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Natural enemy impact on eggs of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), in organic agroecosystems: A regional assessment

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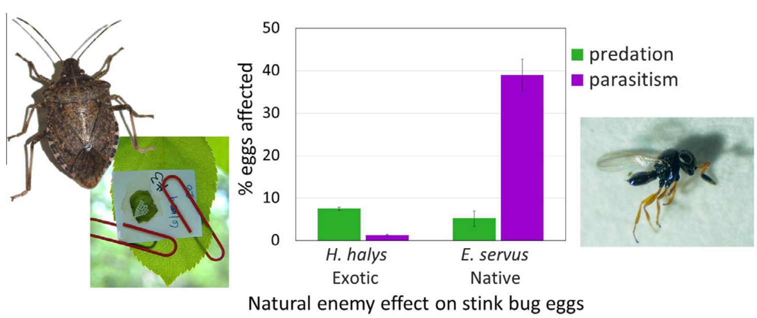
HIGHLIGHTS

- Broad-scale assessment of natural enemies' effect on invasive *H. halys* eggs in eastern US crops.
- Predation, mainly by chewing predators, accounted for the majority of control of *H. halys* eggs.
- Parasitism of *H. halys* eggs by native parasitoids was very low.
- Baseline data to evaluate potential future biocontrol programs and native parasitoid adaptation.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding native natural enemy impacts on the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål), offers insight into the population dynamics of this invasive pest and the potential for biological control. This two-year study offers a broad-scale assessment of mortality factors affecting sentinel and naturally laid *H. halys* eggs in agroecosystems in the pest's invaded range in eastern North America. Predation and parasitism rates varied among states and crops, but overall were low. Average maximum levels of biological control were estimated to be about 19% and 20% in 2013 and 2014, respectively. Of the eggs destroyed by natural enemies, chewing predation was the most prevalent. Parasitism by native parasitoids was very low, with adult parasitoids emerging from <1% of eggs averaged across crops, locations, and years; an additional 2.8% of eggs contained partially developed parasitoids. Lower percentages of sentinel *H. halys* hatched in organically versus conventionally managed crops, and in most cases had higher percentages of predation. Parasitism of sentinel and naturally laid eggs of the native

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stink bugs *Euschistus servus* (Say) and *Chinavia hilare* (Say) averaged 49.3% (±8.6 SE) and 0.6% (±0.3), respectively, across locations and years. *Telenomus podisi* (Ashmead) was the most common parasitoid parasitizing *E. servus* and *H. halys* eggs, but rarely did >1 individual parasitoid emerge from a *H. halys* egg mass. Parasitism of *H. halys* eggs by a complex of parasitoids is an important population regulation factor in its native Asian range, but this study found that parasitoids native to eastern US agroecosystems do not provide that service in this introduced region. The greatest potential for biological control of *H. halys* may be via classical biological control by the Asian parasitoid *Trissolcus japonicus* (Ashmead), which has recently been detected in both the eastern and western US.

1. Introduction

Invasive species are known to have serious ecological and economic consequences (Pimentel et al., 2005). Agriculture pays a particularly high price for invasive pests, as nonnative species are the major pests of many crops in the temperate region (Mack et al., 2000; Pimentel et al., 2005; Sakai et al., 2001). The spread and success of alien species can often be attributed to their escape from the natural enemies that evolved with these exotic species in their native habitat (Keane and Crawley, 2002; Mack et al., 2000; Sakai et al., 2001).

The invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), was accidentally introduced to the eastern United States from its native range in East Asia (Xu et al., 2014), with its first recorded discovery in Allentown, Pennsylvania in 1996 (Hoebeke and Carter, 2003). Populations of *H. halys* soon established throughout the mid-Atlantic states, where the pest has caused the most damage to crops thus far (Leskey et al., 2012a; Rice et al., 2014). Currently, *H. halys* is an agricultural problem in 17 states and has been detected in 42 states and 2 Canadian provinces (www.stopbmsb.org, accessed April 2016).

Adults enter diapause in the fall and overwinter in dead, standing trees and human-made structures, making them a severe nuisance pest to homeowners in areas with high *H. halys* populations (Lee et al., 2014a; Wallner et al., 2014). In the eastern US, overwintering adults emerge from April to June and move to host trees in non-managed, wooded habitats (Nielsen and Hamilton, 2009a; Bakken et al., 2015). Here, females mate and lay eggs and adults and nymphs begin to move to most agricultural crops in June and July. In the eastern US, *H. halys* is known to complete one to two generations per year (Nielsen and Hamilton, 2009a; Bakken et al., 2015).

The polyphagous *H. halys* feeds on numerous vegetable and tree fruit crops, costing growers in unmarketable or entirely lost produce (Leskey et al., 2012b; Nielsen and Hamilton, 2009b). Corn, beans, pepper, tomato, eggplant, and okra are among the preferred vegetables of *H. halys* and can incur heavy damage (Leskey et al., 2012a). In 2010, the pest abruptly increased in abundance and caused severe damage to many agricultural and ornamental crops, mainly in the mid-Atlantic states (Leskey et al., 2012a). The U.S. Apple Association estimated *H. halys* cost $37 million in fruit loss in 2010 (Seetin, 2011), and some stone-fruit growers lost >90% of their crops (Leskey and Hamilton, 2010). The response in 2011 by some growers was adoption of an intense insecticide program, using up to four times the amount of pesticide used in 2010, most of which were broad spectrum chemicals (Leskey et al., 2012b). This unsustainable management approach increases production costs, the threat of secondary pest outbreaks, insecticide resistance, and health and environmental risks (Leskey et al., 2012b). Management of *H. halys* in organic agriculture is even more challenging because growers do not have access to insecticides that are as effective as those used by conventional growers (Lee et al., 2014b).

In its native range of Asia, *H. halys* is found on many host plants, but is not typically a major pest of agricultural crops (Funayama, 2004), suggesting that natural control factors suppress population growth. In Japan, five hymenopteran egg parasitoid species (within the genera *Anastatus* (Eupelmidae), *Ooencyrtus* (Encyrtidae) and *Trissolcus* (Platygastridae)) attack *H. halys* eggs (Arakawa and Namura, 2002). The parasitic wasp *Trissolcus japonicus* (formerly *Trissolcus halyomorphae*) (Ashmead) (Hymenoptera: Platygastridae) is an important natural enemy of *H. halys* in northern China, where parasitism of *H. halys* eggs averages 50%, with rates sometimes reaching 70–80% (Qui, 2007; Talamas et al., 2013; Yang et al., 2009). Release from co-evolved natural predator and parasitoid pressure may be one factor contributing to the success of *H. halys* in the United States (Keane and Crawley, 2002; Mack et al., 2000). There is anticipation that biological control by native natural enemies can play a role in managing *H. halys* in organic agriculture in the eastern US, but little is known about its current impact.

Reported here are results from a large-scale, multi-state, multi-crop assessment of the role of native natural enemies of *H. halys* in organic systems in the invaded regions of the eastern US. This report focuses on predation, parasitism, and overall mortality of *H. halys* and native stink bug eggs in organic as well as conventional cropping systems.

2. Material and methods

Studies were conducted in the summer growing seasons of 2013 and 2014 to determine the effect of natural enemies on *H. halys* (and native stink bugs when possible) populations in organic agriculture systems in the eastern US. Studies focused on assessing the outcome of sentinel and naturally laid egg masses in organic crops and determining the percentages of eggs parasitized or destroyed by predators. Effects on native stink bug species were also determined for naturally laid eggs found at study sites and, in a few instances, sentinel eggs.

2.1. Locations

Study sites included locations in seven states in the eastern US: Michigan, New Jersey, North Carolina, Ohio, Tennessee, and West Virginia (Fig. 1). In 2013, eggs were deployed in the following states and crops (number of sites per crop): KY, apple (1 site) and pepper (1 site); MI, apple (2) and tomato (2); NC, apple (2), pepper (3), okra (2), tomato (2); NJ, apple (2), pepper (2), soybean (2), sunflower (1); OH, blackberry (2), corn (1), pepper (3), Swiss chard (2), tomato (1); TN corn (1), pepper (1), soybean (1); WV, corn (1), okra (1), pepper (1), tomato (1), soybean (1), sunflower (1). The 2014, eggs were deployed in the following states and crops (sites per crop): KY, apple (1) and pepper (1); MI, apple (2) and pepper (2); NC, apple (2) and pepper (2); NJ, pepper (2), raspberry (2); OH, corn (1) and pepper (1); TN, corn (1) and pepper (1); WV, sunflower (1) and pepper (1).

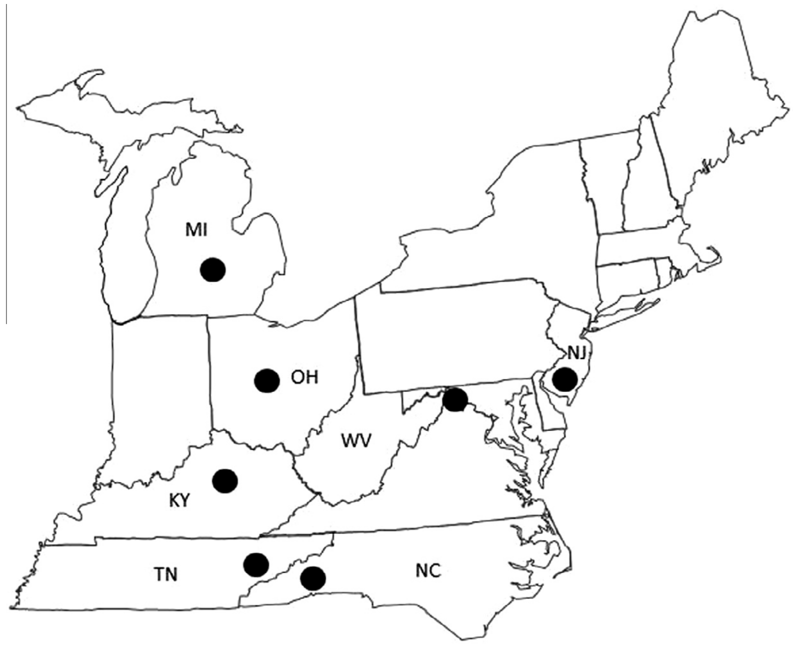

Fig. 1. Map of sample areas where sentinel eggs were deployed.

In NC in both 2013 and 2014, sentinel *H. halys* eggs were also deployed in conventionally managed sites to compare predation, parasitism, and egg mortality in organic versus (vs.) conventionally managed crops. In 2013 eggs were deployed in two conventional sites each of apple, pepper, and tomato, and in 2014 two sites each of conventional apple and pepper. Although the list of organically produced crops used for egg deployment differed among states, efforts were made to include at least one common crop in all states, and at least two common crops in several different states. Pepper was sampled in all states both years (except MI in 2013) and apple was sampled in four and three states in 2013 and 2014, respectively. Additional crops sampled in multiple states in one or both years included corn, okra, soybean, and tomato. Sample sites in each state included USDA certified organically produced crops grown commercially and/or on research stations.

2.2. Sentinel egg mass preparation, deployment, and assessment

Sentinel egg masses were collected from *H. halys* laboratory colonies maintained in each state. Colonies were reared in cages containing a whole bean plant (*Phaseolus vulgaris*), bean pods, and sunflower seeds. In a few instances, paper towels were placed in cages for oviposition. Freshly laid egg masses (less than 24 h old) were collected by cutting around the mass and including a portion of the surrounding bean leaf (or paper towel) on which they were laid. Sentinel eggs of the native brown stink bug (*Euschistus servus*) (Say) and green stink bug (*Chinavia hilare*) (Say) (Hemiptera: Pentatomidae) collected from laboratory colonies using the same protocol were also deployed in KY in 2013, and in KY and WV in 2014. The leaf substrate with the egg mass was attached with doubled sided tape to a cardstock square to create a deployable sentinel egg mass. Prior to deployment in the field, each egg mass was numbered and the number of eggs in each mass counted and recorded. Because adult stink bugs sometimes fed on eggs before they were removed from colonies, in 2014 the number of eggs in each mass exhibiting a feeding tube indicative of cannibalism was recorded and tubes were recounted when collected. Cannibalized eggs were <0.5% of all eggs and were subtracted from the total egg count in that mass.

In most fields, *H. halys* eggs were deployed on multiple dates between June and August. Sentinel egg masses were attached with pins or paperclips to the underside of leaves at the mid-level of plants 3 m apart within a field. At most sites and dates, 20 sentinel egg masses per site and deployment date were set, but numbers were sometimes restricted by fecundity of stink bugs in colonies; at several sites as few as 10 egg masses were deployed on a sample date and in three instances only 4, 9, and 9 masses were deployed on a sample date and collected retaining usable data. Mostly fresh eggs (<24 h old) were used, but frozen eggs were deployed in instances when the supply of fresh eggs was insufficient, therefore the number of fresh masses used varied among some sample dates. In 2013 and 2014, 22.4% and 15.7%, respectively, of deployed *H. halys* egg masses were frozen. Frozen eggs originated from stink bug colonies and were less than 24 h old when collected and held at −20 °C for no more than 30 days before deployed in the field. In 2013, NC, MI, TN and WV, deployed both freshly laid and frozen *H. halys* eggs. All masses were retrieved after a minimum of 48 h and a maximum of 5 days in the field and placed in individual small petri dishes or vials.

An initial assessment of the outcome of each egg within all egg masses was conducted usually within a week of removal from the field. The following data were recorded during this initial assessment: date collected from field, number of eggs hatched, number unhatched, number of eggs missing, number chewed by predators, number of sunken eggs, and number of eggs with an emerged parasitoid. All emerged parasitoids were preserved in ethanol and identified to species where possible. Identifications were verified by the USDA-ARS-Beneficial Insects Introduction Research Lab (Newark, DE).

In 2014, several changes in the assessment protocol enabled us to more clearly differentiate the fate or outcome of eggs. In 2014, the initial assessment included recording the number of eggs with stylet sheaths/puncture holes (indicative of attack by sucking predators), number of intact unhatched white eggs, and number intact unhatched discolored (dark) eggs. The masses were held under varying conditions among states (24–30 °C, 14:10–16:08 L:D, 40–70% RH) for a minimum of 6 weeks to allow parasitoids to develop and emerge. Those eggs that did not hatch after the 6-

week period were dissected to attempt to determine the reason for mortality. Through the dissections, the number of eggs with unemerged parasitoids (partially developed but failed to emerge from the egg) and the number of eggs containing dark undifferentiated substance were recorded. Those unemerged parasitoids recovered through dissections that were developed sufficiently were identified to species where possible.

2.2.1. Naturally laid egg masses

When deploying eggs in fields, plant foliage was also surveyed for naturally laid stink bug egg masses, which were collected (mostly in organically managed fields, but occasionally some were found when in conventionally managed fields). When possible, recently laid masses (i.e., those with no stink bug egg bursters present) were flagged in the field, the number of eggs in the mass upon discovery was recorded and left in the field for 48 h, allowing time for predation and/or parasitism to occur. The species of the stink bug egg mass (Kamminga et al., 2009) and of the host plant on which it was found were recorded, and these naturally laid masses were assessed in the same manner as described above. All stink bug egg masses discovered were collected, including those from which stink bugs had eclosed, those with parasitoid emergence holes, and those without signs of parasitism. However, it was not possible to determine the precise number of eggs missing from naturally laid masses, because the original number of eggs was unknown.

2.3. Data analysis

Egg predation and parasitism were examined as percentages of both total individual eggs and number of egg masses. Frozen stink bug eggs were not viable and could not hatch, so frozen eggs were not included in the percentage hatched and unhatched categories. All other outcomes were calculated out of total frozen plus fresh eggs.

All data analysis was conducted in SAS (SAS, 2012), with differences in individual egg outcomes tested using generalized linear mixed models (GLMM) with a binomial response distribution and logit link. Tukey's method was used for p-value adjustment for all post hoc comparisons. In both years, outcomes (dependent variables) of eggs within state were tested, with crops and egg type (fresh or frozen) as factors (independent variables). In both years, egg outcomes within peppers and also within apples were tested with states as independent variables. In both years for NC data, differences in the egg outcomes within crops were tested with conventional vs. organic sites as independent variables. KY (and WV in 2014) deployed sentinel eggs from stink bug species native to North America and differences were tested for each state and year with stink bug species as a factor.

3. Results

3.1. Overview

A total of 3210 *H. halys* sentinel egg masses were deployed in organic crops across all states in 2013 and 2014. These masses represented a total of 85,677 eggs, of which 68,359 (79.8%) were fresh and 17,318 (20.2%) were frozen. There was an average of 26.7 eggs per mass. Of the 44,394 and 23,965 fresh eggs deployed in 2013 and 2014, respectively, nymphs successfully hatched from 48.0% (±3.8 SE) in 2013 and 44.7% (±3.9) in 2014 averaged across crop and state. Eggs considered to be "unhatched" (i.e., nonviable eggs,

Table 1
Outcome of *Halyomorpha halys* sentinel eggs deployed in organic crops across the eastern US. 2013.

State	Crop	N (eggs)		Egg masses	Percentage of total eggs					
					Hatched[a]	Unhatched[a]	Missing	Emerged Parasitoids	Predation	
		Fresh	Frozen						Chewed	Sucked
KY	Apple	3009	0	115	36.2	56.0	7.8	0	0	0
	Pepper	3610	0	136	30.5	63.4	5.9	0	0.2	0
MI	Apple	1529	1565	116	49.8	32.2	12.2	0.4	0.8	0.1
	Tomato	1637	1731	124	54.4	43.9	1.7	0.3	0	0.1
NC	Apple	6720	271	255	73.0	12.1	2.7	0	12.1	0.2
	Okra	2617	208	105	65.8	26.7	2.5	0.2	3.0	1.6
	Pepper	7020	561	277	56.6	29.1	5.6	0.2	6.4	2.8
	Tomato	2778	277	113	78.0	20.7	0.6	0.1	0.1	0.4
NJ	Apple	1353	0	50	64.9	4.6	6.0	0.9	0.6	23.0
	Pepper	2447	0	83	58.3	6.5	3.1	0.1	2.1	29.9
	Soybean	1184	0	41	46.4	13.8	6.8	2.5	9.1	21.4
	Sunflower	113	0	4	48.7	6.2	5.3	4.4	0	35.4
OH	Blackberry	1605	0	60	50.7	35.9	5.6	0	7.1	0.7
	Corn	1333	0	49	42.7	36.5	3.2	1.3	15.6	0.7
	Pepper	3344	0	125	54.4	39.4	2.6	0	3.0	0.6
	Swiss chard	283	0	10	83.4	12.7	3.9	0	0	0
	Tomato	542	0	20	63.8	31.0	0	0	5.2	0
TN	Corn	385	1642	74	49.6	10.6	50.5	0.8	0.9	1.6
	Pepper	297	2465	102	60.6	14.8	7.0	0.7	3.9	1.2
	Soybean	507	1192	63	21.9	6.1	48.0	0	9.8	1.5
WV	Corn	864	259	45	34.8	36.3	18.9	0.1	13.4	0.5
	Okra	82	130	9	30.5	56.1	5.7	0	7.1	0
	Pepper	28	653	26	0	100.0	10.0	0	1.0	0.1
	Soybean	532	686	47	51.3	26.1	7.0	0	15.7	0.2
	Sunflower	218	923	44	22.5	63.8	11.9	0.6	6.8	0
	Tomato	357	95	17	19.3	56.3	18.8	1.1	7.3	4.4

[a] Hatched and unhatched (i.e., nonviable eggs, those that did not hatch and were not missing, preyed upon, or parasitized) outcomes were calculated out of the total fresh (non-frozen) sentinel eggs deployed, as freezing destroys the viability of developing stink bugs. Missing, emerged parasitoids, chewed, and sucked outcomes were calculated out of total fresh + frozen eggs.

those that did not hatch and were not missing, preyed upon, or parasitized) accounted for 32.3% (±4.5) in 2013 and 37.4% (±4.7) in 2014. In addition, a total of 1492 naturally laid *H. halys* eggs from 57 egg masses were collected from various crops in 2013 and 2014, of which 31.7% (±7.5) successfully hatched and 44.9% (±9.5) eggs were considered unhatched averaged across years and states.

3.2. Outcomes of sentinel H. halys among crops

The outcomes of sentinel *H. halys* eggs varied considerably among crops in both years. In 2013, the percentage of emerged parasitoids was very low in all states and crops, with an average across all states and crops of 0.5% (±0.2 S.E., range of total percent values by crop and state: 0–4.4%) (Table 1). Predation varied widely among states and crops, with chewing predation affecting 5.0% (±1.0, 0–15.7%) and sucking predation 4.9% (±2.0, 0–35.4%) of total eggs. Egg mortality due to sucking predation was especially high in NJ, ranging from 21.4–35.4% by crop. Chewing predation mortality was particularly low in KY and MI compared to all other states.

In 2014, the percentage of successful parasitoid emergence was again very low in all states and crops, with emergence from an average of only 0.3% (±0.1, 0–2.0%) of all eggs (Table 2). However, with the dissection of unhatched eggs in 2014, it was determined that a total of 4.2% of unhatched eggs, or averaged across crops and states 2.8% (±1.0) of total eggs, contained a partially developed parasitoid. When unemerged parasitoid outcomes were combined with the total number of eggs from which parasitoids emerged, the percentage of total parasitized eggs increased to an average of 3.2% (±1.1, 0–12.6%). With the exception of apples in NC (33.1%), chewing predation was low in 2014, averaging only 4.1% (±2.3, 0–33.1%). In 2014, only eggs with a stylet sheath or punctures (clearly indicating predation opposed to a potential abiotic cause of mortality) were classified as "sucking predation" and only 0.6% (±0.3, 0–2.9%) of all eggs were affected by sucking predators.

The number of missing eggs, which may have represented predation, averaged 9.7% (±2.5% S.E., range of 0–50.5%) and 12.8% (±3.0 S.E., range of 0.7–42.1%) in 2013 and 2014, respectively. Instances where the percentage of missing eggs were highest included corn and soybean in TN in 2013 and sunflower in WV in 2014. Also, in states that deployed eggs in apples, the percentage of missing eggs tended to be higher than eggs deployed in other crops in those states. For example, in a total of 11 within-state comparisons between apple and another crop in 2013 and 2014, apples had higher percentages of missing eggs than the other crop(s) in 8 of 11 instances.

3.3. Outcomes among states

In both 2013 and 2014, *H. halys* sentinel eggs were deployed in the same crops in several different states. In 2013, eggs were deployed in pepper in six states (KY, NC, NJ, OH, TN, WV), and in 2014 eggs were deployed in pepper in all seven states. Also, eggs were deployed in apple in four (KY, MI, NC, NJ) and three states (KY, NC, MI) in 2013 and 2014, respectively. Statistical comparisons of egg outcomes among states in apple and peppers are shown in Table 3 with some trends apparent. In both years, chewing predation in peppers was significantly higher in NC compared with all other states. Percentages of sucking predation were only significant in 2013, when the total in NJ pepper and apple was greater than in all other states. Total parasitism differed among states only in 2014, when KY had higher levels of parasitism in both peppers and apples than all other states. In both years, the percentages of missing eggs were higher in sentinels deployed in pepper in WV compared to sentinels deployed in pepper in all other states.

3.4. Outcome of egg masses vs. total eggs

In addition to examining the percentage of total eggs affected by natural enemies, data were also expressed as the percentage of egg masses affected; i.e., percentage of masses that had ⩾1 egg in a mass attacked. For instance, while a total of only 26.2% of total eggs were destroyed by sucking predators in NJ crops in 2013, a total of 75.3% of the egg masses had one or more egg attacked by a sucking predator (Fig. 2). Averaged across all states and crops, the percentage of egg masses vs. eggs attacked by sucking predators, chewing predators and emerged parasitoids in 2013 was 14.6 (±10.2) vs. 4.9 (±2.0), 11.0 (±3.1) vs. 5.0 (±1.0), and 2.0 (±0.6) vs. 0.5 (±0.2), respectively. Averaged across all states in 2014, the percentage of masses vs. eggs attacked was 3.7 (±1.7) vs. 0.6 (±0.3), 10.5 (±3.3) vs. 4.1 (±2.3), 3.8 (±2.0) vs. 0.4 (±0.1), and 10.8 (±3.7) vs. 2.8 (±1.0) for sucking predators, chewing

Table 2
Outcome of *Halyomorpha halys* sentinel eggs deployed in organic crops across the eastern US. 2014.

State	Crop	N (eggs)		Masses	Percentage of total eggs							
					Hatched[b]	Unhatched[b]	Missing	Parasitoids[a]			Predation	
		Fresh	Frozen					Emerged	Unemerged	Total	Chewed	Sucked
KY	Apple	328	0	14	41.8	43.9	13.1	0.3	0.9	1.2	0	0
	Pepper	1253	0	57	13.5	64.2	13.0	2.0	7.1	9.1	0.2	0
MI	Apple	2121	55	83	44.9	50.8	5.6	0	0.5	0.5	0.4	0.2
	Pepper	1430	0	54	49.5	45.9	3.6	0	0.2	0.2	0.4	0.4
NC	Apple	3114	0	116	32.8	16.2	17.7	0.1	0.1	0.2	33.1	0.1
	Pepper	2879	0	113	56.6	27.9	7.2	0.6	3.9	4.5	3.8	0
NJ	Pepper	3780	0	138	43.0	38.6	15.7	0.6	1.1	1.7	0.8	0.3
	Raspberry	3906	0	145	31.7	42.2	21.8	0.4	0.6	1.0	1.0	2.4
OH	Corn	1754	0	73	47.1	46.1	0.7	0	0	0	6.1	0
	Pepper	1935	0	78	41.2	56.3	0.8	0.1	0.4	0.5	1.1	0.1
TN	Corn	211	1378	58	68.2	31.8	3.5	0.2	7.9	8.1	0.8	2.9
	Pepper	1226	2759	152	61.4	19.2	9.1	0.6	4.2	4.8	3.2	2.6
WV	Pepper	0	223	9	–	–	24.7	0	12.6	12.6	0.9	0
	Sunflower	28	245	10	50	3.6	42.1	0	0	0	5.1	0

[a] Emerged parasitoids are those eggs from which a live parasitoid emerged, while unemerged parasitoids are those eggs that contained a partially developed parasitoid. Total includes emerged + unemerged parasitoids.
[b] Hatched and unhatched (i.e., nonviable eggs, those that did not hatch and were not missing, preyed upon, or parasitized) outcomes were calculated out of the total fresh (non-frozen) sentinel eggs deployed, as freezing destroys the viability of developing stink bugs. Missing, emerged parasitoids, chewed, and sucked outcomes were calculated out of total fresh + frozen eggs.

Table 3
Statistical comparisons (GLMM) of the outcome of *Halyomorpha halys* sentinel eggs among states when deployed in organic crops. Post-hoc comparisons with Tukey's p-value adjustment, alpha level of 0.05.

Year	Crop	Egg outcome category	F	df	P	Statistical differences
2013	Pepper	Chewing predation	40.33	5, 747	<0.001	NC > TN > OH > NJ, WV > KY
		Sucking predation	308.75	5, 747	<0.001	NJ > all states NC > TN, OH, WV, KY TN > OH, WV, KY KY < all states
		Emerged parasitism	562.53	5, 747	<0.001	TN > all states TN, NC, NJ > KY, OH, WV
		Missing eggs	25.50	5, 747	<0.001	WV > all states TN > KY, NC, NJ, OH NC, KY > NJ, OH
	Apple	Chewing predation	91.01	3, 534	<0.001	NC > all states
		Sucking predation	145.33	3, 534	<0.001	NJ > all states
		Emerged parasitism			NS	
		Missing eggs	103.89	3, 534	<0.001	MI > KY > NJ > NC
2014	Pepper	Chewing predation	18.31	6, 593	<0.001	NC > all states TN > NJ, WV, MI, KY
		Sucking predation			NS	
		Total parasitism (emerged + unemerged)	37.5	6, 593	<0.001	KY > all states NC, WV > TN, NJ, OH, MI OH, MI < all states
		Missing eggs	67.91	6, 593	<0.001	WV > all states NJ > KY, NC, MI, OH TN, KY > NC > MI > OH
	Apple	Chewing predation	99.95	2, 209	<0.001	NC > MI > KY
		Sucking predation			NS	
		Total parasitism (emerged + unemerged)	4.66	2, 209	0.0105	KY > NC
		Missing eggs	73.73	2, 209	<0.001	NC > KY > MI

predators, emerged parasitoids, and unemerged parasitoids, respectively (Fig. 2).

3.5. Outcomes in conventional vs. organic crops

In 2013, of sentinel *H. halys* eggs deployed in conventionally and organically managed apples (two orchards used for egg deployment per management type), there was a higher percentage of eggs chewed by predators ($F_{1,521}$ = 424.34, P < 0.0001) and missing ($F_{1,521}$ = 54.36, P < 0.0001) in organic vs. conventional orchards (Fig. 3). There was no difference between organic and conventional egg outcomes in apples for sucking predation or for emerged parasitoids.

In 2013, eggs placed in the three organically managed peppers had a higher percentage of chewing predation ($F_{1,570}$ = 229.66, P < 0.0001), sucking predation ($F_{1,570}$ = 106.89, P < 0.0001), missing eggs ($F_{1,570}$ = 199.51, P < 0.0001) and emerged parasitoids ($F_{1,570}$ = 4.19, P = 0.0412) than those in the two conventionally managed pepper fields.

In 2013, eggs placed in the two conventionally managed tomato fields had a higher percentage of chewing predation ($F_{1,403}$ = 13.70, P = 0.0002) and eggs missing ($F_{1,403}$ = 15.26, P < 0.0001) compared to those placed in the two organically managed fields. Sucking predation and emerged parasitoids did not differ between organic and conventional tomato crops.

In 2014, sentinel *H. halys* eggs deployed in conventionally and organically grown apples (two orchards of each management type) had a higher percentage of eggs missing ($F_{1,232}$ = 33.28, P < 0.0001) and destroyed by chewing predation ($F_{1,232}$ = 432.07, P < 0.0001) in organic vs. conventional apples, but the percentage of eggs destroyed by sucking predation ($F_{1,232}$ = 8.57, P = 0.0038) and unemerged parasitoids ($F_{1,232}$ = 28.55, P < 0.0001) was greater in conventional compared to organic apples (Fig. 3).

In 2014, sentinel eggs placed in conventionally and organically grown peppers (two fields each) showed greater chewing predation ($F_{1,230}$ = 22.89, P < 0.0001), emerged parasitoids ($F_{1,230}$ = 13.37, P = 0.0003), unemerged parasitoids ($F_{1,230}$ = 13.37, P = 0.0003), total parasitism (emerged + unemerged) ($F_{1,230}$ = 14.13, P = 0.0002) and missing eggs ($F_{1,230}$ = 66.35, P < 0.0001) in organic compared to conventional orchards (Fig. 3).

3.6. Fresh vs. frozen eggs

Data from states where fresh and frozen eggs were deployed in 2013 were pooled together for statistical analysis and the percentage of chewing ($F_{1,1419}$ = 74.53, P < 0.0001) and sucking predation ($F_{1,1419}$ = 38.10, P < 0.0001) was higher with fresh compared to frozen eggs (Fig. 4). There was a higher percentage of missing frozen eggs vs. fresh eggs ($F_{1,1419}$ = 1132.93, P < 0.0001) but there was no difference between fresh and frozen eggs in the proportion parasitized ($F_{1,1419}$ = 1.38, P = 0.2399).

In 2014, TN was the only state in which comparable, large amounts of frozen and fresh masses were deployed (all but two masses were fresh in MI, one was frozen in WV) and only TN data were used for statistical analyses. Percentages of emerged parasitoids ($F_{1,208}$ = 10.99, P = 0.0011) and missing eggs ($F_{1,208}$ = 78.33, P < 0.0001) were significantly higher in fresh vs. frozen TN eggs (Fig. 4). Percentages of unemerged parasitoids ($F_{1,208}$ = 53.20, P = <0.0001) and eggs chewed ($F_{1,208}$ = 5.10, P = 0.0250) were significantly higher in frozen vs. fresh TN eggs.

3.7. Naturally laid H. halys eggs

In 2013, 34 naturally laid *H. halys* egg masses were found in four states. NJ had a high percentage of eggs attacked by sucking predators at 26.1% but this is based on only 14 egg masses (Table 4). In 2014, only 23 naturally laid *H. halys* masses were detected in three states (Table 4). WV eggs had a high percentage of total parasitism (65.9%) but this was based on outcomes from only 3 egg masses. There were too few naturally laid *H. halys* egg masses detected to conduct statistical analyses or to interpret broadly.

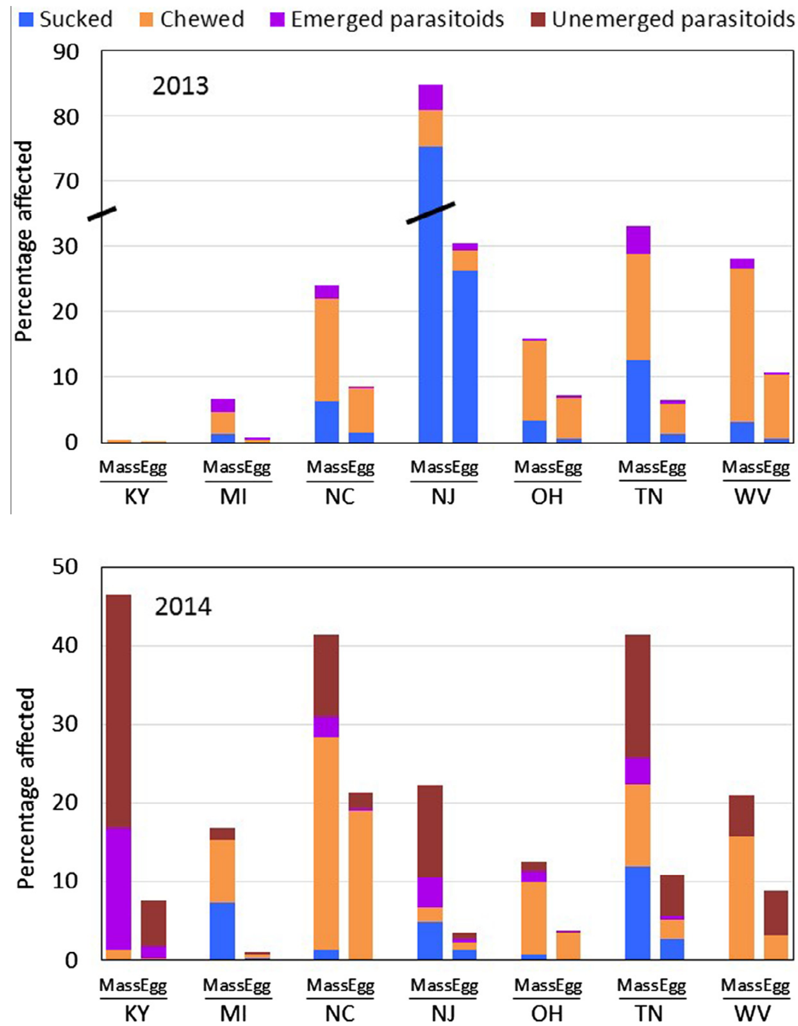

Fig. 2. Percentage of sentinel *H. halys* egg masses (MASS) vs. total eggs (EGG) affected by predation and parasitism. 2013 and 2014.

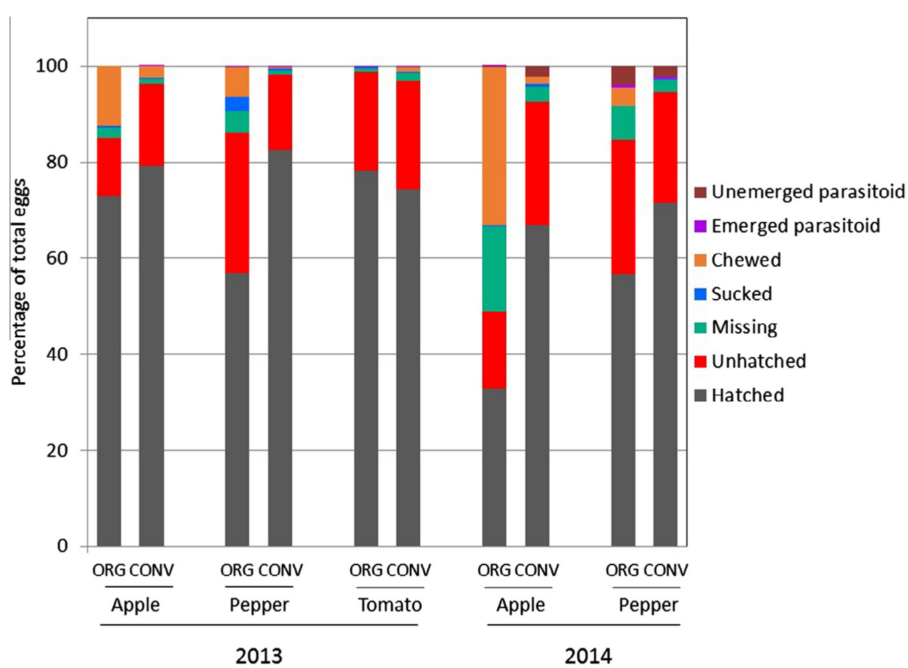

Fig. 3. Outcome of sentinel *H. halys* egg deployed in organic (ORG) vs. conventional (CONV) crops in 2013 and 2014 in NC.

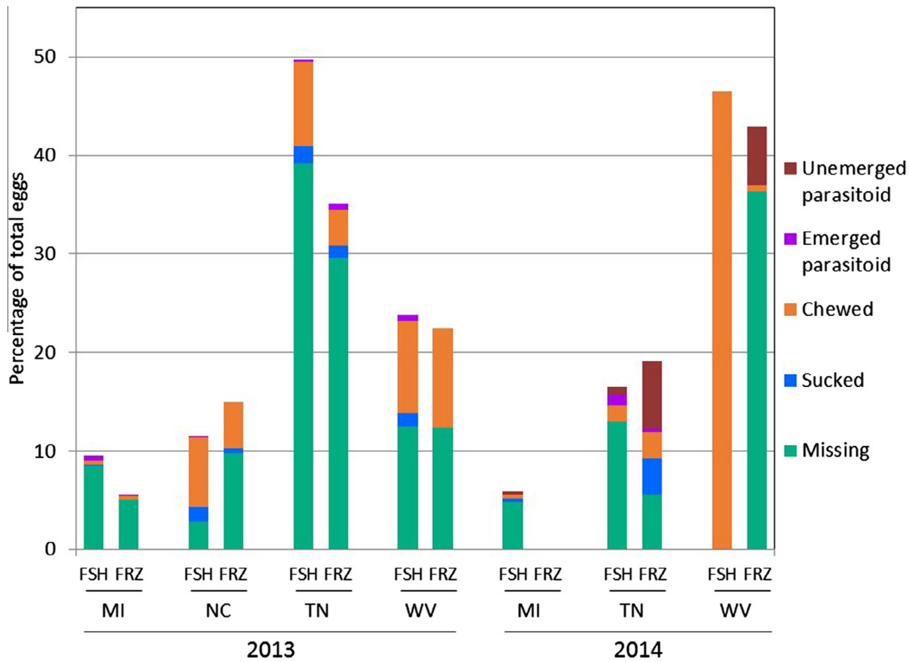

Fig. 4. Outcome of fresh (FSH) vs. frozen (FRZ) sentinel *H. halys* eggs. 2013 and 2014.

Table 4
Outcome of naturally laid *Halyomorpha halys* eggs discovered in various crops.

Year	State	N (eggs)	Egg masses	Percentage of total eggs						
				Hatched	Unhatched[b]	Parasitoids[a]			Predation	
						Emerged	Unemerged	Total	Chewed	Sucked
2013	NC	56	2	7.1	91.1	1.8	–	–	0	0
	NJ	348	14	45.4	21.0	7.5	–	–	0	26.1
	TN	377	15	27.9	50.1	7.7	–	–	9.3	5.0
	WV	79	3	40.5	59.5	0	–	–	0	0
2014	NC	176	6	51.1	22.7	10.8	14.2	25	0	1.1
	TN	374	14	47.3	45.2	3.5	1.6	5.1	2.4	0
	WV	82	3	2.4	24.4	31.7	34.2	65.9	7.3	0

[a] Emerged parasitoids are those eggs from which a live parasitoid emerged, while unemerged parasitoids are those eggs that contained a partially developed parasitoid. Total includes emerged + unemerged parasitoids.
[b] Nonviable eggs, those that did not hatch and were not missing, preyed upon, or parasitized.

3.8. Naturally laid native stink bug eggs

In 2013, naturally laid egg masses of stink bug species native to North America were found in only two states (NC and NJ) and few were found in these states. Brown stink bug (*Euschistus servus*) eggs were found in corn and apples in NC and had high proportions of parasitized eggs (Table 5). Eggs found in NJ had a high proportion of native eggs affected by sucking predators (23.9%). These results are based on only four egg masses found in each state.

In 2014, naturally laid native stink bug eggs were found in three states (NC, TN, and WV). The eggs of both *E. servus* and *Euschistus tristigmus* (Say) had in these states, ranging from 74.6 to 100% (Table 5). However, the very low egg mass numbers found in both years make general conclusions unfeasible.

3.9. Sentinel native brown and green stink bug eggs

In 2013 in KY, sentinel eggs of *E. servus* and *C. hilare* were deployed in apple and pepper. Predation of both species was very low in both crops, although 33.9% (apple) and 20.7% (pepper) of *C. hilare* eggs were missing at the time of collection (Table 6). In addition, parasitism of *E. servus* was quite high in both crops, while none of the *C. hilare* eggs were parasitized. No (0%) parasitoids emerged from any sentinel KY *H. halys* eggs in 2013 compared with sentinel KY *E. servus* eggs with 22.2% emerged parasitoids in apple and 38.5% in pepper. A higher percentage of KY *H. halys* eggs hatched (36.2%) compared with *C. hilare* (18.8%) and *E. servus* (21.6%) eggs in apples. A higher percentage of *H. halys* eggs hatched (30.5%) compared with *E. servus* (5.1%) eggs in peppers. However, these comparisons are based on relatively few native sentinel eggs (and egg masses) and a larger number of *H. halys* eggs (and egg masses). There were 9x and 14x more *H. halys* than *E. servus* eggs deployed in apples and peppers, respectively (5x and 9x more *H. halys* in terms of egg masses and even fewer *C. hilare* masses). Therefore, statistical comparisons were not feasible.

In 2014, comparable numbers of native and *H. halys* eggs (and masses) were deployed in 2014 and statistical comparisons were possible. Sentinel eggs of native species deployed in KY in 2014 showed similar trends in egg outcomes to those observed in KY in 2013, with overall predation fairly low and parasitism of *E. servus* higher than that of *C. hilare* (Table 7). In KY peppers, total parasitism varied among species ($F_{2,226} = 390.28$, $P < 0.0001$), with *E. servus* (53.3%) higher than both *C. hilare* (0.6%) and *H. halys* (9.1%). There was also a larger percentage of sucking predation

Table 5
Outcome of naturally laid eggs of native stink bug species discovered in various crops.

Year	State	Stink bug species	N (eggs)	Egg masses[c]	Percentage of total eggs						
					Hatched	Unhatched[b]	Parasitoids[a]			Predation	
							Emerged	Unemerged	Total	Chewed	Sucked
2013	NC	*E. servus*	53	4	28.3	34.0	37.7	–	–	0	0
	NJ	*E. servus*	109	4	16.5	35.8	23.8	–	–	0	23.9
2014	NC	*E. servus*	221	8	3.2	22.2	73.7	0.9	74.6	0	0
	TN	*E. servus*	86	3	0	20.9	69.8	9.3	79.1	0	0
		E. tristigmus	28	1	0	0	100.0	0	100.0	0	0
		C. hilare	100	3	0	99.0	1.0	0	1.0	0	0
	WV	*E. servus*	21	1	0	0	0	100.0	100.0	0	0

[a] Emerged parasitoids are those eggs from which a live parasitoid emerged, while unemerged parasitoids are those eggs that contained a partially developed parasitoid. Total includes emerged + unemerged parasitoids.
[b] Nonviable eggs, those that did not hatch and were not missing, preyed upon, or parasitized.
[c] Few naturally laid egg masses were found, therefore egg outcomes listed are based on a small sample size.

Table 6
Outcome of sentinel eggs of native stink bug species deployed in organic crops in Kentucky. 2013.

State	Crop	Stink bug species	N (eggs)[a]	Egg masses	Percentage of total eggs					
					Hatched	Unhatched[b]	Missing	Emerged parasitoids	Predation	
									Chewed	Sucked
KY	Apple	*E. servus*	329	21	21.6	25.8	8.5	22.2	1.8	0
		C. hilare	165	5	18.8	47.3	33.9	0	0	0
	Pepper	*E. servus*	257	15	5.1	6.2	1.9	38.5	0	0
		C. hilare	203	6	62.1	17.2	20.7	0	0	0

[a] All fresh (non-frozen) sentinel eggs.
[b] Nonviable eggs, those that did not hatch and were not missing, preyed upon, or parasitized.

Table 7
Outcome of sentinel eggs of native stink bug species deployed in organic crops in Kentucky and West Virginia. 2014.

State	Crop	Stink bug species	N (eggs)		Egg masses	Percentage of total eggs							
						Hatched[b]	Unhatched[b]	Missing	Parasitoids[a]			Predation	
			Fresh	Frozen					Emerged	Unemerged	Total	Chewed	Sucked
KY	Apple	*E. servus*	192	0	17	35.4	19.8	1.5	18.8	24.0	42.8	0.5	0
		C. hilare	2719	0	87	16.2	77.1	5.2	0.3	1.0	1.3	0.1	0.1
	Pepper	*E. servus*	597	0	38	10.6	25.1	10.2	25.0	28.3	53.3	0	0.8
		C. hilare	4336	0	134	31.2	56.8	11.0	0	0.6	0.6	0.3	0.1
WV	Pepper	*E. servus*	13	161	12	0	30.8	0	19.5	1.1	20.7	8.0	0
	Sunflower	*E. servus*	35	173	10	57.1	2.9	19.2	17.8	4.8	22.6	37.5	0

[a] Emerged parasitoids are those eggs from which a live parasitoid emerged, while unemerged parasitoids are those eggs that contained a partially developed parasitoid. Total includes emerged + unemerged parasitoids.
[b] Hatched and unhatched (i.e., nonviable eggs, those that did not hatch and were not missing, preyed upon, or parasitized) outcomes were calculated out of the total fresh (non-frozen) sentinel eggs deployed, as freezing destroys the viability of developing stink bugs. Missing, emerged parasitoids, chewed, and sucked outcomes were calculated out of total fresh + frozen eggs.

on *C. hilare* compared with *E. servus* eggs ($F_{2,226} = 5.85$, $P = 0.0033$). In KY apples, parasitism was higher in *E. servus* (total parasitism 42.8%) vs. *C. hilare* (total 1.3%) and *H. halys* eggs (total 1.2%) (emerged parasitoids $F_{2,115} = 65.13$, $P < 0.0001$; un-emerged $F_{2,115} = 96.06$, $P < 0.0001$; total $F_{2,115} = 173.47$, $P < 0.0001$).

In WV peppers, total parasitism (20.7 vs. 12.6%, $F_{1,19} = 4.70$, $P = 0.0431$) and chewing predation (8.0 vs. 0.9%, $F_{1,19} = 8.84$, $P = 0.0078$) was significantly higher in *E. servus* vs. *H. halys* eggs. The proportion of unemerged parasitoids was higher in *H. halys* (12.6%) than *E. servus* eggs (1.1%) ($F_{1,19} = 11.56$, $P = 0.0030$). In WV sunflowers, a higher proportion of *E. servus* (37.5%) were chewed than *H. halys* eggs (5.1%) ($F_{1,18} = 60.47$, $P < 0.0001$) and a higher proportion of *H. halys* were missing (42.1%) vs. *E. servus* eggs (19.2%) ($F_{1,18} = 27.16$, $P < 0.0001$). WV comparisons were based on comparable numbers of *E. servus* and *H. halys* masses, but few masses were deployed overall (range 6–12 masses by crop and species), therefore a broad interpretation of these results is not applicable.

3.10. Parasitoid species

In 2013, a total of 5 species of parasitoids were represented, with 86 individual parasitoids from *H. halys* eggs and 189 individual parasitoids from *E. servus* eggs identified (Table 8). *Anastatus mirabilis* (Walsh and Riley), *Telenomus podisi* (Ashmead), and a *Trissolcus* sp. parasitized both stink bug species, while *Trissolcus brochymenae* (Ashmead) and *Ooencyrtus* sp. parasitized only *H. halys*.

In 2014, a total of 163, 353, and 44 individual parasitoids representing 8 species were identified from *H. halys*, *E. servus*, and *C. hilare* eggs, respectively (Table 9). In addition to those species represented in 2013, three additional parasitoids occurred in *H. halys* in 2014 – *Anastatus reduvii* (Howard), *Trissolcus edessae* (Fouts), and *Trissolcus euschisti* (Ashmead). *T. podisi* was most common, accounting for 54.0%, 100%, and 77.3% of all parasitoids from *H. halys*, *E. servus* and *C. hilare*, respectively.

Table 8
Parasitoids from sentinel and naturally laid stink bug eggs collected from various organic crops. 2013.

Species	Crop	State	N (parasitoids)	*Anastatus mirabilis*	*Ooencyrtus* sp.	*Telenomus podisi*	*Trissolcus* sp.	*Trissolcus brochymenae*
H. halys	Corn	OH	17	0	17	0	0	0
		WV	1	0	0	0	0	1
	Okra	NC	1	0	0	1	0	0
	Peach	NC	1	0	0	1	0	0
	Pepper	KY	1	0	0	1	0	0
		NC	12	0	0	12	0	0
		NJ	3	0	0	3	0	0
	Tomato	NC	4	0	0	4	0	0
		WV	5	0	5	0	0	0
	Soybean	NJ	29	28	0	1	0	0
	Sunflower	NJ	5	0	0	5	0	0
		WV	7	0	0	0	2	5
E. servus	Apple	KY	50	0	0	50	0	0
	Pepper	KY	113	0	0	92	21	0
	Soybean	NJ	26	26	0	0	0	0

Table 9
Parasitoids from sentinel and naturally laid stink bug eggs collected from various organic crops. 2014.

Species	Crop	State	N (parasitoids)	*Anastatus* sp.	*A. mirabilis*	*A reduvii*	*Ooencyrtus* sp.	*Telenomus podisi*	*Trissolcus brochymenae*	*Tr. edessae*	*Tr. eushisti*
H. halys	Apple	NC	21	0	0	17	0	4	0	0	0
	Corn	TN	24	0	0	0	22	2	0	0	0
		WV	18	0	0	0	0	16	2	0	0
	Pepper	KY	25	0	0	0	0	25	0	0	0
		OH	2	0	0	0	0	2	0	0	0
		NC	20	0	0	0	0	10	0	9	1
		NJ	14	0	0	0	0	14	0	0	0
		TN	15	0	0	0	9	2	0	4	0
	Raspberry	NJ	16	0	8	0	0	5	1	0	2
	Sunflower	WV	8	0	0	0	0	8	0	0	0
E. servus	Apple	KY	34	0	0	0	0	34	0	0	0
	Corn	NC	56	0	0	0	0	56	0	0	0
		TN	7	0	0	0	0	7	0	0	0
	Peach	NC	54	0	0	0	0	54	0	0	0
	Pepper	KY	149	0	0	0	0	149	0	0	0
	Tomato	NC	53	0	0	0	0	53	0	0	0
C. hilare	Pepper	KY	8	0	0	0	0	0	0	0	8
	Sunflower	WV	36	1	0	0	0	34	1	0	0

4. Discussion

Understanding the impact of natural enemies on *H. halys* populations in their invaded range provides insight into the population dynamics and potential for conservation biological control of this pest. We focused our studies on eggs, because of the ability to quantify egg outcome, the capability to identify types of natural enemy attack—egg predation type (see Morrison et al. 2016) and parasitism, the established knowledge base on sentinel eggs of stink bugs native to eastern North America, their vulnerability to hymenoptera parasitoids, and history of classical biocontrol in stink bugs species. For example, *Trissolcus basalis* was released in Australia, Hawaii, and New Zealand to control the southern green stink bug, (*Nezara viridula*) which resulted in full control of the pest in Australia and reduced populations of *Nezara viridula* in New Zealand and Hawaii (Caltagirone, 1981). Conducting these studies in commercial organic production systems provided an opportunity to measure the potential impact of natural control agents in diverse cropping systems free of synthetic broad-spectrum pesticides. Finally, studies were conducted across a wide area of the eastern US (Fig. 1) that included a diversity of agroecosystems and length of time that *H. halys* has been established, ranging from at least the late 1990's in New Jersey (Hamilton, 2009) to as recent as 2010 in Michigan (Michigan State University Integrated Pest Management Program).

The overall level of natural control of *H. halys* eggs was low in this study; the percentage of sentinel eggs lost to predation plus parasitism across all crops and states was estimated to be only 10.4 ± 2.2% and 7.9 ± 2.2% in 2013 and 2014, respectively. This is similar to the level of predation recently reported by Morrison et al. (2016), who found that 9.1% of frozen sentinel *H. halys* eggs deployed in apples and organic crops were lost to predation. However, an additional 9.7 ± 2.5% and 12.8 ± 3.0% of our eggs in 2013 and 2014, respectively, were classified as missing, and it is likely that many of these were consumed by chewing predators. Predators in the family Tettigoniidae have been shown to consume whole egg masses (Stam et al., 1987; Morrison et al., 2016), as have ants (Tillman, 2008; Olson and Ruberson, 2012).

Although parasitism of *H. halys* eggs was low throughout this study, it was probably slightly underestimated in 2013 when unhatched eggs were not dissected to detect undeveloped, unemerged parasitoids. In 2014, when unhatched eggs were dissected, an additional average of 2.8 ± 1.0% of sentinel *H. halys* eggs contained an unemerged parasitoid. Hence, assuming that all missing eggs were consumed by predators and 2.8% of eggs in 2013 contained an unemerged parasitoid, the maximum percentage of eggs that could have been lost to natural enemies was estimated to be 19.1% in 2013 and 19.9% in 2014.

Predation and parasitism varied among states, crops, years, sites, and sample dates. These differences may be due to landscape factors including: the abundance, connectivity, complexity, quality, and type of non-crop habitat (Gardiner et al., 2009; Östman et al., 2001; Thies and Tscharntke, 1999). Such habitats offer a species pool for dispersal, nectar and alternative hosts for parasitoids, and refuge areas from disturbances from agricultural practices such as tillage and for overwintering (Bommarco, 1998; Lee et al., 2001; Thies et al., 2003). Predation of sentinel eggs of the pest *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) was higher in vineyards with adjacent wooded habitat compared to vineyards that lacked neighboring woody vegetation (Thomson and Hoffmann, 2010). While landscape factors were not quantified at our sites, a number studies have shown their influence on natural enemy populations and support the hypothesis that the differences in natural enemy activity on eggs that we recorded may have been driven by landscape structure and composition (reviewed in Bianchi et al., 2006; Letourneau et al., 2011). Considering that *H. halys* is a perimeter pest with non-managed wooded areas serving as reservoirs for infestations in crops (Leskey et al., 2012b; Venugopal et al., 2014; Bakken et al., 2015), these habitats may also be important reservoirs of natural enemies.

In every comparison of the outcome of sentinel eggs placed in organic vs. conventionally-managed crops, the percentages of *H. halys* hatching were lower in organic systems. Also, with the exception of tomatoes in 2013, predation was significantly higher in organic systems. These results are based on two locations per production system for each crop in both years (with the exception of three organically-managed pepper sites in 2013). These results may reflect higher plant diversity, higher field perimeter-to-area ratio, and/or more heterogeneous habitats (Bommarco, 1998; Östman et al., 2001) surrounding and within our organic sites. The differences might also have been influenced by the frequent use of broad-spectrum insecticides in conventional crops, which were likely more harmful to predators than the practices of control used at our organic sites (Hummel et al., 2002). Finally, potentially higher abundance of stink bug hosts in organic agroecosystems may have contributed to higher parasitoid abundance in these systems.

Predation of sentinel *H. halys* eggs was much higher than parasitism; conservatively assuming that half of the missing eggs were removed by predators, predation accounted for at least 80% of biological control activity. Average predation of *H. halys* sentinel eggs across all states was greater by predators with chewing vs. sucking mouthparts in 2013 (5.0% vs. 4.9%) and 2014 (4.1 vs. 0.6%) (Tables 1 and 2).

The protocol used in 2013 likely overestimated the number of eggs destroyed by sucking predator. In 2013, eggs that were sunken, regardless of the presence or absence of a style sheath, were classified as destroyed by sucking predators. In 2014, eggs were further classified to differentiate those with a stylet sheath or punctures indicative of a sucking predator. Morrison et al. (2016) demonstrated that frozen sentinel *H. halys* eggs deployed in the field and surrounded by predator exclusion cages were sometimes sunken with no stylet sheath, indicating sunken eggs without stylet sheaths were not necessarily sunken due to predation. In NJ 2013, the presence/absence of a stylet sheath within the "sucking" predation category was noted, in addition to the standard 2013 protocol. Among those eggs classified as destroyed by sucking predators in NJ, only 22.5% had a stylet sheath. This would still result in a considerably higher percentage of eggs destroyed by sucking predators (total of 5.9% across crops) in NJ compared to all other states (0.8% ± 0.2 averaged across all other states and crops, which included all sunken eggs as classified by 2013 protocol). Nonetheless, this does not change the conclusion that predation by sucking predators was lower than that of chewing predators in both years.

We were not able to determine the cause of non-viable eggs – i.e., those that did not hatch and exhibited no signs of predator or parasitism. Possible causes of include biotic factors that may have led to egg desiccation, non-fertilized eggs, or eggs attacked by a parasitoid in which no parasitoid development occurred.

Although identification of predators was not a component of this study, a diversity of generalist predators are reported predators of stink bugs. *Podisus maculiventris*, *Orius insidiosus*, and salticids were sucking predators of *H. halys* eggs in laboratory studies (Morrison et al., 2016). These and the lygaeids *Geocoris punctipes* (Fallén) and *G. uliginosus* (Say) have been reported as sucking predators of native stink bug species in the southeastern US (Abram et al., 2015; Yeargan, 1979; Tillman, 2008, 2010, 2011). A number of different generalist predators with chewing mouthparts have been reported as common predators of stink bug eggs, including coccinellids, ants, and grasshoppers (see Abram et al., 2015; Krispyn and Todd, 1982; Olson and Ruberson, 2012; Ragsdale et al., 1981; Stam et al., 1987; Tillman, 2011). Of the commonly found WV predators tested in a laboratory setting, members of Tettigonnidae (*Atlanticus testaceous*, *Conocephalus strictus*, and *Orchelimum* spp.), Carabidae (*Harpalus* spp.), Dermaptera (*Forficulidae* spp.), and Gryllidae (*Oecanthus* spp.) most frequently and efficiently chewed *H. halys* eggs (Morrison et al., 2016). Additional predators that we observed feeding on eggs when retrieving sentinel egg masses included soldier beetle larvae (Cantharidae) and several different arachnids and slugs (Gastropoda).

Our observation that predation by chewing predators was more important than that of sucking predators has also been observed by others in the eastern US. For instance, Yeargan (1979) reported 37% predation rates of *E. servus* and *C. hilare* sentinel eggs in KY soybean and alfalfa, with eggs damaged by chewing compared to sucking predators occurring at a ratio of about 3.5:1. In corn, peanut, and cotton in Georgia, predation rates varied by crop and date, but predation by chewing predators frequently exceeded 90%, while that of sucking predators was usually less than 20% (Tillman, 2011). Morrison et al. (2016) reported that native predators common to WV fruit orchards and vegetable crops with chewing mouthparts were 4x more efficient (measured as percentage of eggs consumed per egg mass) at *H. halys* egg predation than those with piercing-sucking mouthparts in the laboratory.

While our rates of predation were somewhat lower than those reported for native stink bug species in field crop systems, our data were from numerous dates and crops, both of which affect predation. Shepard et al. (1994) observed relatively high rates of predation of *N. viridula* eggs in soybeans (~50%), but no predation in tomatoes on 11 of 14 sample dates, with low predation (10–20%) on the remaining three dates. In addition, predation of sentinel *E. servus* and *C. hilare* eggs placed in both field and vegetable crops in Virginia was often zero and always <10% (Koppel et al., 2009). Furthermore, low rates of predation have been reported for *N. viridula* eggs in tomato and bean fields in California (Ehler, 2002) and predators were observed to be more efficient at locating and destroying *N. viridula* eggs in macadamia orchards than in nearby weeds (Jones et al., 1996). The fact that many of our sample sites were vegetable fields may have contributed to an overall low rate of predation. In this study, in sentinel *H. halys* eggs the highest predation rates were most frequently from eggs deployed in apple, corn, soybean, and sunflower.

Overall, levels of parasitism of *H. halys* eggs by native parasitoids were low compared to native stink bug eggs in our study and others. Our estimated percentage of parasitized *H. halys* sentinel eggs was only ~3% both years, averaged across states and crops, the majority of which were unhatched eggs with unemerged parasitoids. Parasitism of sentinel *E. servus* eggs placed in apples and peppers in KY and WV ranged from about 22–50%. Interestingly, parasitism of *C. hilare* was very low, with none in 2013 and only 1% of eggs parasitized in 2014. Yeargan (1979) observed similar results in KY soybeans and alfalfa, with higher parasitism of *E. servus* (20–60%) vs. *C. hilare* sentinel eggs (0–19%). In southeast Virginia, parasitism of sentinel *E. servus* eggs in a diversity of crops averaged ~50% (Koppel et al., 2009). Parasitism of *E. servus* and *N. viridula* in Georgia varied greatly among sample dates and years, but parasitism rates of >50% were not uncommon (Tillman, 2008, 2010, 2011). Similarly, parasitism rates of *N. viridua*, *C. hilare*, and *Euschistus* spp. exceeding 50% were common in multiple cropping systems in South Carolina (Jones et al., 1996; Shepard et al., 1994).

The low level of parasitism of *H. halys* by native parasitoids that we observed was not unexpected in view of similar results in regions where this insect is a recent invasive pest. Of 5864 fresh and frozen eggs deployed in soybean, apple and wooded areas in Maryland, native parasitoids emerged from only 4.5% of eggs, and these were primarily from frozen eggs in wooded areas (Talamas et al., 2015). In Switzerland, only 0.5% and 4.4% of sentinel *H. halys* eggs placed in wooded habitats were parasitized (Haye et al., 2015). It should be noted that sentinel eggs may underestimate parasitism, as Jones et al. (2014) observed considerably higher parasitism of *H. halys* eggs that were naturally laid (30–35%) vs. sentinel eggs (<5%) placed in ornamental trees. They hypothesized that their sentinel eggs may have been missing semiochemicals used by adult parasitoids to locate host eggs. In contrast to Jones et al. (2014), who removed eggs from the oviposition substrate with the aid of water and placed them on filter paper, our sentinel eggs remained on the section of bean leaf (or in a few instances the section of paper substrate) on which it was oviposited. Nonetheless, we did observe higher parasitism rates in naturally laid vs. sentinel *H. halys* eggs in 2014.

Among the seven species of parasitoids from *H. halys* eggs, *T. podisi* was the most commonly encountered, likely due to the prevalence of this parasitoid in the agroecosystems we sampled rather than suitability of *H. halys* as a host (Abram et al., 2014). In fact, *H. halys* appeared to be a poor host based on higher parasitism rates of egg masses vs. total eggs. *T. podisi* is a common parasitoid of *Euschistus* stink bugs in eastern US cropping systems (Jones et al., 1996; Koppel et al., 2009; Orr et al., 1986; Tillman, 2008, 2010, 2011; Yeargan, 1979) and has also been recovered from *H. halys* in Maryland (Jones et al., 2014; Talamas et al., 2015). Although infrequently encountered in our survey, *T. edessae* (Fouts), and *Ooencyrtus* sp. have not previously been reported parasitizing *H. halys* eggs.

In contrast to our low rates of parasitism by native *Trissolcus* spp. and *T. podisi*, several native *Anastatus* spp. appear to readily parasitize *H. halys* eggs. In particular, *A. reduvii* parasitized upwards of 50% of fresh sentinel eggs in woody ornamental trees in Maryland (Jones et al., 2014). In Switzerland, the native *A. bifasciatus* successfully parasitized fresh and frozen *H. halys* eggs at a rate of about 30% in a laboratory setting (Haye et al., 2015). Agricultural crops do not appear to be a preferred habitat for native *Anastatus* spp.; we have encountered it most frequently from eggs collected in wooded areas (J.F.W. unpublished data), similar to the findings of Jones et al. (2014) and Talamas et al. (2015).

Egg parasitism is an important population regulation mechanism of stink bugs that does not appear to be effectively operating against *H. halys* outside of its native range in Asia. In the pest's introduced ranges, the absence of highly effective *H. halys* egg parasitoids that occur in China and Japan (Arakawa et al., 2004; Arakawa and Namura, 2002; Yang et al., 2009) is consistent with the natural enemy release hypothesis (Keane and Crawley, 2002) and has likely contributed to the high population densities of this insect in the US. *Trissolcus japonicus* (Ashmead), an Asian parasitoid of *H. halys* studied in US quarantine facilities since 2007 as a candidate for classical biological control, was recently detected in the field in Maryland (Talamas et al., 2015) and Washington state (Milnes and Beers, 2016). As *Trissolcus basalis* classical biological control programs demonstrate, release of the laboratory strain could increase the probability of establishment and success of this biocontrol agent, as introduction of multiple parasitoid strains increases the chance of establishment of an optimal a strain, best adapted to the new environment and most effective at control (Caltagirone, 1981). There likely have been several accidental introductions of *T. japonicus* in the US and natural spread of the parasitoid along with the potential for releases of the laboratory strain offer promise of more effective parasitism of *H. halys*.

This study provides a broad-scale assessment of the effect of natural enemies on *H. halys* eggs in agricultural crops in the eastern US. Biological control in this study was primarily restricted to predators, whose success as control agents may be influenced by local landscape factors and plant composition (Gardiner et al., 2009; Thies et al., 2003). It is possible that resident natural enemies in the invaded US may become more effective at control of *H. halys* over time (Carroll et al., 2005; Grabenweger et al., 2010). The spread or introduction of Asian parasitoids, particularly *T. japonicus*, offers greater opportunities for biological control. The results of this study provide key baseline information to monitor the future impact of biological control on *H. halys* eggs in agricultural settings.

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