

Landscape Factors Influencing Stink Bug Injury in Mid-Atlantic Tomato Fields

Kevin B. Rice,¹ Rachael R. Troyer, Kristal M. Watrous, John F. Tooker, and Shelby J. Fleischer

Department of Entomology, The Pennsylvania State University, University Park, PA (ricekevinb@gmail.com; troyerachael@gmail.com; kwatrous@gmail.com; tooker@psu.edu; sjf4@psu.edu), and ¹Corresponding author, e-mail: ricekevinb@gmail.com

Subject Editor: Allan Showler

Received 3 June 2016; Editorial decision 15 October 2016

Abstract

Landscape structure and diversity influence insect species abundance. In agricultural systems, adjacent crop and non-crop habitats can influence pest species population dynamics and intensify economic damage. To investigate the influence of landscape factors on stink bug damage in agricultural systems, we assessed stink bug damage from 30 processing tomato fields in the mid-Atlantic United States and analyzed landscape structure and geographic location. We found that forest shape and size, and geographic location strongly influenced stink bug damage. Landscapes with larger forest edge in southern portions of the mid-Atlantic region experienced the greatest damage, perhaps owing to the introduction of the invasive brown marmorated stink bug. We conclude that landscape structure will likely influence damage rates in nearby agricultural fields.

Key words: tomato, landscape diversity, *Halyomorpha halys*, BMSB

Landscapes can influence insect population dynamics by providing pest species with alternative host plant species and overwintering sites that effect insect pest pressure (With 2002, Moeser and Vidal 2004, Gardiner et al. 2009, Bahlai et al. 2010, Woltz et al. 2012). Local crop and non-crop habitats surrounding agricultural fields can exacerbate damage caused by pest species. For instance, soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is an exotic, invasive insect species in North America that is a major pest of soybeans, *Glycine max* L. Merrill (Ragsdale et al. 2004, 2007), and common buckthorn, *Rhamnus cathartica* L., an invasive shrub, is the principle overwintering host (Voegtlin et al. 2005). Soybean fields with surrounding landscapes containing buckthorn experience earlier infestations, higher probabilities of establishment (Orantes et al. 2012), and greater soybean aphid densities (Bahlai et al. 2007, Heimpel et al. 2010). In Asia, landscape factors affect the spread of invasive rice water weevil, *Lissorhoptus oryzophilus* Kuschel, and manipulating landscape structure aids in managing this species (Wang et al. 2011). Therefore, landscapes which support high insect populations can increase pest pressure and economic damage.

In the United States, processed tomatoes are a \$1.3-billion industry (Hartz et al. 2008, USDA, NASS 2014), and stink bug feeding injury can result in economic damage. Stylet punctures and salivary enzymes from stink bug feeding cause deformed fruit (“cat-facing”), blemishes on outer skins of tomatoes, and internal tissue damage (Peiffer and Felton 2014, Rice et al. 2014). Stink bug damage reduces economic value of processing tomatoes because those processed as sauce due to

stink bug damage receive a lower price for growers than cut or whole-pack tomatoes (Letter of permission from Scott Hoffman enclosed with this submission). Stink bugs are highly mobile (Oda et al. 1980, Yanagi and Hagihara 1980, Zhang et al. 1993, Rice et al. 2014), and adults often move among multiple host plant species (Wang and Wang 1988; Fujisawa 2001; Lee et al. 2013, 2014; Wiman et al. 2015). Therefore, agricultural fields surrounded by an abundance and diversity of alternative host plant species may increase pest pressure, resulting in greater crop injury. Determining landscape factors associated with increased stink bug damage in agricultural commodities will help managers focus scouting efforts and target insecticide treatments in areas with high probability of damage.

Brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), is an invasive, herbivorous insect species introduced to the mid-Atlantic (Garipey et al. 2014, Xu et al. 2014) that feeds on hundreds of host plant species (Bergmann et al. 2013), often resulting in severe economic damage (American/Western Fruit Grower 2011, Rice et al. 2014); thus, landscape composition may influence agricultural damage caused by *H. halys*. Therefore, agricultural fields surrounded by an abundance and diversity of alternative host plant species may allow *H. halys* to increase pest pressure, inflicting greater damage on crops.

This study investigates landscape factors associated with stink bug damage in processing tomato in mid-Atlantic states. We hypothesized that surrounding landscape classification (agricultural, orchard, forest, miscellaneous), shape, and size will influence stink bug damage.

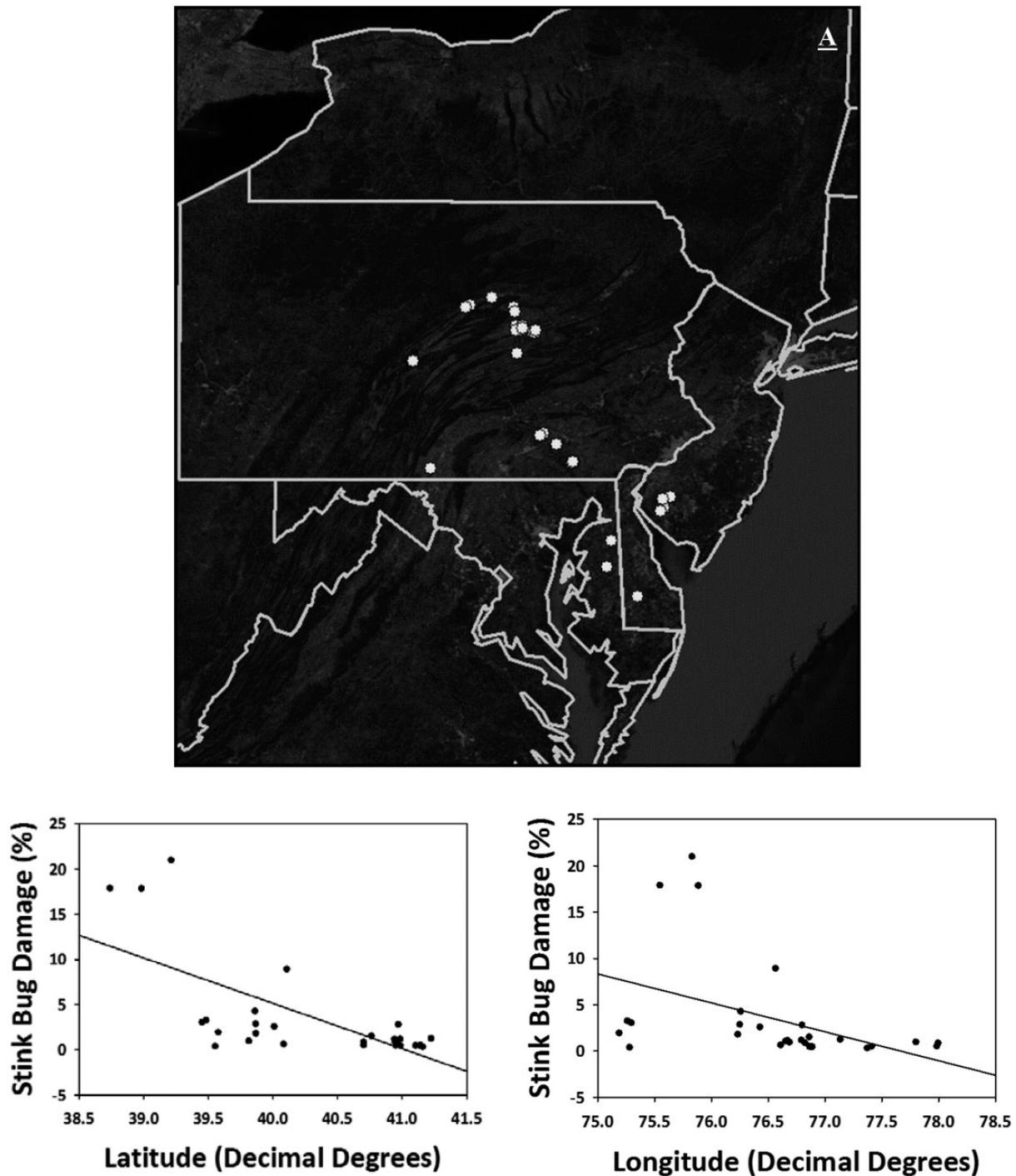


Fig. 1. (A) Location of 30 processing tomato fields in the mid-Atlantic United States sampled for stink bug damage and (B) increased percent field damage from stink bug feeding in southern (best fit regression line: $Y = -0.05x + 2.06$) and (C) eastern ($Y = 0.031X + 2.42$) locations.

We quantified stink bug damage for five fields in central Pennsylvania in 2012, and 30 fields growing processing tomato from four states in 2013, and analyzed surrounding landscapes at each field to determine the influence of landscape factors on damage rates.

Materials and Methods

Preliminary studies in 2012 to estimate stink bug densities with visual counts prior to insecticide treatments within fields resulted in

very low numbers, even though fruit damage was observed (S.J.F., unpublished). Therefore, we turned to measuring damage rates directly, aiming for a metric most relevant to the production of processing tomatoes. During 2012, we quantified stink bug damage from five processing tomato fields in Pennsylvania, and in 2013, we evaluated damage from 30 mid-Atlantic tomato fields (Fig. 1A). Damage was assessed as fruit arrived at a commercial processing plant in central Pennsylvania. A mechanical probe, consisting of a cylinder and bottom claw, collected two ~ 11.3 kg (~ 25 lb.) subsamples from each truck. Samples were pooled, washed, weighed,

Table 1. Landscape factors associated with stink bug damage (β , R^2 , and P values, $\alpha = 0.1$) for three landscape classifications in processing tomato in central Pennsylvania during 2012

Area	Landscape factor	Landscape class		
		Forest ns	Agriculture ns	Miscellaneous ns
	Class area			
Patch	Number of patches	ns	ns	−0.0075, 0.82, 0.035
	Mean patch size	ns	ns	0.0000034, 0.79, 0.042
	Median patch size	ns	ns	ns
	Patch size CV	ns	ns	ns
	Patch size SD	0.0000022, 0.66, 0.096	ns	ns
Edge	Total edge	ns	ns	ns
	Edge density	ns	ns	ns
	Mean patch edge	ns	ns	ns
Shape	Mean shape index	ns	ns	ns
	Area weighted mean shape index	ns	−0.073, 0.81, 0.037	ns
	Mean perimeter-area ratio	ns	1.3, 0.68, 0.086	ns
	Mean patch fractional dimension	ns	ns	ns
	Area weighted mean patch fractional dimension	ns	ns	ns

and then placed on a conveyer belt for visual survey of stink bug feeding damage. We recorded the number of damaged fruit per sample. If outer damage signs were inconclusive, we verified stink bug damage by peeling the skin and inspecting for white corky tissue, a defining stink bug damage trait (Rice et al. 2014). We recorded the mass of 100 tomatoes from each sample. To estimate percent field damage for each sample, we divided sample mass by mass of 100 fruits that was then divided into the number of damaged fruits in a sample (Eq. 1). Shapiro–Wilk test indicated normality violation ($P < 0.0001$); therefore, we log-transformed percent field damage.

$$\begin{aligned} \% \text{ field damage} \\ = \frac{\# \text{ of damaged fruit per sample}}{(\text{Sample mass/mass of 100 tomatoes from field})} \end{aligned}$$

Eq. 1. Calculation of percent stink bug damage from each sample.

Multiple truckloads arrived at the processing plant for each field, depending on the size and yield of that field. We averaged percent damage for each field (average of 7.5 truckloads per field). We considered each field a replicate, and at least 922 m separated each field from another (average 10 km to the nearest field). To determine sugar concentration, we analyzed four fruit per sample with a Reichert AR200 refractometer to calculate brix content.

We estimated landscape classes, and factors about patches of each landscape class (McGarigal and Marks 1995) in the area surrounding each field, using spatial databases and Arc GIS software (ArcGIS 10.1). We recorded in a .csv file in (X,Y) format, the decimal degree GPS coordinates of the center of each sampled field. ArcCatalog transformed the .csv file into a feature class using the World Geodetic System (WGS; 1984 coordinate format), which was then projected onto an empty map in ArcGIS. Tracing each field's outline at a constant resolution of 200 m utilizing National Agriculture Imagery Program aerial photography created a polygon feature class. Buffering each field outline by 250 m made a polygon feature class that represented surrounding landscape area while excluding the field. The National Agricultural Statistics Service (NASS) Cropscape Cropland raster layer provided detailed landscape and cropscape information. We used the extract-by-mask tool to cut the NASS raster layer to buffer polygon outlines that output a raster layer, which we converted into a polygon feature class.

We re-assigned the NASS landscape categories within the buffer zone into four classes: 1) agriculture (vegetables, field crops, and small fruit), 2) forest (deciduous and coniferous trees), 3) orchard (apple and peach), and 4) miscellaneous. The miscellaneous category included development, bodies of water, and all other rare landscape classes. Intersecting the reclassified polygon NASS layer with the original buffer layer related individual fields with their corresponding landscape patches in one concise attribute table. Converting the final feature class into a shape file saved outside of the geodatabase allowed Patch Analyst, a software extension in ArcView GIS, to analyze landscape patches by field. We calculated 14 landscape factors for each landscape class using the Patch Analyst software extension in ArcView (Table 1) for each field, determining the shape and size of each landscape category within the 250-m buffer zone.

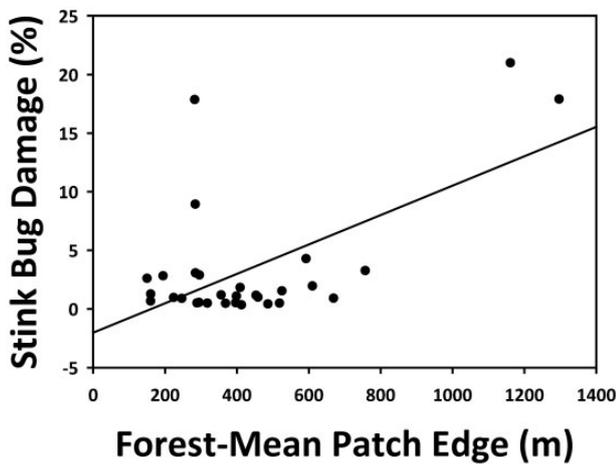
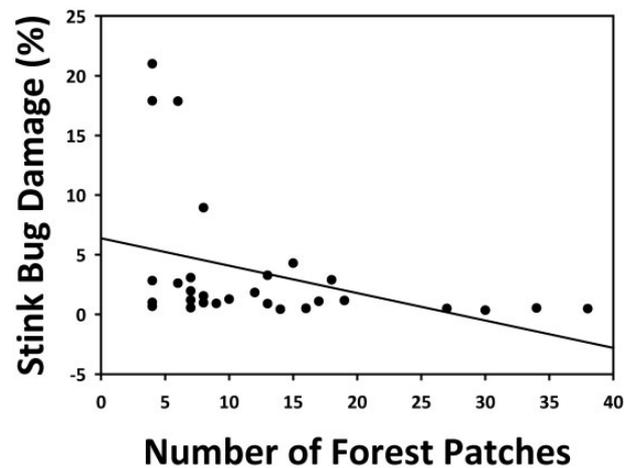
Samples included four cultivars. To determine if cultivar (variety 3402, 3406, 4007, and 5108) influenced damage rates, we compared percent damage with ANOVA (SAS Institute 2004 version 9.4 Proc GLM; $\alpha = 0.05$). We used simple linear regression to examine the effect of brix content and geographic location (latitude and longitude) on percent damage ($\alpha = 0.05$). We analyzed landscape classes extracted from the NASS database and landscape factors estimated with Patch Analysis with simple linear regression (SAS Proc REG), using percent farm damage as the response variable, retaining classes and factors with significant ($\alpha = 0.1$) prediction of damage. We used Pearson's correlation (SAS Proc CORR) to detect correlated predictor variables. When variables were correlated, we retained the variable with the most biological relevance. We analyzed the relationship of field damage with remaining landscape factors, latitude, and longitude using multiple regression (SAS Proc REG), and ranked models using Akaike's information criteria (AIC). Damage rates between years were compared using Wilcoxon–Mann–Whitney because of violation of normality.

Results

Damage rates differed between 2012 and 2013 ($\chi^2 = 9.3$, $P = 0.002$); thus, each year was analyzed independently. During 2012, brix content did not affect stink bug damage ($F_{1,5} = 2.52$, $P = 0.19$), and because all but one field planted the same variety, effects of cultivar were not compared. Also, because all fields in 2012 came from a similar geographic area, we did not analyze for a latitude or

Table 2. Landscape factors associated with stink bug damage (β , R^2 , and P values, $\alpha = 0.1$) for three landscape classifications in processing tomato from 30 farms in 2013

Area	Landscape factor	Landscape class			
		Forest ns	Agriculture ns	Orchard ns	Miscellaneous
	Class area				
Patch	Number of patches	-0.068, 0.28, 0.0024	ns	ns	ns
	Mean patch size	0.00004, 0.22, 0.009	ns	ns	ns
	Median patch size	0.00004, 0.15, 0.03	ns	ns	ns
	Patch size CV	ns	ns	ns	-0.005, 0.16, 0.03
	Patch size SD	ns	ns	ns	-0.00002, 0.18, 0.02
Edge	Total edge	-0.0001, 0.12, 0.06	ns	ns	-0.0002, 0.26, 0.004
	Edge density	ns	ns	ns	-152, 0.19, 0.02
	Mean patch edge	0.002, 0.22, 0.009	ns	ns	ns
Shape	Mean shape index	ns	ns	ns	ns
	Area weighted mean shape index	ns	ns	ns	ns
	Mean perimeter-area ratio	ns	ns	ns	ns
	Mean patch fractional dimension	ns	ns	ns	ns
	Area weighted mean patch fractional dimension	ns	ns	ns	ns

**Fig. 2.** Positive relationship between forest mean patch edge and percent field damage from stink bug feeding (best fit regression line: $Y = 0.002X - 5.04$).**Fig. 3.** Negative relationship between percent field damage from stink bug feeding and number of forest patches (best fit regression line: $Y = -0.068X - 3.29$).

longitude effect. During 2013, damage did not differ among cultivars ($F_{3,30} = 1.86$, $P = 0.16$) or brix content ($F_{1,30} = 0.27$, $P = 0.61$). During 2013, damage rates did, however, vary significantly among geographic locations. Fields at southern sites experienced greater damage compared with northern sites ($F_{1,30} = 24.43$, $P < 0.0001$, $R^2 = 0.47$; Fig. 1B), and eastern sites had greater damage than western sites ($F_{1,30} = 6.5$, $P = 0.017$, $R^2 = 0.19$; Fig. 1C).

2012 Landscape Analysis

Stink bug damage in processing tomato correlated with six patch-analysis landscape factors distributed among three landscape classes (Table 1). After correlated variables were removed, only two remained. Forest patch size standard deviation was positively correlated and the mean patch size of the miscellaneous class was negatively associated with stink bug damage.

2013 Landscape Analysis

Stink bug damage in processing tomato correlated with nine patch-analysis landscape factors distributed between two landscape classes (Table 2). Unexpectedly, we did not detect an effect on stink bug

damage from agricultural and orchard landscape classes; in simple linear regressions, only factors associated with forest and miscellaneous landscape classes predicted damage. After removing correlated variables, only two landscape factors, both in the forest landscape class, remained. Forest mean patch edge was positively and significantly associated with stink bug damage (Fig. 2; $F_{1,30} = 7.83$, $P = 0.009$), and the number of forest patches was negatively correlated with damage (Fig. 3; $F_{1,30} = 11.12$, $P = 0.002$). We combined the four significant predictor variables (forest mean patch edge, number of forest patches, longitude, and latitude), analyzed eight candidate multiple regression models, and ranked them using AIC. Forest mean patch edge and latitude produced the model with the lowest AIC, and an adjusted R^2 of 0.52 (Table 3).

Four fields had high damage rates, ranging from 9 to 21%, and thus held potential to exert a relatively larger influence on the regression analyses. We believe these are not outliers, and accurately represent fields with high damage, because each of the data points used in our analyses represents a mean of multiple truckloads per field. Nevertheless, when we removed these fields and reanalyzed the data, 20 factors predicted damage, including factors in the forest, agriculture, orchard, and miscellaneous classes (Table 4). Agriculture edge

density, miscellaneous total edge, and longitude produced the model with the lowest AIC, and an adjusted R^2 of 0.37 (Table 5).

Discussion

Landscape structure can affect establishment, spread, and impact of pest species (Sakai et al. 2001, With 2002, Venugopal et al. 2014).

Table 3. Summary of models for predicting stink bug damage in processing tomato

Model	AIC	Adjusted R^2
Forest mean patch edge, latitude	-193.0873	0.52
Forest mean patch edge, latitude, longitude	-192.0810	0.52
Forest mean patch edge, number of forest patches, latitude	-191.6131	0.52
Forest mean patch edge, number of forest patches, latitude, longitude	-190.4337	0.51
Latitude, longitude	-189.4352	0.45
Latitude, longitude	-187.7968	0.43
Number of forest patches, latitude	-187.5363	0.43
Number of forest patches, latitude, longitude	-185.8470	0.41
Forest mean patch area, number of forest patches	-186.4868	0.41

Because stink bug adults appear to move within landscapes to feed upon multiple host plant species, (Yanagi and Hagihara 1980, Hoebeke and Carter 2003, Funayama 2004, Nielson and Hamilton 2009, Martinson et al. 2013), we explored the influence of landscape structure and geographic location on stink bug damage to tomatoes. By analyzing loads of tomato fruit as they arrived at the processing plant, we were able to obtain field-scale estimates of damage rates. In both years, forest landscape factors were strongly associated with stink bug damage, suggesting adjacent patches of forest in agricultural systems may increase stink bug population abundance.

Among the forest landscape class, forest patch size standard deviation in 2012 and mean patch edge, mean patch size, and median patch size in 2013, correlated positively with damage. Furthermore, multiple regression models with the lowest AIC retained forest mean patch edge as an explanatory variable. Thus, forest shape and size most strongly influenced stink bug damage.

This effect was likely driven by several life-history traits of *H. halys*, the most abundant stink bug in the mid-Atlantic (Leskey and Hogmire 2005, Nielsen et al. 2011). For instance, *H. halys* are strongly associated with forest because they feed upon woody stems, flowers, fruits, and leaves of deciduous trees (Hoebeke and Carter 2003, Nielson and Hamilton 2009, Martinson et al. 2013), and adults often move between trees and agricultural systems (Yanagi

Table 4. β , R^2 , and P values ($\alpha = 0.1$) for landscape factors associated with stink bug damage in processing tomato during 2013 with four potential outliers removed

Area	Landscape factor	Landscape class			
		Forest ns	Agriculture ns	Orchard 0.00011, 0.099, 0.065	Miscellaneous -0.0000033, 0.21, 0.011
	Class area				
	Number of patches	-0.038, 0.20, 0.013	ns	0.16, 0.097, 0.066	ns
Patch	Mean patch size	ns	ns	0.00077, 0.16, 0.024	ns
	Median patch size	ns	ns	0.0011, 0.17, 0.022	ns
	Patch size CV	ns	ns	0.01, 0.075, 0.095	-0.0034, 0.18, 0.017
	Patch size SD	ns	ns	ns	-0.000013, 0.16, 0.024
	Total edge	-0.000064, 0.083, 0.084	ns	0.0010, 0.10, 0.063	0.000043, 0.21, 0.011
Edge	Edge density	ns	97.75, 0.20, 0.046	693.37, 0.10, 0.063	
	Mean patch edge	ns	ns	0.007, 0.17, 0.023	ns
	Mean shape index	ns	ns	0.87, 0.17, 0.021	ns
Shape	Area weighted mean shape index	ns	ns	0.81, 0.17, 0.021	-0.48, 0.16, 0.024
	Mean perimeter-area ratio	ns	ns	7.81, 0.17, 0.022	ns
	Mean patch fractional dimension	ns	ns	0.72, 0.17, 0.022	ns
	Area weighted mean patch fractional dimension	ns	ns	0.72, 0.17, 0.022	ns

Table 5. Summary of models for predicting stink bug damage in processing tomato with four potential outliers removed

Model	AIC	Adjusted R^2
Agricultural edge density, forest total edge, miscellaneous total edge, longitude	0.37	-23.10
Agricultural edge density, miscellaneous total edge, longitude	0.37	-23.87
Agricultural edge density, forest total edge, orchard total edge, longitude	0.36	-23.02
Agricultural edge density, forest total edge, longitude	0.36	-23.8
Agricultural edge density, forest total edge, orchard total edge, longitude	0.36 miscellaneous total edge	-21.99
Agricultural edge density, forest total edge, longitude, latitude	0.35	-22.36
Agricultural edge density, orchard total edge, miscellaneous total edge, longitude	0.35	-22.32
Agricultural edge density, miscellaneous total edge, longitude, latitude	0.35	-22.22
Agricultural edge density, forest total edge, miscellaneous total edge, longitude,	0.34 latitude	-22.33
Agricultural edge density, forest total edge, orchard total edge, longitude	0.34 latitude	-21.29
Agricultural edge density, miscellaneous total edge, latitude	0.33	-22.4
Agricultural edge density, forest total edge, orchard total edge, latitude	0.33	-21.52
Agricultural edge density, forest total edge, orchard total edge, longitude	0.33 latitude, miscellaneous total edge	-20.08

and Hagihara 1980, Funayama 2004, K.B.R., unpubl.), possibly to optimize nutritional intake (Raubenheimer et al. 2009). This movement behavior among plant species may be typical for pentatomid species, including *H. halys*, which may experience higher fitness and survival when mixing diets (Panizzi 1987, Panizzi and Slansky 1991, Panizzi and Saraiva 1993, Velasco and Walter 1993, Panizzi 1997, Medal et al. 2012). Agricultural fields that border forests may, therefore, experience higher stink bug densities, especially in region invaded by *H. halys*.

Halyomorpha halys is an “edge species” because populations typically concentrate along field margins (Leskey et al. 2012a, Rice et al. 2014, Venugopal et al. 2014). Adult *H. halys* emerging from overwintering sites in the forest may initiate these edge populations (Leskey et al. 2012a, Lee et al. 2014), and then they may benefit from higher plant species diversity at the field margin. As a result, crop fields adjacent to forest patches may experience greater *H. halys* damage as larger bug populations move away from these edges owing to competition or as they seek various nutrients at different points in their lives. Although our sampling from truckloads at a processing plant could not distinguish the species of stink bug causing the damage, the 2012 preliminary in-field sampling revealed only *H. halys* as the stink bug species in the field. Sweep net and black light sampling indicate that *H. halys* is the most abundant stink bug species in mid-Atlantic field crops and orchards (Leskey and Hogmire 2005, Nielsen et al. 2011). Also, stink bug damage rates associated with harvested processing tomatoes in the mid-Atlantic were extremely low prior to the arrival of *H. halys* (S.J.F., unpublished data). Therefore, we believe the majority of stink bug damage was due to *H. halys*.

Unexpectedly, number of forest patches correlated negatively with stink bug damage during 2013. Forest edge, or edge density regardless of land use class, may be more important than the number or size of forest or other patches. When we removed the influence of potential outliers (fields that had the highest damage rates), geographic position continued to be a significant factor, and while the relevant landscape classes expanded to include both forest, agricultural, and miscellaneous, edge density (in this case, agricultural edge density) remained the highest ranked variable.

In addition to landscape edges, geography influenced stink bug damage. Fields in southern and eastern locations had greater injury, which is likely an artifact of *H. halys* invasion history. *Halyomorpha halys* was first reported from eastern Pennsylvania in 1996 (Hoebeke and Carter 2003); therefore, eastern locations are closer to the invasion epicenter and likely had greater *H. halys* densities. As the invasion front spreads westward, this pattern could diminish. Greater damage in warmer southern locations may be attributable to environmental influences that strongly affect *H. halys* phenology and population dynamics (Nielsen et al. 2016).

The “miscellaneous landscape” class contained areas without host plants, such as bodies of water, and human developments (homes and outbuildings). Railroads and urban development have been implicated for facilitating geographic expansion of *H. halys* soon after establishment (Wallner et al. 2014). Railroads were not located near our fields, but we found negative relationships between damage rates in tomatoes and miscellaneous landscape metrics that included human-made structures, such as outbuildings. Human developments might positively influence *H. halys* populations during establishment and spread but have less effect on agricultural damage rates as populations increase and host plant availability becomes more important.

The best fit model for predicting stink bug damage in processing tomato prioritized 2 out of 64 measured variables: forest mean

patch edge and latitude. These variables with the lowest AIC scores are likely good predictors for stink bug damage in other agricultural commodities. Forests provide *H. halys* with overwintering sites (Hoebeke and Carter 2003, Nielson and Hamilton 2009, Martinson et al. 2013, Lee et al. 2014), and deciduous trees may provide important nutritional benefits. In our landscape, latitude may reflect population development, as influenced by invasion history and degrees days for development. It should be noted, however, that landscapes with less forested areas may produce different predictor variables.

In both years, forest landscape factors were important predictors of damage from stink bugs in agricultural systems. Targeted management decisions along forest edges, such as increased scouting, trap cropping, or, at the extreme, treating field edges with insecticides, may help alleviate damage (Soergel et al. 2015). Alternatively, crop managers may be able to expect decreased levels of damage by moving particularly sensitive crops farther from forest edges. Landscape analysis can be a useful tool for predicting potential pest damage and locating high-risk landscapes that will likely experience greater economic damage. Modifying these habitats or scouting more intensively in these landscapes may deter establishment or mitigate damage from pest species.

Acknowledgments

We thank William Mitchell for helping quantify stink bug damage. We thank Debbie Masser, Scott Hoffman, Ken Martin, and Furman Foods for allowing access to the processing facility, and contributing supporting data about farms and fields. This material is based on work that is supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award number 2011-01413-30937.

References Cited

- American/Western Fruit Grower 2011. Brown marmorated stink bug causes \$37 million in losses to mid-Atlantic apple growers. (<http://www.growingproduce.com/article/21057/brown-marmorated-stink-bug-causes-37-million-losses-to-mid-atlantic-apple-growers>) (accessed 9 August 2013).
- Arc GIS 2012. Arc GIS, version 10.1, Redlands, CA
- Bahlai, C. A., J. A. Welsman, A. W. Schaafsma, and M. K. Sears. 2007. Development of soybean aphid (Homoptera: Aphididae) on its primary overwintering host, *Rhynchospora cathartica*. *Environ. Entomol.* 36: 998–1006.
- Bahlai, C. A., S. Sikkema, R. H. Hallett, J. Newman, and A. W. Schaafsma. 2010. Modeling distribution and abundance of soybean aphid in soybean fields using measurements from the surrounding landscape. *Environ. Entomol.* 39: 50–56.
- Bergmann, E., K. M. Bernhard, G. Bernon, M. Bickerton, S. Gill, C. Gonzales, G. C. Hamilton, C. Hedstrom, K. Kamminga, C. Koplinka-Loehr, et al. 2013. Host plants of the brown marmorated stink bug in the U.S. (http://www.stopbmsb.org/where-is-bmsb/host-plants/#host_plants_table) (accessed 15 September 2013).
- Fujisawa, T. 2001. Damage and control of the brown marmorated stink bug in apple orchards. *Jpn. Agric. Technol.* 45: 42–47.
- Funayama, K. 2004. Importance of apple fruits as food for the brown-marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae). *Appl. Entomol. Zool.* 39: 617–623.
- Gardiner, M. M., D. A. Landis, C. Gratton, N. Schmidt, M. O’Neal, E. Mueller, J. Chacon, G. E. Heimpel, and C. D. DiFonzo. 2009. Landscape composition influences patterns of native and exotic lady beetle abundance. *Divers. Distrib.* 15: 554–564.
- Gariepy, T. D., T. Haye, H. Fraser, and J. Zhang. 2014. Occurrence, genetic diversity, and potential pathways of entry of *Halyomorpha halys* in newly invaded areas of Canada and Switzerland. *J. Pest Sci.* 87: 17–28.

- Hartz, T., G. Miyao, J. Mickler, M. LeStrange, S. Stoddard, J. Nunez, and B. Aegerter. 2008. Processing tomato production in California. University of California, Cooperative Extension. Publication 7228.
- Heimpel, G. E., L. E. Frelich, D. A. Landis, K. R. Hopper, K. A. Hoelmer, Z. Sezen, M. K. Asplen, and K. Wu. 2010. European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. *Biol. Invasions* 12: 2913–2931.
- Hoebeke, E. R., and M. E. Carter. 2003. *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): A polyphagous plant pest from Asia newly detected in North America. *Proc. Entomol. Soc. Wash.* 105: 225–237.
- Lee, D. H., J. C. Cullum, J. L. Anderson, J. L. Daugherty, L. M. Beckett, and T. C. Leskey. 2014. Characterization of overwintering sites of the invasive brown marmorated stink bug in natural landscapes using human surveyors and detector canines. *PLoS ONE* 9: e91575. doi:10.1371/journal.pone.0091575.
- Lee, D. H., B. D. Short, S. V. Joseph, J. C. Bergh, and T. C. Leskey. 2013. Review of the biology, ecology, and management of *Halyomorpha halys* (Hemiptera: Pentatomidae) in China, Japan, and the Republic of Korea. *Environ. Entomol.* 42: 627–641.
- Leskey, T. C., and H. W. Hogmire. 2005. Monitoring stink bugs (Hemiptera: Pentatomidae) in mid-Atlantic apple and peach orchards. *J. Econ. Entomol.* 98: 143–153.
- Leskey, T. C., G. C. Hamilton, A. L. Nielsen, D. F. Polk, C. Rodriguez-Saona, J. C. Bergh, D. A. Herbert, T. P. Kuhar, D. Pfeiffer, G. P. Dively, et al. 2012a. Pest status of the brown marmorated stink bug, *Halyomorpha halys* in the USA. *Outlooks Pest Manage.* 23: 218–226. DOI: 10.1564/23oct07.
- Martinson, H. M., M. J. Raupp, and P. M. Shrewsbury. 2013. Invasive stink bug wounds trees, liberates sugars, and facilitates native Hymenoptera. *Ann. Entomol. Soc. Am.* 106: 47–52.
- McGarigal, K., and B. J. Marks. 1995. Spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. US Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Medal, J., T. Smith, A. Fox, A. Santa Cruz, A. Poplin, and A. Hodges. 2012. Rearing the brown marmorated stink bug *Halyomorpha halys* (Heteroptera: Pentatomidae). *Fla. Entomol.* 95: 800–802.
- Moeser, J., and S. Vidal. 2004. Do alternative host plants enhance the invasion of the maize pest *Diabrotica virgifera* (Coleoptera: Chrysomelidae) in Europe? *Environ. Entomol.* 33: 1169–1177.
- Nielson, A. L., and G. C. Hamilton. 2009. Seasonal occurrence and impact of *Halyomorpha halys* (Hemiptera: Pentatomidae) in tree fruit. *Ann. Entomol. Soc. Am.* 102: 608–616.
- Nielsen, A. L., G. C. Hamilton, and P. W. Shearer. 2011. Seasonal phenology and monitoring of the non-native *Halyomorpha halys* (Hemiptera: Pentatomidae) in soybean. *Environ. Entomol.* 40: 231–238.
- Nielsen, A. L., S. Chen, and S. J. Fleischer. 2016. Coupling developmental physiology, photoperiod, and temperature to model phenology and dynamics of an invasive Heteropteran, *Halyomorpha halys*. *Front. Physiol.* 7: 165. doi: 10.3389/fphys.2016.00165
- Orantes, L. C., W. Zhang, M.A.R. Mian, and A. P. Michel. 2012. Maintaining genetic diversity and population panmixia through dispersal and not gene flow in a holocyclic heteroecious aphid species. *Heredity* 109: 127–134.
- Oda, M., T. Sugiura, Y. Nakanishi, and Y. Uesumi. 1980. Ecological studies of stink bugs attacking the fruit trees. Observations of the seasonal prevalence by light trap, ecology, and occurrence on fruit trees and mulberry by field observations. *Bull. Nara Agric. Exp. Stn.* 11: 53–62.
- Panizzi, A. R. 1987. Nutritional ecology of seed-sucking insects of soybean and their management. *Mem. Inst. Oswaldo Cruz, Rio de Janeiro* 82: 161–175.
- Panizzi, A. R. 1997. Wild hosts of pentatomids: ecological significance and role in their pest status on crops. *Ann. Rev. Entomol.* 42: 99–122.
- Panizzi, A. R., and S. I. Saraiva. 1993. Performance of nymphal and adult southern green stink bug on an overwintering host plant and impact of nymph to adult food-switch. *Entomol. Exp. Appl.* 68: 109–115.
- Panizzi, A. R., and F. Slansky. 1991. Suitability of selected legumes and the effect of nymphal and adult nutrition in the southern green stink bug (Hemiptera: Heteroptera: Pentatomidae). *J. Econ. Entomol.* 84: 103–113.
- Peiffer, M., and G. W. Felton. 2014. Insights into the saliva of the brown marmorated stink bug *Halyomorpha halys* (Hemiptera: Pentatomidae). *PLoS ONE* 9: e88483. doi: 10.1371/journal.pone.0088483
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004. Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97: 204–208.
- Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter, I. V. MacRae, E. W. Hodgson, M. E. O'Neal, K. D. Johnson, R. J. O'Neil, C. D. DiFonzo, et al. 2007. Economic threshold for soybean aphid (Hemiptera: Aphididae). *J. Econ. Entomol.* 100: 1258–1267.
- Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. Nutrition, ecology, and nutritional ecology: Toward an integrated framework. *Funct. Ecol.* 23: 4–16.
- Rice, K. B., C. J. Bergh, E. J. Bergmann, D. J. Biddinger, C. Dieckhoff, G. P. Dively, H. Fraser, T. D. Garipey, G. C. Hamilton, T. Haye, et al. 2014. Biology, ecology and management of brown marmorated stink bug (*Halyomorpha halys*). *J. Integr. Pest Manage.* 5: 1–13.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, et al. 2001. *Ann. Rev. Ecol. Syst.* 32: 305–332.
- SAS Institute 2004. SAS, version 9.4. SAS Institute, Cary, NC.
- Soergel, D. C., N. Ostiguy, S. J. Fleischer, R. R. Troyer, E. G. Rajotte, and G. Krawczyk. 2015. Sunflower as a potential trap crop of *Halyomorpha halys* (Hemiptera: Pentatomidae) in pepper fields. *Environ. Entomol.* 44: 1581–1589.
- USDA, NASS 2014. Census of agriculture. US Department of Agriculture, National Agricultural Statistics Service, Washington, DC.
- Velasco, L.R.L., and G. H. Walter. 1993. Potential of host-switching in *Nezara viridula* (Hemiptera: Pentatomidae) to enhance survival and reproduction. *Enviro. Entomol.* 22: 326–333.
- Venugopal, P. D., P. L. Coffey, G. P. Dively, and W. O. Lamp. 2014. Adjacent habitat influence on stink bug (Hemiptera: Pentatomidae) densities and the associated damage at field corn and soybean edges. *PLoS ONE* 9: e109917. doi:10.1371/journal.pone.0109917.
- Voegtlin, D. J., R. J. O'Neil, W. R. Graves, D. Lagos, and H.J.S. Yoo. 2005. Potential winter hosts of soybean aphid. *Ann. Entomol. Soc. Am.* 98: 690–693.
- Wallner, A. M., G. C. Hamilton, A. L. Nielsen, N. Hahn, E. Green, and C. R. Rodriguez-Saona. 2014. Landscape factors facilitating the invasive dynamics and distribution of the brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae), after arrival in the United States. *PLoS ONE* 9: e95691.
- Wang, Y., and Y. Wang. 1988. Studies on the pear bug, *Halyomorpha picus*. *Acta Agric. Bor-Sin.* 3: 96–101.
- Wang, Z., J. Wu, H. Shang, and J. Cheng. 2011. Landscape connectivity shapes the spread pattern of the rice water weevil: A case study from Zhejiang, China. *Environ. Manage.* 47: 254–262.
- Wiman, N. G., V. M. Walton, P. W. Shearer, S. I. Rondon, and J. C. Lee. 2015. Factors affecting flight capacity of brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae). *J. Pest Sci.* 88: 37–47.
- With, K. A. 2002. The landscape ecology of invasive spread. *Conserv. Biol.* 16: 1192–1203.
- Woltz, J. M., R. Isaacs, and D. A. Landis. 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. *Agric. Ecosyst. Environ.* 152: 40–49.
- Xu, J., D. M. Fonesca, G. C. Hamilton, K. A. Hoelmer, and A. L. Nielsen. 2014. Tracing the origin of US brown marmorated stink bugs, *Halyomorpha halys*. *Biol. Invasions* 16: 153–166.
- Yanagi, T., and Y. Hagihara. 1980. Ecology of the brown marmorated stink bug. *Plant Prot.* 34: 142–148.
- Zhang, C. T., D. L. Li, H. F. Su, and G. L. Xu. 1993. A study on the biological characteristics of *Halyomorpha picus* and *Erthesina fullo*. *For. Res.* 6: 271–275.