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RAPID COMMUNICATION

Fruit availability influences the seasonal abundance of invasive stink bugs in ornamental tree nurseries

Holly M. Martinson[1] · P. Dilip Venugopal[1] · Erik J. Bergmann[1] ·
Paula M. Shrewsbury[1] · Michael J. Raupp[1]

Abstract Invasive plant-feeding insects cause billions of dollars in economics losses annually around the world. Understanding how they utilize different host plants directly informs their management. The highly invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), has destroyed crops and invaded homes since its discovery in the U.S. in the mid-1990s. In this study, we test the hypothesis that in diverse resource environments, the presence and maturity of fruits on trees influences the abundance of *H. halys*. Observational surveys of the abundance of *H. halys* life stages (egg masses, nymphs, and adults) on 3884 trees of 223 cultivars in woody plant nurseries revealed that fruit maturity was a strong predictor of the seasonal abundance and within-tree distribution of *H. halys*. We next explicitly tested whether fruits themselves were the key resource for *H. halys* through a manipulative field experiment. Removal of fruits from trees suppressed stink bug abundance throughout the season. Despite being considered a broad feeding generalist, our results highlight that in landscapes with highly heterogeneous and ephemeral resources, *H. halys* specializes on finding mature fruits. Therefore, *H. halys* can be controlled by designing landscapes with fruitless varieties of popular trees, exploiting phenological mismatches between the pest and its host plants, and through targeted management of *H. halys* on fruiting trees in the landscape.

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✉ Holly M. Martinson
hmartins@umd.edu

1 Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, USA

Key message

- *Halyomorpha halys* is a highly invasive and broadly polyphagous plant-feeding bug. Thus, identifying factors that influence its abundance across host plants will inform management.
- In an extensive field survey and a season-long experiment, the abundance of *H. halys* was strongly influenced by the presence and maturity of fruit.
- Considering this pest as a fruit specialist may aid in management, monitoring, and the development of landscapes refractory to stink bugs.

Introduction

Biotic introductions are one of the leading causes of global environmental change (Vitousek 1994; Sala et al. 2000; Pimentel et al. 2005). Species that successfully establish and spread in a new range engage in a host of unprecedented ecological relationships, including novel consumer-resource interactions (Parker et al. 2006; Desurmont and Pearse 2014). Introduced plant-feeding insects are among the most damaging introduced species (Liebhold et al. 1995; Aukema et al. 2011), but predicting the extent of herbivory and damage to plants in the invaded range is a complex function of herbivore dietary breadth (Carvalheiro et al. 2010; Pearse and Altermatt 2013), plant phylogeny (Pearse and Altermatt 2013), plant defense (Gandhi and

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Herms 2010; Desurmont et al. 2011), and the spatial and temporal availability of resources (Forister and Wilson 2013).

The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is a rapidly spreading, economically important herbivore pest originally native to eastern Asia (Leskey et al. 2012; Rice et al. 2014). At first detected in 1996 in the mid-Atlantic region (Hoebeke and Carter 2003), *H. halys* is now reported from at least 41 states in the U.S. and seven additional countries across three continents (Gariepy et al. 2014; Rice et al. 2014; Cesari et al. 2014). In its introduced range, it has progressed quickly from a nuisance pest to a major pest of agriculture, severely damaging fruit, vegetable, and row crops and ornamental plants in nurseries (Holtz and Kamminga 2010; Rice et al. 2014). For example, mid-Atlantic apple growers reported US$37 million in damages in 2010 alone (Rice et al. 2014), and such stark levels of damage have contributed to an up to fourfold increase in the use of chemical insecticides in affected crops (Leskey et al. 2012). Where abundances are high, *H. halys* is also a significant nuisance pest, with large numbers of bugs aggregating on landscape plants and then invading homes and other structures for overwintering shelter (Inkley 2012).

Across its native and introduced ranges, *H. halys* feeds on over 100 host plant species (Rice et al. 2014). Even the most polyphagous herbivores, however, do not feed equally across all potential host plants. The purpose of this study was to determine whether the presence and maturity of fruit, a key resource for many stink bugs (Panizzi 1997), is a significant driver of *H. halys* abundance where diverse host plants are available, and in doing so inform management of this economic pest. To these ends, we combined a comprehensive field survey of *H. halys* abundance on diverse trees at woody plant nurseries with a season-long fruit removal experiment.

Materials and methods

Observational field surveys

In 2013, we conducted field surveys of *H. halys* on trees at two commercial woody plant nurseries in Maryland [Raemelton Farm (Location: 39.299468N, 77.458549W) and Ruppert Nurseries (39.243172N, 77.142069W)]. We conducted one minute visual counts of *H. halys* on the foliage, flowers and fruit, and bark of nursery trees. We recorded the abundance and location on the tree of *H. halys* egg masses, early instar nymphs (stadia 1–3), late instar nymphs (stadia 4–5), and adults. The project directors (primarily MR and EB) trained all personnel to ensure uniformity and consistency in data collection protocols. At each visit, we also recorded the presence and maturity of fruit in three categories: (1) no fruit, (2) immature or partially developed fruit, or (3) mature, fully developed fruit.

We conducted censuses of *H. halys* abundance on nursery trees six times over the growing season of 2013, visiting trees approximately every 2 weeks from late May through early August. The full dataset comprised 3,884 individual trees of 223 cultivated varieties (hereafter, "cultivars"), for a dataset of 22,983 observations. Censuses were initiated on 28 May, 11 June, 24 June, 9 July, 23 July, and 5 August and were conducted over several days in order to visit each of the trees.

To understand the effect of fruiting phenology on *H. halys* abundance, individual trees were then classified according to their seasonal fruiting phenology. Due to tree harvest at these working nurseries, sampling effort among trees was unequal across time. Thus, only those trees visited during each of the six census periods were included in this analysis, leading to a reduced data set of 3,561 trees. This reduced dataset encompassed 91.7 % of the trees in the full dataset, 216 unique cultivars, and 21,366 total observations. Trees were categorized as (1) Non-fruiting: no fruit was ever recorded during the six census periods ($n = 2,097$); (2) Early fruiting: immature or mature fruit was present during either of the first two census periods but not during the last two census periods ($n = 362$); (3) Late fruiting: immature or mature fruit was present during either of the last two census periods but not during the first two census periods ($n = 346$); (4) Continuously fruiting: immature or mature fruit was present during the early, middle, and late census periods ($n = 756$). Alternative classifications of fruiting phenology gave qualitatively similar results (data and results not shown).

Fruit removal experiment

We conducted a whole-tree fruit removal experiment in 2014 at Raemelton farm, where high abundances of *H. halys* had been reported for several years. We selected 16 trees each of four commonly planted ornamental cultivars for this experiment: *Syringa pekinensis* 'Morton,' *Malus* 'Donald Wyman,' *Malus sargentii* 'Select A,' and *Amelanchier x grandiflora* 'Autumn Brilliance.' Each tree was 2–3 m in height.

Because of strong edge effects reported for this and other stink bugs (Venugopal et al. 2014, 2015), we employed a stratified assignment of experimental treatments to trees in their planting rows and only included trees planted within 15 m of a field edge. The first tree in a row was assigned an experimental treatment randomly by coin toss, and then treatments were assigned in an alternating manner on subsequent trees in the row. To ensure canopies

did not overlap, trees used in the experiment were separated by one non-experimental tree.

We conducted pretreatment surveys for *H. halys* on all trees in the experiment on 13 June, following the timed visual count protocol employed in the Observational Field Surveys. After these initial surveys and working with one cultivar at a time, we removed by hand all fruits and any remaining flowers on trees assigned to the fruit removal treatment. Fruit removal was conducted over the period of 13–23 June. Throughout the season, we periodically checked for and removed any additional fruits on removal trees. Weekly from 26 June to 2 Sept 2014, we conducted visual surveys of *H. halys* abundance on removal and control trees and recorded the number and location on the tree (on fruits/flowers, bark, or leaves) of egg masses, early instar nymphs, late instar nymphs, and adults. We also recorded the fruit stage, though not the total abundance of fruit, on control trees. Fruits were present on most control trees throughout the experiment, with the exception of *Amelanchier x grandiflora* 'Autumn Brilliance' from which fruits had dropped by 29 July (Sampling Period 7).

Statistical analysis

For both the observational and experimental studies, we constructed generalized linear mixed models (GLMM) based on Laplace approximation, with a Poisson error distribution and log link function (Bolker et al. 2009). Stink bug life stages (egg masses, early instar nymphs, late instar nymphs, and adults) were each analyzed separately. Model building and model selection for the mixed effects modeling followed the procedures suggested by Zuur et al. (2009). First, several candidate models, each with different random effects but identical fixed effects, were tested to choose the optimal random effect model using both AIC and BIC (Akaike and Bayesian Information Criteria, respectively) values for selection criteria (Pinheiro and Bates 2000). For the GLMMs, the significance of the fixed effects was determined by Wald χ^2 tests. Model estimated means comparisons, when employed, were performed using Tukey's HSD test. Models were evaluated for appropriateness of assumptions by testing for over-dispersion and correlations among random effect terms and by visualizing variances in a location-scale plot with superimposed loess fit (Bolker et al. 2009).

All statistical analyses were performed in the R program (R Core Team 2014) and associated statistical packages. GLMMs were performed with package "lme4" (Bates et al. 2014), significance tests with package "car" (Fox and Wiesberg 2011), and the multiple comparisons of means were computed with the package "multcomp" (Hothorn et al. 2008). GLMM-estimated coefficients were extracted

through package "effects" (Fox 2003) and plotted using "ggplot2" (Wickham 2009).

Observational field surveys

To test the effect of fruit maturity on *H. halys* abundance, we constructed separate GLMMs for each stink bug life stage, with the fixed effect of fruit maturity (absent, immature, or mature). To account for repeated measures, we included a random effect for individual tree nested within sampling period. Candidate models also included the location of the tree in the nursery field row (edge or center) and the cultivar as other random effects. The optimal random effects selected (by AIC and BIC) in the final model for each life stage included two random effects: individual tree nested within sampling occasion and cultivar.

The proportion of *H. halys* distributed within trees on fruits and flowers, bark, and leaves as a function of fruit maturity was tested for each life stage (egg masses, early instar nymphs, late instar nymphs, and adults) using Chi-square tests or two-sample test for equality of proportions with Yate's continuity correction.

We next tested for the effect of tree fruiting phenology throughout the season on *H. halys* abundance with a separate GLMM. Only the adult dataset was used for this analysis, as adults are highly mobile (Wiman et al. 2015) and showed the strongest response to mature fruits in the field surveys. For this analysis, we specified the fixed effects of fruiting phenology, a quadratic term for sampling period (time effect), and their interaction as predictor variables. The optimal random effects for this model included individual tree, location of the tree in the nursery field row (edge or center), and the cultivar.

Fruit removal experiment

We tested for differences in pretreatment *H. halys* abundance on trees assigned to the two treatments through GLMM, with treatment as a fixed effect and cultivar as a random effect. Models for other stink bug life stages were not run, as nymphs and egg masses were rarely recorded in the pretreatment census.

For post-treatment data, to test the effect of fruit removal, we constructed separate GLMMs for each stink bug life stage (except egg masses), with the fixed effects of treatment (fruit removed or present), cultivar, and a quadratic term for the sampling period (time effect). Models for egg masses were not run as only 6 egg masses were recorded in total. To account for repeated measures, we included the individual tree sampled as a random effect term in the GLMM.

Results

Observational field surveys

In repeated visual counts of *H. halys* on 3,884 trees, fruit maturity was a significant predictor of *H. halys* abundance for all life stages except egg masses (Fig. 1). Fruit stage did not affect egg mass abundance (Wald χ^2 Test with $df = 2$ throughout, $\chi^2 = 0.52$; $P = 0.77$) but had a significant effect on the abundances of early instar nymphs (instars 1–3; $\chi^2 = 6.60$; $P = 0.037$), late instar nymphs (instars 4–5; $\chi^2 = 8.43$; $P = 0.015$), and adults ($\chi^2 = 22.33$; $P < 0.001$). In particular, late instar nymphs and adults were far more abundant on trees with mature fruits than immature fruits or no fruits at all (Fig. 1).

Fruit maturity influenced not only *H. halys* abundance but also the distribution of individuals within trees on fruits, leaves, and bark (Fig. 2). Fruit maturity had little effect on the proportion of individuals on fruit for egg masses (comparing mature vs. immature, $df = 1$ throughout; $\chi^2 = 0.28$; $P = 1$) or early instars ($\chi^2 = 1.27$; $P = 0.26$) but led to increased proportions of late instars ($\chi^2 = 13.37$; $P < 0.001$) and adults ($\chi^2 = 14.34$; $P < 0.001$) on fruit. Overall, the proportion of individuals on mature fruits increased with increasing developmental stage ($\chi^2 = 185.72$; $df = 3$; $P < 0.001$; Fig. 2).

Particularly for the highly mobile adults, peak abundances of *H. halys* corresponded well with the peak fruiting
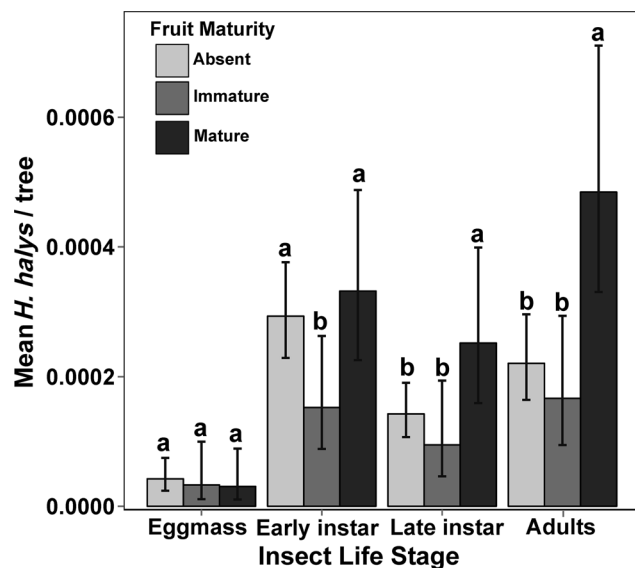
Fig. 1 The relationship between stink bug abundance and fruit maturity across insect life stages. Model estimated mean abundance (and 95 % confidence intervals) of *Halyomorpha halys* on trees with absent, immature, or mature fruits in the observational field survey. Significant differences in mean values based on Tukey's HSD comparisons are indicated by different letters above bars ($\alpha = 0.05$)
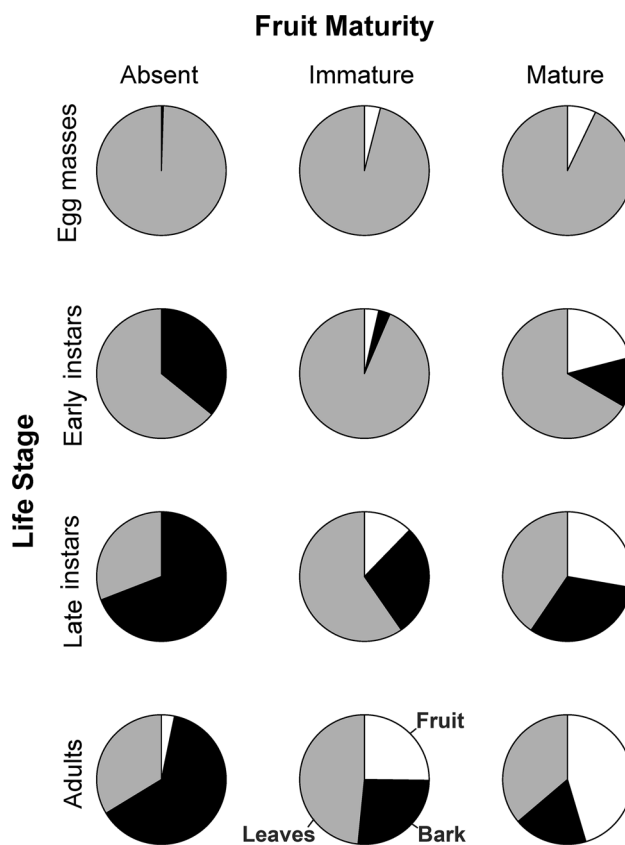

Fig. 2 The distribution of individuals within trees for each stink bug life stage (*rows*) and level of fruit maturity (*columns*). Shown are the proportions of *H. halys* on fruits and flowers (*white*), bark (*black*), and leaves (*gray*) across trees in the field survey

period of trees (Fig. 3). The final GLMM included the effects of fruiting phenology, a quadratic term for sampling period (time effect), and their interaction (Wald's χ^2 for interaction = 147.6; $df = 3$; $P < 0.001$). The abundance of adult *H. halys* increased gradually over the season on non-fruiting trees (Fig. 3a), reflecting the seasonal phenology of *H. halys*. Notably, clear peaks in abundance were evident early in the season on early-fruiting trees (Fig. 3b) and late in the season on late-fruiting trees (Fig. 3c). Abundance increased throughout the season on trees fruiting all season long (Fig. 3d).

Fruit removal experiment

Pretreatment abundances (sampling period 1) did not differ between trees assigned to experimental and control treatments (adults: $\chi^2 = 2.14$; $df = 1$; $P = 0.14$; few nymphs were recorded in Period 1). Removing fruits suppressed *H. halys* colonization of trees throughout the growing season (Fig. 4). The experimental treatment led to significant differences in the abundances of all life stages, which were
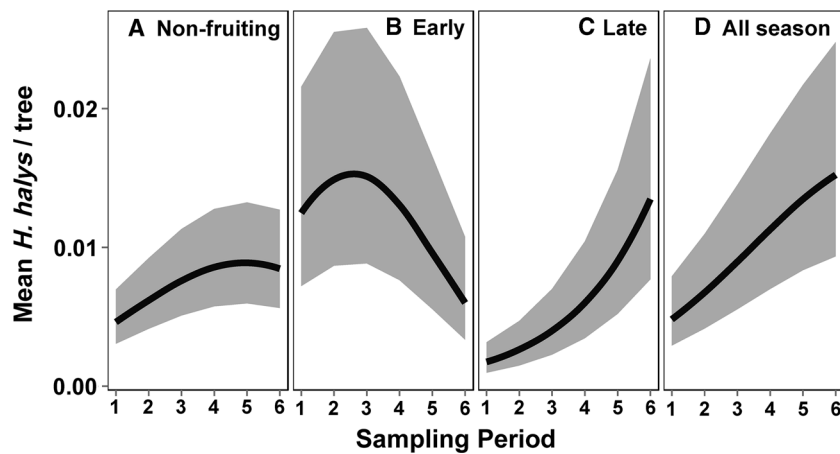
Fig. 3 The relationship between adult stink bug abundance, sampling period, and the fruiting phenology of nursery trees. Model estimated mean adult abundances (and 95 % CI) are plotted across time for **a** non-fruiting trees ($n = 2{,}097$), **b** early-fruiting trees ($n = 362$), **c** late-fruiting trees ($n = 346$), and **d** trees fruiting all season long ($n = 756$). Sampling was initiated fortnightly on the following dates in 2013: 28 May (Sampling Period 1), 11 June (Period 2), 24 June (Period 3), 9 July (Period 4), 23 July (Period 5), and 5 August (Period 6)

more abundant on trees with fruits than without. Experimental fruit removal significantly depressed the abundance of early instar nymphs (effect of treatment in final GLMM model: $\chi^2 = 4.24$; $df = 1$; $P = 0.039$; Fig. 4a), late instar nymphs ($\chi^2 = 17.82$; $df = 1$; $P < 0.001$; Fig. 4b), and adults ($\chi^2 = 41.71$; $df = 1$; $P < 0.001$; Fig. 4c).

Additionally, adult abundances also varied among cultivars (effect of cultivar in final GLMM model: $\chi^2 = 56.16$; $df = 3$; $P < 0.001$). Adult abundances were higher on *Syringa pekinensis* 'Morton' [model estimated mean (lower and upper 95 % CI): 0.37 (0.22, 0.63)] and *Malus* 'Donald Wyman' [0.24 (0.14, 0.42)] compared to *Malus sargentii* 'Select A' [0.015 (0.0056, 0.042)] and *Amelanchier x grandiflora* 'Autumn Brilliance' [0.011 (0.0035, 0.035)].

The distribution of *H. halys* individuals on fruits, leaves, and bark also changed with experimental treatment and differed among insect life stages (Fig. 4, Insets). Notably, most adults were found on the fruits of control (fruit present) trees, whereas early and late instar nymphs were found predominantly on leaves (χ^2 test of association between life stage and proportion of individuals on fruit, bark, and leaves: $\chi^2 = 55.7$; $df = 4$; $P < 0.0001$).

Discussion

H. halys is considered widely polyphagous, feeding on and damaging many vegetables, row crops, small fruits, tree fruits, and ornamental and wild trees (Bergmann et al. 2014; Rice et al. 2014). A broad diet breadth is beneficial in balancing nutrients (Simpson and Raubenheimer 1993; Behmer 2009), diluting toxins (Freeland and Janzen 1974;

Guglielmo et al. 1996), and increasing the availability of acceptable resources for generalist consumers (Bernays and Minkenberg 1997). Despite using a broad range of resources, however, generalists often specialize on particular blends of nutrients to meet dietary and stoichiometric needs (Behmer et al. 2002; Fagan et al. 2002). For instance, high-protein plant parts such as seeds are a key part of the diet of many omnivorous insects (Eubanks and Denno 1999; Eubanks et al. 2003).

Here, we suggest that although it feeds as a broad generalist, *H. halys* could be considered a fruit specialist, seeking and moving among woody plants that differentially bear fruit in space and time. Fruits and seeds have high levels of carbohydrates and nitrogen, providing valuable resources for phytophagous insects (Mattson 1980). Adults and late instar nymphs were three times as abundant on trees with mature compared to immature fruits (Fig. 1), were observed more on the fruits themselves as fruits matured (Fig. 2), and failed to colonize trees from which fruits were removed (Fig. 4).

Furthermore, differences in *H. halys* abundance among cultivars in the fruit removal experiment may also be related to fruit availability. For example, *Amelanchier* fruited early and had dropped its fruits by the end of July. Peak abundances of *H. halys* late instar nymphs and adults, however, occurred mid-summer (see also Nielsen and Hamilton 2009; Haye et al. 2014), leading to a mismatch between the phenology of this stink bug and *Amelanchier* peak fruit production. Further differences in *H. halys* abundance among a broader set of cultivars is part of an ongoing investigation (Bergmann et al. *In Prep*).

Adult *H. halys* were also able to track resources as they became available through the season (Fig. 3). This

Fig. 4 The response of stink bugs to experimental fruit removal over time. Plotted are abundances (mean number per tree ± 1 SE) of *H. halys* on trees with fruits present (*filled symbols, solid lines*; n = 32) and fruits removed (*open symbols, dashed lines*; n = 32) in weekly samples from 13 June to 2 Sept 2014 for early instar nymphs (**a**), late instar nymphs (**b**), and adults (**c**). *Insets* show the distribution of *H. halys* individuals within trees on fruits and flowers (*white*), bark (*black*), and leaves (*gray*) on control (*fruit present*) trees
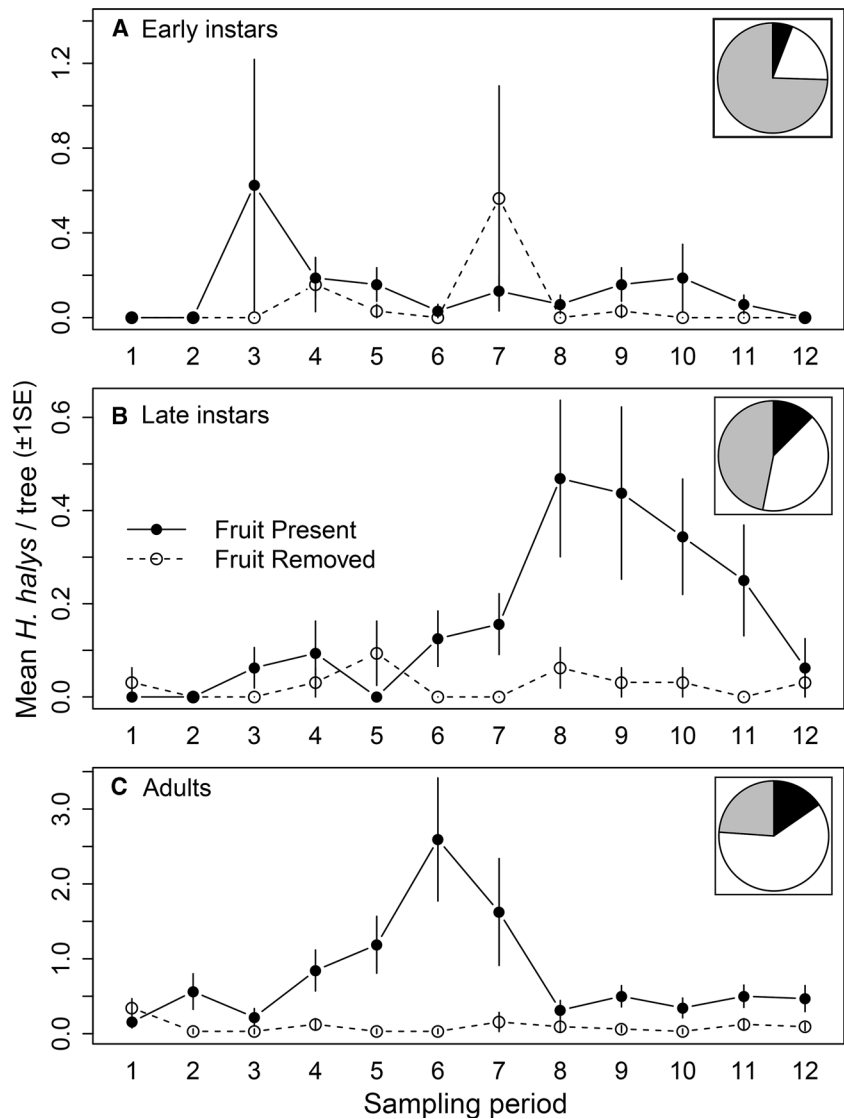
resource tracking behavior, common among many polyphagous insect herbivores (Kennedy and Storer 2000), could be used to develop management strategies for this pest. In regions invaded by *H. halys*, the presence and maturity of fruit will likely dictate where and when *H. halys* will be found, cause damage, and potentially be controlled. We suggest that where *H. halys* is a significant nuisance home invader, the composition of the surrounding landscape may play a key role in determining how much of a nuisance it actually may be, as well as contribute to its potential as a crop pest in the landscape.

Given the importance of mature fruits that we show here, it is reasonable to expect that ornamental and forest plants carrying ripe fruits at the beginning of the growing season are ideal resources for overwintered adults. In temperate regions where *H. halys* undergoes an obligate winter diapause, overwintered adults feed on ornamental

and wild host plants and have a pre-oviposition period when the female undergoes ovarian development (Nielsen and Hamilton 2009). Thus, spring-fruiting trees are key resources for *H. halys* that could potentially be targeted for management. The abundance of spring-fruiting trees likely influences fecundity and local population sizes and, as a result, influences the size of the population that disperses to crops later in summer. Similarly, at the end of the growing season, when *H. halys* may be storing up resources for diapause, the risk of home invasion may be higher where fruiting landscape trees are available and in close proximity to residences.

Breaking the synchrony (both spatially and temporally) between the availability of ripe fruit resources and mobile *H. halys* life stages will be a key strategy to controlling stink bug populations. Given that adult *H. halys* largely utilize residential homes for overwintering (Rice et al.

2014), and ornamental and wild host plants in spring for feeding (Nielsen and Hamilton 2009), control could be achieved by designing landscapes with fruitless cultivars of trees, or with trees fruiting after spring insect emergence and prior to dispersal in the fall. Removal of fruits from existing landscape trees could also be investigated as a potential way to control *H. halys*. These strategies will likely reduce the overall population size of *H. halys* in landscapes, reduce risk to crops, and limit home invasions. Targeting fruiting resources for monitoring and control will also be a key strategy to mitigate and prevent further damage caused by *H. halys* in nascent infestations in Europe and around the world.

Author contribution statement

All authors designed this study and collected data. HM and DV analyzed the data and wrote the manuscript. All the authors contributed substantially to edits and approved the final manuscript.

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