swamp privet lace bug.

Table 2. Mean (±SE) number of *Le. mutica* frass spots on upper, lower, and combined leaf surfaces, eggs laid, and survival of lace bugs on three hosts during no-choice laboratory assays in which they were limited to one of three hosts.*

Plant host	Frass (upper)	Frass (lower)	Frass (combo)	Eggs	Survival
Fringe tree	44.90 ± 7.90 C	139.20 ± 33.8 A	184.10 ± 34.0 A	4.80 ± 2.1 AB	2.80 ± 0.3 A
Swamp privet	95.70 ± 15.6 B	106.70 ± 17.8 A	202.40 ± 30.3 A	10.40 ± 3.8 A	3.20 ± 0.3 A
Chinese privet	161.1 ± 14.4 A	98.10 ± 23.5 A	259.20 ± 31.0 A	1.40 ± 0.5 B	3.60 ± 0.2 A

* Means in the in the same column bearing same letter are not significantly different ($\alpha = 0.05$).

0.035). Lace bug survival was similar on all three host plants ($F_{2,22}$ = 2.38, P = 0.116).

Significantly more frass was deposited on the upper leaf surface of Chinese privet than either fringe tree or swamp privet for bugs collected from fringe tree (Population 1) ($F_{2,8}$ = 17.59, P = 0.0012; Table 3), but there were no differences in frass on the lower leaf surface or when upper and lower frass were combined ($F_{2,8}$ = 2.25, P = 0.168; $F_{2,8}$ = 1.71, P = 0.241, respectively). Lace bugs collected from swamp privet (Population 2) deposited significantly more frass on upper leaf surfaces of swamp privet and Chinese privet than on fringe tree while frass deposits on the lower leaf surfaces were the same among hosts ($F_{2,8}$ = 11.56, P = 0.004; $F_{2,8}$ = 0.55, P = 0.598). Upper/lower frass combined was similar among plant hosts ($F_{2,8}$ = 4.78, P = 0.050).

Lace bugs from fringe tree (Population 1) deposited more eggs on swamp privet than on either fringe tree or Chinese privet despite equal survival on all hosts ($F_{2,8}$ = 9.37, P = 0.008; $F_{2,8}$ = 1.56, P = 0.2687; Table 3). Egg production and survival were not significantly different among any of the hosts for lace bugs collected from swamp privet (Population 2) ($F_{2,8}$ = 0.67, P = 0.539; $F_{2,8}$ = 1.07, P = 0.387).

When fringe tree was the host plant, no differences in the amount of frass on the upper leaf surface, lower leaf surface, upper/lower frass combined, or survival were observed between populations ($F_{1,4}$ = 2.80, P = 0.169; $F_{1,4}$ = 2.69, P = 0.176; $F_{1,4}$ = 2.80, P = 0.169; $F_{1,4}$ = 2.67, P = 0.178; Table 4). Likewise, both populations performed similarly on swamp privet, with no differences in the amount of frass on the upper leaf surface, lower leaf surface, upper and lower frass combined, or survival ($F_{1,4}$ = 5.21, P = 0.085; $F_{1,4}$ = 1.90, P = 0.241; $F_{1,4}$ = 7.12, P = 0.056; $F_{1,4}$ = 1.45, P = 0.294). Egg production, however, was significantly greater in Population 1 lace bugs collected from fringe tree than in Population 2 lace bugs, which were originally collected from swamp privet ($F_{1,4}$ = 12.82, P = 0.023). Lace bugs from both populations had similar levels of frass on upper leaf surfaces ($F_{1,4}$ = 0.68, P = 0.457), lower leaf surfaces ($F_{1,4}$ = 0.22, P = 0.665), and upper/lower frass combined ($F_{1,4}$ = 0.00, P = 0.973) on Chinese privet and they laid equal numbers of eggs ($F_{1,4}$ = 0.00, P = 1.00) and survived equally well ($F_{1,4}$ = 2.67, P = 0.178).

Laboratory choice tests. *Trials 1 and 2*. Lace bugs were observed most frequently on the Petri dish container (n = 144 observations), and were found in equal numbers on Chinese and swamp privet ($F_{2,137}$ = 3.90, P = 0.023; Table 5), which was reflected in feeding damage scores that did not differ between the two hosts Chinese privet and swamp privet ($F_{1,90}$ = 0.04, P = 0.842). Lace bug population source ($F_{2,137}$ = 0.12, P = 0.735) and gender ($F_{2,137}$ = 0.03, P = 0.865) had no effect on location on plant or container, or on damage (population $F_{1,90}$ = 0.20, P = 0.660; gender $F_{1,90}$ = 2.74, P = 0.102).

Trials 3–5. Lace bugs were found most often on green ash and were found similarly among swamp privet, Chinese privet, or the cage ($F_{3,279}$ = 36.28, P < 0.0001; Table 5). Feeding damage was highest on green ash and swamp privet followed by Chinese privet ($F_{2,208}$ = 6.81, P = 0.001). Neither population nor gender affected lace bug location (population $F_{1,279}$ = 1.88, P = 0.172; gender $F_{1,279}$ = 2.04, P = 0.154) or damage (population $F_{1,208}$ = 0.07, P = 0.785; gender $F_{1,208}$ = 0.28, P = 0.595).

Field studies for host plant suitability—choice test. The field choice test confirmed laboratory results. Lace bugs were observed most frequently on green

Table 3. Mean (±SE) number of *Le. mutica* frass spots on upper, lower, and combined leaf surfaces, eggs laid, and survival of lace bugs from two populations during no-choice laboratory assays in which they were limited to one of three hosts.*

Plant host	Frass (upper)	Frass (lower)	Frass (Combo)	Eggs	Survival
Population 1**					
Fringe tree	56.40 ± 12.2 B	192.20 ± 60.2 A	248.60 ± 23.9 A	6.00 ± 3.7 B	3.20 ± 0.4 A
Swamp privet	68.60 ± 7.20 B	89.20 ± 27.5 A	157.80 ± 13.2 A	19.20 ± 5.0 A	3.60 ± 0.2 A
Chinese privet	175.40 ± 26.0 A	85.40 ± 29.7 A	260.80 ± 22.2 A	1.40 ± 0.6 B	3.80 ± 0.2 A
Population 2**					
Fringe tree	33.40 ± 8.00 B	86.20 ± 10.2 A	119.60 ± 7.41 A	3.60 ± 2.2 A	2.40 ± 0.6 A
Swamp privet	122.80 ± 26.1 A	124.20 ± 22.6 A	247.00 ± 21.3 A	1.60 ± 0.5 A	2.80 ± 0.5 A
Chinese privet	146.80 ± 12.6 A	110.80 ± 39.1 A	257.60 ± 19.3 A	1.40 ± 0.9 A	3.40 ± 0.2 A

* Means within populations and in the in the same column bearing the same letter are not significantly different ($\alpha = 0.05$).
** Population 1 = fringe tree lace bug, Population 2 = swamp privet lace bug.

Table 4. Mean (±SE) number of *Le. mutica* frass spots on upper, lower, and combined leaf surfaces, eggs laid, and survival of lace bugs from two populations during no-choice laboratory assays in which they were limited to one of three hosts.*

Population	Frass (upper)	Frass (lower)	Frass (combo)	Eggs	Survival
Fringe tree					
1**	56.40 ± 12.2 A	192.20 ± 60.2 A	248.60 ± 23.9 A	6.00 ± 3.7 A	3.20 ± 0.4 A
2**	33.40 ± 8.0 A	86.2 0 ± 10.2 A	119.60 ± 7.42 A	3.60 ± 2.2 A	2.40 ± 0.6 A
Swamp privet					
1**	68.60 ± 7.2 A	89.20 ± 27.5 A	157.80 ± 13.2 A	19.2 ± 5.0 A	3.60 ± 0.2 A
2**	122.80 ± 26.1 A	124.20 ± 22.6 A	247.00 ± 21.3 A	1.60 ± 0.5 B	2.80 ± 0.5 A
Chinese privet					
1**	175.40 ± 26.0 A	85.40 ± 29.7 A	260.80 ± 22.2 A	1.40 ± 0.6 A	3.80 ± 0.2 A
2**	146.80 ± 12.6 A	110.80 ± 39.1 A	257.60 ± 19.3 A	1.40 ± 0.9 A	3.40 ± 0.2 A

* Means for populations in the same column and the same host bearing the same letter are not significantly different ($\alpha = 0.05$).
** Population 1 = fringe tree lace bug, Population 2 = swamp privet lace bug.

Table 5. Laboratory choice tests of *L. mutica* adults given the choice of two or three hosts. Means ± SE for adult location and percent leaf area damaged.*

	Trials 1 and 2		Trials 3 and 4	
Treatments	**Location of Bug**	**Leaf Area Damaged**	**Location of Bug**	**Leaf Area Damaged**
Swamp privet	0.85 ± 0.1 B	13.42 ± 0.1 A	2.13 ± 0.2 B	22.94 ± 0.2 A
Chinese privet	0.77 ± 0.1 B	13.33 ± 0.2 A	1.22 ± 0.2 B	15.58 ± 0.2 B
Container	1.29 ± 0.1 A	—	1.96 ± 0.2 B	—
Green ash	—	—	7.51 ± 0.9 A	25.07 ± 0.3 A

* Means in the in the same column bearing different letters are significantly different ($\alpha = 0.05$). (—) indicates no data.

Table 6. Field choice test assay with lace bug means ± SE for adult location and percent leaf area damaged.*

Treatments	Location of Lace Bug	Leaf Area Damage
Swamp privet	12.40 ± 0.8 B	39.69 ± 3.5 B
Chinese privet	5.40 ± 0.4 B	31.76 ± 1.1 B
Green ash	51.00 ± 0.5 A	65.66 ± 3.1 A

* Means in the in the same column bearing different letters are significantly different ($\alpha = 0.05$).

ash. Green ash also was most-often damaged (location $F_{2,8} = 20.31$, $P = 0.0007$; damage $F_{2,8} = 76.63$, $P = 0.0001$; Table 6). No significant differences between swamp privet and Chinese privet were noted.

Discussion

Original collections and observations of the two lace bug populations suggested they could have been two different lace bug species. The lace bugs collected from swamp privet (Macon Co.) appeared slightly smaller and more mobile than those collected from fringe trees (Spalding Co.). Also, Wheeler (2002) suggested lace bugs collected from swamp privet could be either *Le. elliptica* Mcatee or *Le. ilicis* Drake, mesophyll feeders known to inhabit swamp privet. However, the two lace bug populations used in this study were subsequently identified as *Le. mutica* (Tom Henry USDA/ARS/SEL, pers. comm.) and they behaved similarly throughout the studies. The no-choice test general comparison of the two lace bug populations (Table 1) revealed few differences in their performance and more egg production by Population 1, probably a direct result of their higher survival in that test. The laboratory host choice test supported their identification as one species in that there were no differences between the populations and their host choice.

Prior to this study, Chinese privet was not a confirmed host of *Le. mutica*, although the lace bug was known to utilize other members of the Oleaceae family including fringe tree, green ash, and swamp privet (Drake 1918, Mead 1975). The no-choice test showed that *Le. mutica* adults could survive, feed, and lay eggs on Chinese privet. Results did indicate less egg production on Chinese privet (Tables 2 and 3). This could mean that lace bugs do not obtain the same amount of energy from Chinese privet, so it was less acceptable, or simply that the lace bugs used were unable to produce eggs. Also, observations of egg placement on the different plant hosts showed occasional exposed eggs on the Chinese privet whereas egg placement on other hosts was deeper in the plant tissue (J.K. unpubl. data). These observations could help explain why Chinese privet is not a preferred host plant. The nutritional composition of Chinese privet leaf tissue may not be optimum for *Le. mutica* fitness, or Chinese privet leaves could be an unsuitable host for best egg placement and development. The optimal oviposition theory states that females will lay their eggs where their offspring will be able to perform best (Jaenike 1978); also, plant surfaces are one of the most critical confluences affecting host acceptance by insects (Eigenbrode and Espelie 1995). For example, the azalea lace bug, *S. pyrioides*, is thought to consider hosts based on leaf wax chemistry (Wang et al. 1999), leaf pubescence (Schultz 1993), stomatal characters (Kirker et al. 2008), and leaf moisture content (Wang et al.1998), so even among azalea cultivars there are different levels and mechanisms of resistance to lace bugs. These complex selection criteria may explain tingid host specificity and why *Le. mutica* does not host-shift in the wild to the increasingly abundant Chinese privet.

Our studies suggest that the reason *Le. mutica* does not readily utilize Chinese privet is because it is not a preferred host. When given only the choice of swamp privet and Chinese privet, the lace bug did not prefer one to the other, but whenever green ash was present the lace bugs always preferred it. In most forest areas where *Le. mutica* were established, green ash was also present, so it is likely that ash was the primary host supporting the population. This restricted host preference makes *Le. mutica* an unlikely candidate for control of Chinese privet without a host shift, but it is encouraging for the potential of the similar Asian lace bug, *Le. hospita*, to be a biological control agent. Chinese privet is the preferred host of this lace bug and, if released and acting similarly, it would not shift to other native plant hosts.

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