ABSTRACT

Title of Document:	SPATIAL HETEROGENEITY OF STINK BUG (HEMIPTERA: PENTATOMIDAE) POPULATIONS IN AGRICULTURAL SYSTEMS.
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Knowledge on spatial patterns of insect pest populations and the ecological processes influencing these patterns can be directly applied to the management of pests in agricultural systems. Recent increases in stink bug populations, importantly the invasive *Halyomorpha halys* (Stål 1855), has caused unprecedented economic losses in the mid-Atlantic United States. To inform integrated pest management programs, I quantified the spatial heterogeneity of stink bug population density in field crops at multiple spatial scales (field edge, entire fields and regional), and identified the associated environmental factors and the underlying ecological mechanisms (i.e. climatic tolerances, resource quality and availability).

At corn and soybean field edges, highest density of stink bugs was limited to the first few crop rows. At some study sites, fields adjacent to woods and buildings harbored higher density of stink bugs than those adjacent to open areas. Injury to corn

kernel damage, and soybean pod and seed increased with stink bug density, and was highest at the field edges. Stink bug density was also positively associated with yield loss in soybean.

In entire fields of corn-soybean, *H. halys* was found in very low density or absent beyond 25m from the field edge. At study sites with high stink bug populations, interpolated density values showed potential dispersal of *H. halys*, particularly adults and large nymphs, from corn into soybean, coinciding with the end of dough stage in corn and beginning of soybean seed development stage.

Temperature and developed areas, and proportion of forest and crop areas were important predictors of regional patterns in *H. halys* and *Chinavis hilaris* abundance, respectively. For *Euschistus servus*, temperature and forest cover influenced patterns at broad spatial scale. Adjacent habitat influence, with highest abundance along woods, on stink bug density was limited to within field scale, and difference in abundance between sites was driven primarily by temperature gradient.

These results directly inform field level stink bug management strategies through planting date and orientation of fields in the landscape, and for timing and intensity of treatments, as well as area-wide management. This research also identified roles of temperature and landscape in facilitating or impeding invasive pest populations.

SPATIAL HETEROGENEITY OF STINK BUG (HEMIPTERA:
PENTATOMIDAE) POPULATIONS IN AGRICULTURAL SYSTEMS

By

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2014

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Preface

This dissertation contains an overall abstract, introduction, three research chapters, and a project summary with management implications. Each research chapter is presented in a manuscript form; therefore, some of the background and methods may be repeated. Tables and figures are embedded within each of the research chapters, as appropriate. A single reference section is provided at the end, for literature cited throughout the dissertation.

Dedication

To Amma and Appa, for giving me the best possible education despite all the

struggles and hardships.

To Sahana and Sara

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Introduction

Spatial context of ecological processes in landscapes

Understanding patterns over space and time is central to ecology and the assessment of spatial patterns is a fecund paradigm in ecology (Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004; Jombart, Dray, & Dufour, 2009; Legendre, 1993). Biological communities and associated biota interact with the physical environment at definite spatial and temporal scales resulting in spatial structures (clustered, random or dispersed). Therefore, assessment and identification of the spatial structures in populations or communities is an important step toward unraveling the ecological processes that structure them (Borcard *et al.*, 2004; Dray *et al.*, 2012; Jombart *et al.*, 2009; Legendre & Fortin, 1989).

Spatial heterogeneity (*sensu* Dutilleul & Legendre, 1993), is vastly important for the study of populations, communities, ecosystems, and landscapes (Vinatier, Tixier, Duyck, & Lescourret, 2011). Environmental conditions, individual species traits, habitat characteristics (Tscharntke, Steffan-Dewenter, Kruess, & Thies, 2002) and neutral processes (Rosindell, Wong, & Etienne, 2008) all cause spatial heterogeneity in populations and communities. Species traits such as climatic tolerances, dispersal ability (Tscharntke & Brandl, 2004), sexual attraction by pheromones, or aggregative behaviors impact population dynamics and species distributions (Samalens & Rossi, 2011). Spatially correlated patterns of species distribution and abundance, or of communities, are influenced by environmental and

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habitat variables which are also spatially structured. Such an association is generally

referred to as environment induced spatial dependence (Jombart *et al.*, 2009;

Legendre, 1993; Wagner & Fortin, 2005). Besides environmental influences, species

distribution or abundance may also exhibit spatial dependence due to biotic processes

such as dispersal, intra- and inter-specific interactions and their own population

dynamics – commonly referred to as pure spatial dependence or spatial

autocorrelation (Borcard *et al.*, 2004; Dray *et al.*, 2012; Legendre, 1993; Peres-Neto

& Legendre, 2010) .

The spatial structures produced through environment induced spatial

dependence are expected predominantly to occur at broad spatial scales, while those

arising due to pure spatial dependence / spatial autocorrelation (biotic processes) at

intermediate to small spatial scales. Also, a combination of several processes

occurring at different scales could lead to an observed spatial pattern (Borcard *et al.*,

2004; Dray *et al.*, 2012; Jombart *et al.*, 2009; Legendre, 1993; Wagner & Fortin,

2005; Wiens, 1989). Thereby, testing for spatial pattern and identifying the scale of

occurrence could lead us to the ecological processes structuring species abundance (S.

Dray *et al.*, 2012).

Empirical studies linking species dispersal, species interactions, and resource

selection to spatial patterns of species distributions can inform basic and applied

ecology (Taylor, 1984; Tscharntke, Rand, & Bianchi, 2005; Vinatier *et al.*, 2011).

Studies that link ecological processes with observed spatial patterns in the field have

broad implications for managing natural populations (e.g., effect of habitat

fragmentation on endangered species conservation; Matern, Drees, Kleinwächter, & Assmann, 2007) or anthropogenic landscapes such as agricultural ecosystems. For example, relating crop damage to the spatial distribution of populations may indicate improved methods for controlling pest species (Eber, 2004; Rodeghiero & Battisti, 2000). Dispersal of pest species between crop and non-crop habitats is central to many ecological processes important for managing agricultural ecosystems, and concepts in spatial ecology are relevant for developing management strategies for controlling agricultural pest species (Tscharntke *et al.*, 2005).

Community structure, species distribution and abundance, and biotic interactions may depend on habitat characteristics at spatial scales greater than the local habitat patch (Thies, Steffan-Dewenter, & Tscharntke, 2003; Tscharntke *et al.*, 2005). Therefore, a landscape (*sensu* Turner, 1989) perspective considering the areal extent, spatial arrangement, and connectivity of habitats across different spatial scales is needed to determine the mechanisms controlling ecological patterns and processes occurring at the local (i.e., patch) scale (Gardiner *et al.*, 2009; Kareiva, Mullen, & Southwood, 1990; O'Rourke, Rienzo-Stack, & Power, 2010; Polis, Anderson, & Holt, 1997; Thies & Tscharntke, 1999; Tischendorf & Fahrig, 2000; Turner, 1989). Landscape connectivity is the linkage among habitat patches (e.g., fields) through the dispersal of the organism of interest (With, Gardner, & Turner, 1997), which is mediated by the abundance and configuration of habitats (or land-use types) in the landscape (structural connectivity) and by the ability of organisms to access them (functional connectivity). Pest insects might require more time and energy to locate their preferred hosts in diverse landscapes than in simple landscapes (O'Rourke *et al.*,

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2010). This may result in increased mortality, acceptance of lower quality hosts, and less energy available for reproduction (den Belder, Elderson, van den Brink, & Schelling, 2002; O'Rourke *et al.*, 2010). Species population dynamics are largely dependent on the spatial arrangement of habitat patches, the interaction between landscape structure and individual species traits (Goodwin & Fahrig, 2002), and indirect effects of the landscape (e.g. natural enemy distribution; Kruess & Tscharntke, 1994). For instance, landscapes dominated by a single preferred habitat or crop type allow easy movement between habitats, however even heterogeneous or apparently fragmented landscapes are connected if species dispersal abilities are sufficient to colonize neighboring patches or fields (Margosian, Garrett, Hutchinson, & With, 2009).

Many factors determine how a species perceives landscape structure, such as - individual responses to spatial heterogeneity of habitats with regards to insect movement (rate and tortuosity of movement in different habitats, response to edges, dispersal range), habitat affinities, and assessment of habitat quality (With *et al.*, 1997). The influence of landscape context differs between species, and communities constitute species that are differently influenced by the landscape (Kareiva *et al.*, 1990; With, 2002) due to species specific traits. Species dispersal abilities and resource specificity determine the magnitude of effect of landscape structure on pest abundance (Dunning, Danielson, & Pulliam, 1992; Tscharntke & Brandl, 2004). By facilitating or impeding movement of organisms among resource patches, landscape composition and configuration affect dispersal, source–sink dynamics, neighborhood effects, and metapopulation dynamics (Dunning *et al.*, 1992). Thus, characterizing the

spatial heterogeneity in populations of target pest species may help understand the relationships between landscape structure and species-specific responses (Tischendorf & Fahrig, 2000).

Spatial variation in agricultural insect pest populations and their management

Insect population densities typically are spatially heterogeneous (Liebhold, Rossi, & Kemp, 1993; van Helden, 2010). This heterogeneity is important to understand predator-prey and predator-parasite relationships, intraspecific competition, and for development of insect pest management strategies (Liebhold *et al.*, 1993). Knowledge of the spatial distribution of insect pest abundances directly informs pest monitoring planning (Taylor, 1986), prediction of abundances (Liebhold *et al.*, 1993), and strategies for pest management (Cocu, Harrington, Hullé, & Rounsevell, 2005; Nestel, Carvalho, & Nemny-Lavy, 2004). This leads to the formation of integrated pest management (IPM) systems such as site-specific IPM or regional/area wide IPM. Knowledge of the spatial pattern of insect pest abundance and distribution within fields through the growing season is required for precision farm management practices and effective insect pest management (Blom, Fleischer, & Smilowitz, 2002; Winder, Perry, & Holland, 1999). For example, management of insect pests based on localized insect density within a field, rather than uniform management of insect pests based on average densities throughout the field, is the crux of site-specific insect pest management (review by Park, Krell, & Carroll, 2007).

Beyond the purview of a single field, and instead of the field-by-field approach of most traditional control programs, area-wide pest management is a

strategy aimed at suppressing key pest populations by applying a uniform tactic over large geographic areas encompassing multiple fields (Marcos Kogan, 1998). Area wide or regional pest management strategies have succeeded in slowing the spread of insect pests (Sharov, Leonard, Liebhold, & Clemens, 2002), suppressing pests to reduce densities below economic injury threshold levels (Vargas *et al.*, 2001), and eradicating insect pests (reviews by Brewer & Goodell, 2012; Kogan, 1998). Area wide or regional pest management is an option that could be suitable for pests such as stink bugs as they are mobile, have a wide host range, and are distributed through a large geographic area. Insect pests with these characteristics can escape from single fields where control measures are applied and colonize other non-treated fields (Park, Perring, Farrar, & Gispert, 2006). As part of both site–specific and area-wide IPM strategies, however, frequent scouting and measurement of the spatial variability of insect pest abundances within a field or across fields in a larger landscape is required. Spatially explicit distribution maps of pest insects showing within-field/ landscape level variability of abundance can allow spatially targeted pest management strategies at field and landscapes scales (Park *et al.*, 2007).

Agricultural landscapes in the United States and economic costs of insect pests

Homogenization of agricultural landscape (i.e., few crops types accounting for a significant proportions of overall crop area) can facilitate widespread disease and pest outbreaks, which can cause widespread economic loss and jeopardize the food supply (Margosian *et al.*, 2009). Simplification of landscapes through agricultural intensification and reduction in natural habitats reduces natural enemy populations

and may inhibit natural biocontrol services and increase pest problems (Bianchi, Booij, & Tscharntke, 2006; Landis, Gardiner, Werf, & Swinton, 2008). Just four crop types (corn – 385,933 km^2, soybean – 309,721 km^2, wheat – 227,258 km^2, and cotton – 42116 km^2) constitute a third of the total crop area in conterminous United States (NASS - USDA, 2014). Due to the regional concentration of crops (Parker, 2002) and the accidental introduction of potential crop pests from other continents into the United States (42 insect species between 1997-2001 (Work, McCullough, Cavey, & Komsa, 2005), crop production in the United States is highly vulnerable to disease and damage by insect pests (Margosian *et al.*, 2009).

The economic damage and the potential for future damage caused by the spread of exotic insect crop pests are enormous. Within the United States an estimated 217,724 metric tonnes of chemicals are used in agricultural lands, contributing to the $11 billion spent on pesticides (Fernandez-Cornejo, Nehring, Sinha, Grube, & Vialou, 2009). Despite this, about 37 % of crop yields in the United States are lost to pests (Pimentel *et al.*, 1992), with losses and damages due to invasive insect crop pests estimated at $13.5 - $14.4 billion. This loss includes $500 million per annum for control costs of insect pests alone (Pimentel, Lach, Zuniga, & Morrison, 2000; Pimentel, Zuniga, & Morrison, 2005). It has to be noted that these estimates are derived from years prior to the adoption of transgenic crop technology and the wide use of prophylactic seed treatments that have eliminated additional insecticide use in many crops. Parker (2002) reported that the United States Dept. of Agriculture and other government organizations annually spend more than $1 billion

for research, risk assessment, response to outbreaks, public outreach, education, and extension.

Throughout the world, stink bugs are major pests of economically important crops (Panizzi & Slansky, 1985; Panizzi, 1997). This includes legumes (e.g. soybean), cereals (e.g. rice and wheat), cotton, tree crops (e.g. citrus, oil palms, coconut, and cocoa) and coffee (see review by Panizzi 1997). In North America, most phytophagous pentatomid species of economic importance belong to the subfamily Pentatominae. Of the approximately 40 genera and 180 species in this subfamily found in North America, only five species are considered serious economic pests (McPherson & McPherson, 2000). They are the southern green stink bug (SGSB) *Nezara viridula* (Linnaeus 1758), rice stink bug (RSB) *Oebalus pugnax* (Fabricus 1775), green stink bug (GSB) *Acrosternum hilare* Say 1832, brown stink bug (BSB) *Euschistus servus* (Say 1832), and one spotted stink bug (OSSB) *Euschistus variolarius* (Palisot de Beauvois 1837).

Information on the nationwide economic losses due to the stink bugs in the United States is sparse, but few reports indicate that in the Southern States, approximately an economic loss of $73 million due to stink bug damage to soybean crops alone (Akin *et al.*, 2011). Further, Musser & Catchot, (2008) reported that about $28.2 million was lost due to stink bug damages to soybean in Mississippi, while the annual estimated losses in Georgia soybean during 1971 to 1998 ranged from $1 million to $24 million (McPherson & McPherson, 2000). While stink bugs cause economic losses in the southern parts of United States, they were not considered

serious pests of crops in Mid-Atlantic States until recently. The most common stink

bugs in agricultural fields in Maryland are GSB and BSB, but these stink bugs were

not considered an important pest on corn and soybean and had little economic impact

in the Mid-Atlantic region (CABI, 2014; Leskey *et al.*, 2012; Nielsen, Hamilton, &

Shearer, 2011; Nielsen & Hamilton, 2009b). The recent explosion in populations of

the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål 1855) however,

has led to significant ecological impacts that may increase through time.

Ecological and economic effects of the invasive stink bug, *Halyomorpha halys*

H. halys is native to Asia with distributions in China, Japan and Korea, and

has steadily expanded in population number and distributional range since its

introduction into the United States near Allentown, PA during late 1990s (Hoebeke &

Carter, 2003). *H. halys* is now found in 41 states within conterminous United States.

It is polyphagous and feeds on more than 150 host plants including many fruit and

shade trees, woody ornamentals, legumes, and other various vegetables.

Phytophagous stink bug species generally feed on corn and soybean plants, but only a

small percentage of corn or soybean fields in the Mid-Atlantic States were affected by

stink bugs prior to the introduction of *H. halys*. In recent years, *H. halys* abundance

and associated crop damages have steadily increased in the region. *H. halys* is now a

serious agricultural pest and nuisance in residential and commercial buildings in

multiple Northeastern and Mid-Atlantic States (CABI, 2014; Leskey *et al.*, 2012).

Invasion by an introduced species may alter the community composition of

native stink bug communities by increasing the dominance of the invader and

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suppressing the abundance of native species (Daehler, 2003; Hejda, Pyšek, & Jarošík, 2009; Pimentel *et al.*, 2005). An increase in invasive species abundance may alter the effectiveness of existing management practices of agricultural ecosystems (Nielsen *et al.*, 2011). During the past two years, *H. halys* was commonly the most abundant stink bug species in both fruit crops and grain crops in the Mid-Atlantic region and had caused unprecedented damage during 2009 and 2010 (CABI, 2014; Leskey *et al.*, 2012; Nielsen & Hamilton, 2009b). In particular, *H. halys* was responsible for economic losses in apples and pears in NJ & PA (Nielsen & Hamilton, 2009b) and damage to an estimated 20% of the apples in the mid-Atlantic region amounting to economic loss of $37 million (Leskey *et al.*, 2012).

The scale and intensity of the *H. halys* outbreak in the Mid-Atlantic region has led to increased research efforts and the formation of the *H. halys* working group. Research efforts focused on understanding the *H. halys* invasion and developing management strategies have also recently increased. While the working group for the *H. halys* has included the assessment of landscape features associated with their abundances as a research priority, empirical studies and surveys at the landscape scale are lacking. The ability of farmers to manipulate pests such as *H. halys* requires knowledge of its distribution within fields and across large landscapes and of how prevailing environmental factors and regional land use / cover may inhibit or support pest outbreaks (O'Rourke *et al.*, 2010). However, there are currently no detailed assessments of the spatio-temporal patterns of *H. halys* populations within fields or at landscape scales. Very few studies quantify the stink bug related damage and yield loss in field crops (Owens, Herbert, Dively, Reisig, & Kuhar, 2013). Other than

climate related distributional range (Musolin, 2007) and predictive distribution models (Zhu, Bu, Gao, & Liu, 2012), detailed assessment on spatial structures in stink bug populations across large study area and the underlying ecological process, are currently not available.

The effect of landscape configuration and composition on the spread or containment of exotic pests informs how spatial patterns of resource distributions affect the various stages of the invasion process (With, 2002) and such an understanding of the landscape influences on pest invasion is important for developing effective management strategies. Therefore, an assessment of the spatial distribution and influence of resources and other landscape features on the populations of exotic pests may aid prediction and management of the spread of invasive species. Examining the environmental and landscape influences on *H. halys* populations at different spatial scales, can inform pest management decisions.

Research objectives and dissertation format

The main goals of my research were to (1) characterize the spatial heterogeneity of stink bug pest population dynamics in field crops, at multiple spatial scales (i.e. field edge, entire fields and regional landscape), (2) identify the environmental factors, potential underlying mechanisms (i.e. climatic tolerances, resource quality and availability), and their spatial scale of influence on stink bug population dynamics, and (3) inform field level and area-wide management of stink bug pests in field crops.

My first chapter characterized the density of stink bugs in the field edges of (0- 15m from field edge) field corn and soybean at different study sites. Specifically, I examined the influence of adjacent managed and natural habitats, and buildings on the density of stink bugs at different distances from the edge of corn and soybean fields. I also quantified the damage to corn grain, soybean pods and seeds and yield in relation to the observed stink bug densities, at different distances from field edge. Thereby, this chapter related the pattern of stink bug density at field edge to the crop damages. Results from this chapter have implications for stink bug pest management strategies in the form of crop placement and suggestions on spatially targeted timing and intensity of pest treatment solutions.

In the second chapter, I characterized the density of stink bugs throughout the entire fields of adjacent corn and soybean, and broadly examined the role of adjacent corn as a source of stink bugs that invade soybean. Specifically, I determined the influence of crop phenology on stink bug density and compared stink bug age class structure at various phenological stages of corn and soybean crops. As this was spatially explicit, I was able to document the spatial heterogeneity in stink bug density, through the growing season, across fields with adjacent corn and soybean. Finally, I compared the density of stink bugs in corn adjacent soybean field edges between sites with high and low overall stink bug density. Results from this chapter could provide inputs for decisions on planting date and orientation of fields in the landscape, and implications for timing and intensity of pest management treatments particularly at the interface of corn and soybean crops.

My third research chapter determined the environmental and multi-scale landscape factors that influenced spatial structures in stink bug abundances across mid-Atlantic region. I also tested several hypotheses to identify ecological mechanisms that structured stink bug populations at multiple spatial scales. Specifically, I examined the scale at which the abundance of stink bug species in the mid-Atlantic region were structured; the environmental and multi-scale landscape factors that were associated with stink bug abundance; and at which spatial scales they influenced stink bug abundance. Results from this chapter have implications for field level and area-wide management of stink bug pests. Finally, I summarized the results from the three chapters and discussed the various strategies for managing stink bugs in field crops of the mid-Atlantic region.

Chapter 1: Adjacent habitat influence on stink bug (Hemiptera: Pentatomidae) populations, and associated damage inflicted at field corn and soybean edges

Introduction

Agricultural systems are components within a heterogeneous landscape that strongly connect to and interact with the surrounding environment (Nestel *et al.*, 2004). The movement of insects between natural and agricultural environment has important implications for agricultural ecosystem functioning (Ekbom, Erwin, & Robert, 2000). The movement of pest insects to seasonal crop resources can be non-random and directional as pest species move in groups and settle in a contiguous manner over space (Stinner, Barfield, Stimac, & Dohse, 1983). This movement might result in the insect pest immigrating into the agricultural habitats in an aggregated manner in certain areas within the field (Nestel *et al.*, 2004). However, species-specific characteristics might influence the observed pest populations within agricultural habitats, and may cause different distribution patterns across other habitats into crops. For e.g. aggregations may occur along the field edges for some pest species immigrating between habitats.

The seasonal availability and suitability of source and recipient habitats in relation to the life stages of the mobile, polyphagous insect pest influence the dispersal dynamics of pests from sources to recipient habitats (Ekbom *et al.*, 2000; Kennedy & Margolies, 1985; Kennedy & Storer, 2000). Thus the knowledge about insect pest immigration and settlement within the field, with reference to habitats

adjacent to crops, can be used to effectively predict infestation risk of insect pests prior to their colonization and subsequent population increase (Nestel *et al.*, 2004).

Stink bugs in the family Pentatomidae are major pests of economically important crops (Panizzi, 1997) globally, and considered important pests in soybean *Glycine max* (L.) Merr. producing areas of the world (Panizzi & Slansky, 1985). While stink bugs cause economic losses in the southern parts of United States, they were not considered serious pests of crops in mid-Atlantic region until recently. The most common stink bugs in agricultural fields in the mid-Atlantic are *Chinavia hilaris* (Say 1832) and *Euschistus servus* (Say 1832), but these species have had little economic impact in the region (Nielsen *et al.*, 2011). The recent explosion in populations of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål 1855) however, has led to significant economic and ecological impacts.

Since its accidental introduction and discovery near Allentown, Pennsylvania, USA, *H. halys* has been detected in 41 states, and local populations and detections from Europe (Switzerland, France, Canada, Germany, Italy and Liechtenstein) have also been reported (CABI, 2014) . This polyphagous stink bug has a wide range of host plants including tree fruits, vegetables, field crops, ornamental plants, and native vegetation in its native and invaded ranges. Since 2010, serious crop losses have been reported for apples, peaches, sweet corn, peppers, tomatoes and row crops such as field corn and soybeans in the mid-Atlantic region(Leskey *et al.*, 2012). *H. halys* is also a nuisance pest in human dwellings. In this context, information on the buildup and movement of stink bugs into crops adjacent to managed and natural habitats and

the associated crop damage has direct implications for integrated pest management.

The dispersal and movement of various stink bug species between crops and other habitats has been addressed by many studies in the context of dispersal between habitats, adjacent habitat influences on populations in field edges and associated crop damage (Toscano & Stern, 1976; Jones & Sullivan, 1982; Outward, Sorenson, & Bradley, 2008; Tillman, Northfield, Mizell, & Riddle, 2009; Toews & Shurley, 2009; Pease & Zalom, 2010; Reay-Jones, 2010; Reeves, Greene, Reay-Jones, Toews, & Gerard, 2010; Reisig, 2011; Herbert & Toews, 2011; Olson, Ruberson, Zeilinger, & Andow, 2011; Tillman, 2011). However, these studies mainly pertain to stink bug communities in crops of southern U.S. and currently only anecdotal reports of high *H. halys* abundance in the edges of fields adjacent to woodlots (Leskey *et al.*, 2012) are available. Many stink bug species cause significant seed quality and yield losses in field corn *Zea mays* L. and soybean (Reisig, 2011; Brier & Rogers, 1991; Corrêa-Ferreira & De Azevedo, 2002; Daugherty *et al.*, 1964; McPherson, Douce, & Hudson, 1993; McPherson, Newsom, & Farthing, 1979; Ni *et al.*, 2010; Todd & Turnipseed, 1974), and stink bugs are also associated with the transmission of bacteria, fungi and other diseases (Clarke & Wilde, 1971; Medrano *et al.*, 2009; Mitchell, 2004). However, very few studies quantify field crop damage in relation to abundance of stink bug in the mid-Atlantic region (Owens *et al.*, 2013). Soybean is one of the preferred hosts for *H. halys* (Hoebeke & Carter, 2003), and both field corn and soybean constitute a very high proportion of overall crop area in the mid-Atlantic region and throughout the U.S. (NASS - USDA, 2014). Research efforts aimed at determining the role of adjacent habitat in influencing stink bug dispersal, population

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density and pattern of settlement into crops, hence, are indispensible for developing

control and management strategies of *H. halys* in row crops.

In this study I a) documented the species composition and within-field

distribution of stink bugs in field corn and soybean; b) examined the influence of

adjacent managed and natural habitats, and buildings on the density of stink bugs; and

c) related stink bug density to seed quality in field corn and soybean, and pod

development and yield in soybean. I expected *H. halys* to be the most abundant stink

bug in my study based on previous reports of stink species composition in mid-

Atlantic row crops (Nielsen *et al.*, 2011). I predicted higher density of stink bugs

along woods and buildings than open areas as they provide host plants and over-

wintering refuge (Lee, Short, Joseph, Bergh, & Leskey, 2013). I also predicted high

density of stink bugs at the field edge, reducing with distance into the field interior as

observed by anecdotal reports for *H. halys* (Leskey *et al.*, 2012).

Methods

Field selection & stink bug sampling strategy

The study was conducted at the USDA Beltsville Agricultural Research

Center at Beltsville*,* MD and University of Maryland Research and Education Center

facilities at Beltsville, Clarksville and Keedysville, MD. At these sites, field corn (30'

row spacing) and full season soybean (7' row spacing) fields with a portion of their

perimeter directly adjacent to wooded areas (henceforth woods), buildings (buildings,

houses and barns; henceforth buildings), mixed crops (alfalfa, sorghum, and

vegetable crops) and open, non-crop areas (henceforth open) were selected for sampling in 2012 and 2013. Corn fields were chosen as one of the adjacent habitat types *in lieu* of mixed crops for several soybean fields. In each field, the sampling layout included 4 transects, each with 8 sampling plots for a total of 32 samples. The sampling plots along four transects spaced 20 m apart were marked at distances 0, 1.5, 3, 4.5, 6, 9, 12, and 15 m from the edge to field interior. Stink bugs were enumerated at each sampling plot by carefully examining 10 consecutive corn plants and later converted to densities, or all plants within a semicircular area of 0.5 m radius (1.57 m^2) in soybean.

Visual counts were converted to densities and recorded for stink bug adults, nymphs, and egg masses of *H. halys*, *E. servus*, *C. hilaris*, *Murgantia histronica* (Hahn 1834), and *Thyanta custator* (Fabricius 1803). For corn, details on the planting density were used to calculate the length of 10 consecutive plants and were multiplied by the row distance to derive area sampled. Fields were repeatedly sampled weekly, between mid July – mid August in field corn and mid August – late September in soybean. Sampling coincided with the kernel development stages of corn (R2-R5; blister – dent; Hanway, 1963) and the seed development stages of soybean (R4-R7; full pod to physiological maturity (Fehr, Caviness, Burmood, & Pennington, 1971), which are associated with high *H. halys* and other stink bug species density (Leskey *et al.*, 2012; Nielsen *et al.*, 2011; Schumann & Todd, 1982). Details on the number of corn and soybean field edges with different adjacent habitats, and the sampling dates during 2012 and 2013 are provided in Table 1.1. A total of 4835 field corn plots in 32

fields, and 2968 soybean plots in 26 fields across all sites were sampled for stink bugs during 2012 and 2013.

Assessing seed quality in field corn and soybean

   To relate stink bug density to ear damage in corn, eight fields adjacent to different adjacent habitats were selected, which had the highest observed counts of stink bugs in 2013. Of these fields, 3, 3, 1 and 1 were adjacent to woods, buildings, mixed crops and open areas, respectively. In each field, 10 consecutive corn ears were collected at each sampling plot prior to harvest maturity and stored in cloth bags for drying. Planting details of the fields used for assessing corn damage are provided in Table 1.2. For each ear, the following data were recorded: 1) number of kernels damaged by stink bugs (identified by a characteristic puncture scar typically surrounded by a discolored cloudy marking); 2) number of collapsed kernels due to stink bug damage (this type of damage was carefully examined to distinguish between kernels damaged by stink bugs and dusky sap beetles, *Carcophilus lugubris* (Murray); 3) number of kernel rows around the ear; 4) length of one kernel row (mm); and 5) average width of individual kernels (mm). With the individual ear measurements, the total number of kernels was derived by dividing the kernel row length by the width of a kernel times the number of rows. Data were then summed across all ten ears and stink bug damage was expressed as the percentage of damaged and collapsed kernels in relation to total number of kernels per sample. A total of 2326 ears of corn from 252 sampling plots across 8 fields were assessed for stink bug damage.

To relate stink bug density to pod development prior to harvest, samples of 10 consecutive plants at each sampling site across transects of seven soybean fields in 2012-2013 were examined *in situ* to count the total numbers of pods with 3 or more seeds (full pods), pods with less than 3 seeds, and flat, immature pods (flat pods). For standardization, the proportions for each pod type were calculated for each sample. Pod quality data were collected from 64 plots in 2 fields adjacent to woods at Keedysville. Planting details for the fields used for assessing soybean seed damage are provided in Table 1.2. Of the seven fields sampled for seed quality data, two fields were adjacent to buildings and five fields were adjacent to woods, and all had the highest counts of stink bugs observed in each year. Once fields reached full senescence and were ready for harvest, twenty plants from each sampling site across all transects of the 7 fields were collected, stored in mesh bags, and allowed further drying for optimum thrashing. Seeds were removed from pods for each sample by a stationary motor-driven thrasher. Dirt, chaff, or un-thrashed pods were removed, and the remaining seed samples were then weighed to measure yield.

To assess seed quality, subsamples of 200-300 seeds were removed from each sample, counted, and weighed to calculate test weight (expressed as the weight per 100 seeds). Seed samples in 2012 were sieved to remove smaller, immature seed (<0.3 cm), whereas these smaller seeds were not removed from subsamples in 2013. In both years, seeds were individually examined and categorized into six groups as follows: 1) stink bug damaged seed, distinguished by a puncture scar and often surrounded by a discolored cloudy area; 2) moldy seed, characterized by having milky white or grayish crusty growth on surface, sometimes with cracks and fissures;

3) shriveled seed that appeared wrinkled and often undersized; 4) purple seed

recognized as purple or pink areas on the seed coat due to the fungus *Cercospora*

kikuchii Matsumoto & Tomoy 1925 (Walters, 1980); 5) green seed showing

discolored green tissue in cross section, rather than the normal yellow; and 6) normal,

undamaged seed. To standardize across samples, the percentage of seeds in each

category in relation to the total number of seeds were calculated. Due to differences

in the size grading protocol between years, there were minor differences in the

proportions of seeds in each category. Soybean seed quality data were collected for a

total of 154 sampling plots from 6 fields in 2012 and 2013.

Statistical Analyses

Adjacent habitat and distance from edge influences

      The influences of adjacent habitat and distance from field edge on the density

and distribution of stink bugs were analyzed by Generalized Linear Mixed Models

(GLMMs) based on Laplace approximation, with a Poisson-lognormal error

distribution and log link function (Bolker *et al.*, 2009). All analyses were performed

with fields as replicates and transects within fields as subsamples. For corn and

soybean data, analyses were performed on 3 separate datasets - all stink bug stages

combined, nymphs only, and adults only. For each of these datasets, GLMMs were

performed on the data pooled across species, years and study sites, and on data from

each study site pooled across years. Each sampling point along transect at a field edge

was treated as a random factor to control for repeated measurement (Pinheiro &

Bates, 2000); adjacent habitat, distance from edge, and their interaction were the

fixed effects, and stink bug density was the response variable. For the overall data models, study site and year were also treated as random effects.

Model building and selection procedures for the mixed effects modeling followed the procedures used by (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). First, several candidate models, each with different random effects but identical fixed effects, were tested to choose the optimal random effect model using a combination of AIC and BIC values for selection criteria. For all optimum fixed effect models, an initial full model analysis including individual and interactive effects of adjacent habitat (4 levels - woods, buildings, mix crop / corn and open) and distance from edge (8 levels - 0-15m) was performed. The significance of the fixed effects was determined by Wald χ^2 tests. If a significant interaction was found then model-estimated means were compared between all levels of adjacent habitat at each distance from the field edge, with a Bonferroni correction. If there was no significant interaction, then adjacent habitat and distance from edge were independently used as fixed effects and post-hoc model-estimated means comparisons were performed using Tukey's HSD. Models were evaluated for assumption appropriateness 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).

Table 1. 1. Details on field corn and soybean field edges with different adjacent habitats sampled for stink bugs and the sampling occasions at each field in Maryland, USA during 2012-2013.

Crop	Year	Site	Adjacent habitats (number of field edges)	Sampling dates (frequency)
Field Corn	2012	Beltsville	woods (4), buildings (3), mix crops (1), open (4)	10 July – 15 Aug (7 – 10 days)
		Clarksville	woods (1), buildings (1), mix crops (3)	10 July – 15 Aug (7 days)
	2013	Clarksville	woods (3), buildings (2), mix crops (3), open (2)	18 July – 22 Aug (7 days)
		Keedysville	woods (1), buildings (1), mix crops (1), open (2)	16 July – 20 Aug (7 days)
		Overall	woods (9), buildings (7), mix crops (8), open (8)	10 July – 22 Aug (7 - 10 days)
Soybean	2012	Beltsville	woods (2), buildings (3), corn (1), open (2)	23 Aug – 20 Sept (7 – 10 days)
		Keedysville	woods (2), buildings (1), corn (1), open (1)	30 Aug – 26 Sept (7 - 10 days)
	2013	Beltsville	woods (1), buildings (1), corn (1), open (1)	13 Aug – 06 Sept (7 days)
		Clarksville	buildings (1), corn (1), open (1)	16 Aug – 12 Sept (5 - 7 days)
		Keedysville	woods (2), buildings (2), corn (1), open (1)	15 Aug – 18 Sept (5 - 7 days)
		Overall	woods (7), buildings (8), corn (5), open (6)	13 Aug – 26 Sept (5 – 10 days)

Table 1. 2. Details on the field corn and soybean fields used for analyzing grain and seed damage in Maryland, USA during 2012-2013.

Crop	Year	Site	Field ID	Variety	Planting Date	Density / acre
Field Corn	2013	Clarksville	Corn1	Pioneer 1319HR	2-May-13	26000
			Corn2	DK6121	15-May-13	26000
			Corn3	Pioneer 1319HR	2-May-13	26000
			Corn4	Pioneer 1319HR	2-May-13	26000
			Corn5	DK6121	16-May-13	26000
			Corn6	NK74R3000GT	16-May-13	26000
		Keedysville	Corn7	Doebler 633HXR	23-Apr-13	26000
			Corn8	Doebler 633HXR	23-Apr-13	26000
Soybean	2012	Beltsville	Soy1	Asgrow 3030	11-May-12	155555
			Soy2	Asgrow 3030	11-May-12	155555
		Keedysville	Soy3	Doebler 633HXR	26-May-12	180000
			Soy4	Doebler 633HXR	4-Jun-12	180000
			Soy5	Doebler 633HXR	4-Jun-12	180000
	2013		Soy6	Seed Consultants SCS9360RR	22-May-13	180000
			Soy7	Doebler 633HXR	27-May-13	180000

Relating stink bug density and seed damage

Influences of stink bug density on damage to corn kernels were assessed using generalized linear models (GLMs) with poisson or quasi-poisson error distribution and log link function (Ver Hoef & Boveng, 2007). Percentage of collapsed and stink bug damaged seeds were used as response variables and mean stink bug density at distance from the edge as the explanatory variable. Mean stink bug density. For significant results, the coefficient of determination was calculated by Nagalkerke's pseudo R^2 statistic (Nagelkerke, 1991).

Linear regression was used to assess the influence of stink bug density on soybean pod development. To meet normality assumptions, response variable was square root transformed prior to analysis. Influence of stink bug density on soybean seed quality was assessed by linear mixed models (LMMs) with year as a random effect to account for minor differences in grading seed size protocols. LMMs were performed to relate stink bug density to the percentage of seeds in each category of seed quality. Influence of stink bug density on soybean yield was assessed by LMMs with field as a random effect to account for differences in soybean variety and other field conditions between sites. Data were log or square root transformed to meet normality requirements and the significance of the fixed effect was determined by Wald t-tests. Diagnostic plots of the models visualizing within-group residuals (standardized residuals vs fitted values, normal Q-Q plots, and histograms of residuals) and estimated random effects (normal Q-Q plots and pairs-scatter plot matrix) were used to assess model appropriateness. The coefficient of determination for the LMMs, based on the likelihood-ratio test, were calculated using Nagalkerke's

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pseudo R^2 statistic (Nagelkerke, 1991). Patterns in damage to corn kernels, soybean pods and seeds at different distances from edge, juxtaposed to stink bug density, were visualized by plotting average values of damage and stink bugs aggregated by distance.

All statistical analyses were performed in R program (R Development Core Team, 2011) and associated statistical packages. GLMMs were performed with package lme4 (Bates, Maechler, Bolker, & Walker, 2013) and LMMs with package nlme (Pinheiro *et al.*, 2013). Multiple comparisons of means for GLMMs were computed with R packages contrast (Kuhn, Weston, Wing, & Thaler, 2013) and multcomp (Hothorn, Bretz, Westfall, Heiberger, & Schuetzenmeister, 2013). GLMMs and LMMs estimated coefficients were extracted and plotted using package effects (Fox *et al.*, 2013). Coefficient of determination (pseudo R^2) for the GLM was calculated with package rms (Harrell, 2013), and with package MuMin (Bartoń, 2013) for LMMs.

Results

Species Composition and density

A total of 9440 individuals (66% nymphs; 34% adults) of four phytophagous stink bug species (*E servus*, *H. halys*, *C. hilaris*, and *M. histrionica*) were recorded in field corn, of which *H. halys* accounted for 97% of the total. Species composition varied among study sites and crop systems. *H. halys* comprised 57% of the sampled populations in corn at Beltsville, followed by *E. servus* (35%), whereas *H. halys*

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accounted for ~97% of all stink bugs at Clarksville and Keedysville. In soybean, a total of 9867 individuals (68% nymphs; 32% adults) of five phytophagous stink bug species (*E. servus, H. halys, C. hilaris, M. histrionic, T. custator*) were recorded, of which *H. halys* accounted for 93% of the total. *H. halys* comprised 83-85% of the stink bug numbers in soybean at Beltsville, while greater than 92% were *H. halys* at Clarksville and Keedysville. Results obtained from the statistical analyses hence pertained mainly to patterns of *H. halys* density, since this species constituted ~95% of all observed stink bugs in both field corn and soybean.

 Influences of adjacent habitat and distance from field edge

Field corn

For the analysis of overall stink bug data from field corn edges, the random effects used for the GLMM included the field, study site and year (Table 1.3). Results showed significant interactive influences of adjacent habitat and distance from edge on stink bug density (Wald $\chi^2 = 399.2$, df = 21, $P < 0.001$). Multiple comparison of means between adjacent habitats at each distance showed that density of stink bugs was significantly higher along woods compared to density in fields next to mixed crops and open areas at various distances (Figure 1.1A). Density along woods and buildings was not significantly different, although mean numbers of stink bugs were consistently higher along woods. Density at 15 m from field edge was not significantly different among adjacent habitats. Significant interactive influences of adjacent habitat and distance from edge on stink bug density was observed for the Clarksville and Keedysville data (Wald $\chi^2 = 43.9$, df = 21, $P = 0.002$ and Wald $\chi^2 =$

56.7, df = 21, $P < 0.001$, respectively) but not for Beltsville data (Wald $\chi^2 = 0.15$, df = 18, $P = 0.9$).

Multiple comparisons of means of stink bug density at Clarksville showed similar trends to the results of analyses of data pooled over all study sites, with density along woods higher than that of mixed crops and open areas at various distances (Fig 1.1B). However, stink bug density along woods at Keedysville was not significantly different from density at sites adjacent to mixed crops (Fig 1.1C). Also, corn fields at this study site had surprisingly higher stink bug density along the outside rows (0 m) adjacent to mixed crops than levels along outside rows next to woods. At Beltsville, where overall stink bug density was significantly lower in corn fields, adjacent habitat did not significantly influence density (Wald $\chi^2 = 0.21$, df = 3, $P = 0.917$); thus, multiple comparisons were not performed.

Table 1. 3. Summary of models used for selecting the optimal random effect in generalized linear mixed models prior to analyzing fixed effects for stink abundance in field corn and soybean edges. For each model, the fixed effects of adjacent habitat and distance from field edge remained constant. Based on the combination of Akaike Information Criteria (AIC) and the Bayesian information criteria (BIC) values received by each model, the best model (in bold) was chosen as the optimal random effect.

Crop	Random effect terms	df	AIC	BIC
Corn	No random effect	33	25184.19	25394.15
	1 | Year	33	19168.79	19378.99
	1 | Site	33	16586.12	16796.33
	1 | Field	33	15316.72	15526.92
	Year | Site	35	16560.91	16783.85
	1 | Field + 1 | Site	**34**	**15278.99**	**15495.56**
	1 | Site +1| Year	34	16565.34	16781.91
	1 | Field + 1 | Site + 1 | Year	35	15280.99	15503.93
Soybean	No random effect	33	17795.803	17993.3
	1 | Year	33	12833.196	13031.05
	1 | Site	33	11755.366	11953.22
	1 | Field	**33**	**9604.958**	**9802.814**
	Year | Site	35	18391.976	18601.82
	1 | Field + 1 | Site	34	9602.584	9806.436
	1 | Site +1| Year	34	11309.068	11512.92
	1 | Field + 1 | Site + 1 | Year	35	9600.673	9810.521

Soybean

The GLMM analysis of overall stink bug data treated field as the only random effect and showed significant interactive influences of adjacent habitat and distance on stink bug density (Wald χ^2 = 49.1, df = 21, $P < 0.001$; Table 1.3). Multiple comparisons of means showed that density of stink bugs were significantly higher at all distances from field edges along woods compared to density in fields next to open area habitats (Fig. 1.2A). Stink bug numbers along woods were also consistently higher than levels observed at field edges next to buildings and corn fields, but differences were not significant at all distances from field edges. Pooled over all habitat types, the highest density of stink bugs was recorded at the immediate field edge and declined considerably by 9 m and was lowest at 15 m.

GLMMs performed by study site on overall stink bug data showed significant interactive influence of adjacent habitat and distance from edge on density at Keedysville (Wald χ^2 = 47.8, df = 21, $P < 0.001$), but not at Clarksville (Wald χ^2 = 9.2, df = 14, $P = 0.818$) and Beltsville (Wald χ^2 = 26.6, df = 21, $P = 0.315$). Multiple means comparisons for Keedysville data showed significantly higher density at all distances from edge along woods and at distances up to 9 m along corn fields compared to levels next to open areas (Fig. 1.2B). Stink bug numbers were generally higher in soybean fields next to corn, though not statistically significant levels next to woods. Separate GLMMs testing the main effects of adjacent habitat and distance from field edge showed that stink bugs were significant more abundant in Beltsville

fields bordering woods and buildings that in fields next to corn and open habitats (Fig. 1.3A).

Pooled over all adjacent habitats, density at Beltsville was significantly higher along the immediate field edge compared to sample sites farther away from the edge where stink bug numbers were similar between 9-15 m (Fig 1.3B). Separate analysis of the Clarksville data showed a greater influence of buildings and corn fields on stink bug density compared to adjacent open habitats, though no edges of soybean fields next to woods were sampled at this study site (Fig. 1.3C). The gradient of stink bug density at Clarksville from the field edge showed similar patterns observed at Beltsville, with significantly higher numbers at the immediate edge, lower but similar levels between 9-15 m, and then declining further to 50 m (Fig. 1.3D).

The results of analyses performed on data sets of nymphs and adult stink bugs in both corn and soybean edges were broadly similar to that of the overall stink bug results presented above. Since the pattern observed in adult and nymph data sets were similar to that of the overall dataset, these results have not been presented here.

Figure 1. 1. Mean stink bug density in field corn in relation to different adjacent habitats and distance from the field edge. Estimates derived from poisson-lognormal GLMMs are plotted for overall stink bug data pooled over all study sites (A), Clarksville (B) and, Keedysville (C). Values presented here have been reconverted from their original link function estimated model coefficients. Vertical lines represent upper and lower 95% confidence intervals, hence not symmetrical around the estimated means. Mean densities within each distance interval with the same letter above them are not statistically different ($\alpha = 0.05$).
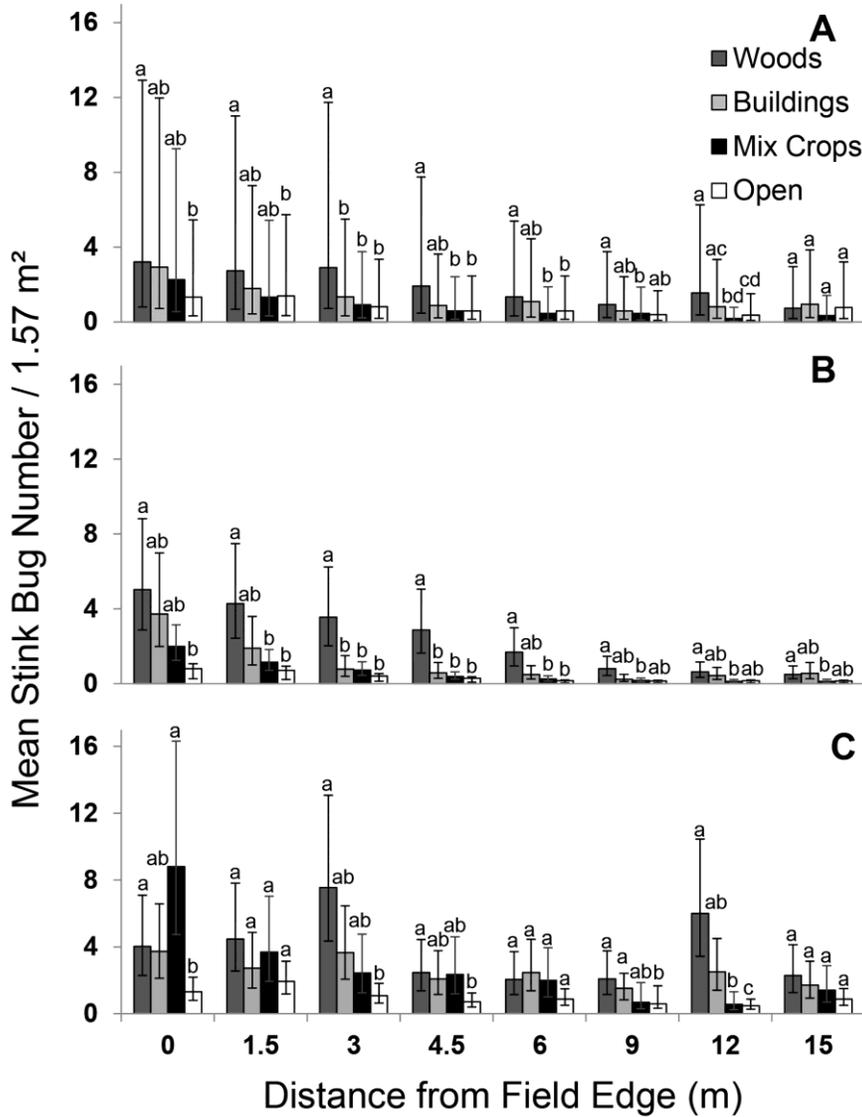
Figure 1. 2. Mean stink bug density in soybean field edges in relation to different adjacent habitats and distance from field edge. Estimates derived from poisson-lognormal GLMMs are plotted for overall stink bug data pooled over all study sites (A), and Keedysville (B). Values presented here have been reconverted from its original link function estimated model coefficients. Vertical lines represent upper and lower 95% confidence intervals, hence are not symmetrical around the estimated means. Mean densities within each distance interval with the same letter above them are not statistically different ($\alpha = 0.05$).
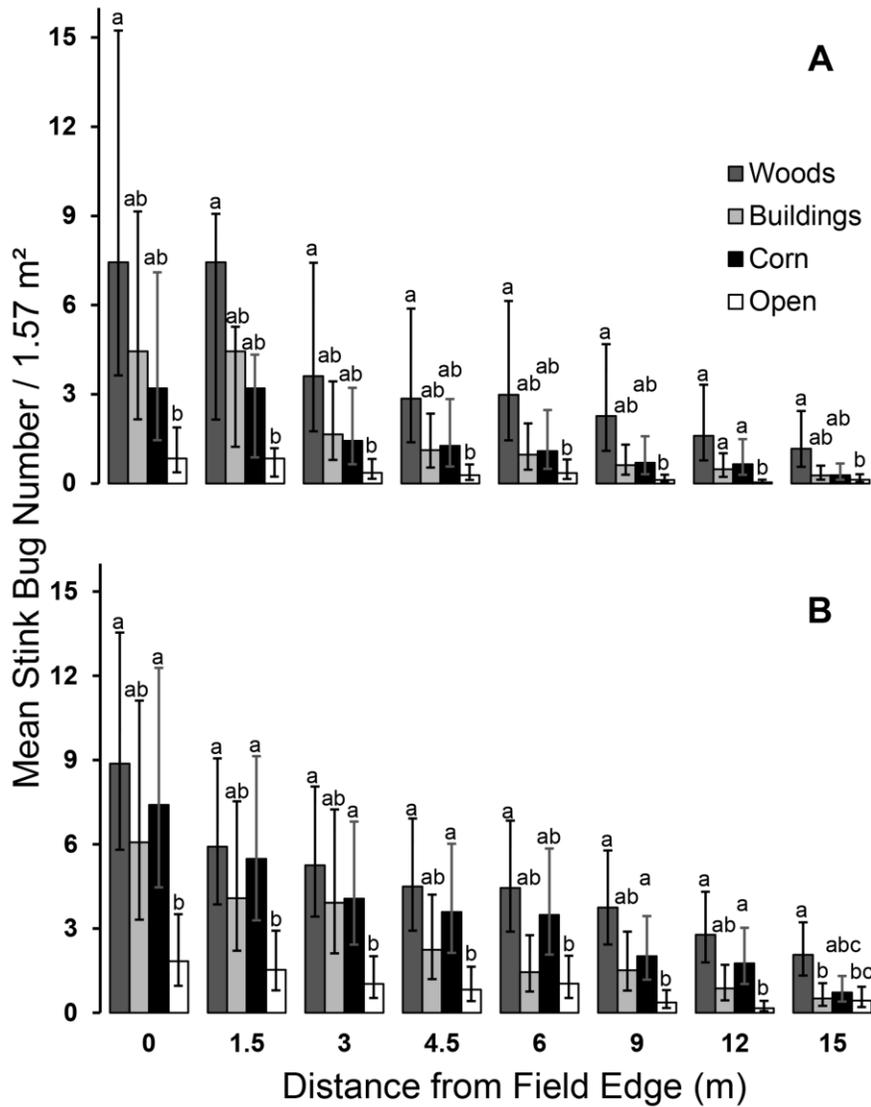
Figure 1. 3. Mean stink bug density in soybean field edges in relation to adjacent habitats and distance from field edge. Data from Beltsville and Clarksville are depicted in graphs A-B and C-D, respectfully. Estimates were derived from poisson-lognormal GLMMs and the values presented here have been reconverted from its original link function estimated model coefficients. Vertical lines represent upper and lower 95% confidence intervals, hence not symmetrical around the estimated means. Mean densities with the same letter above them are not statistically different ($\alpha = 0.05$, Tukey's HSD).
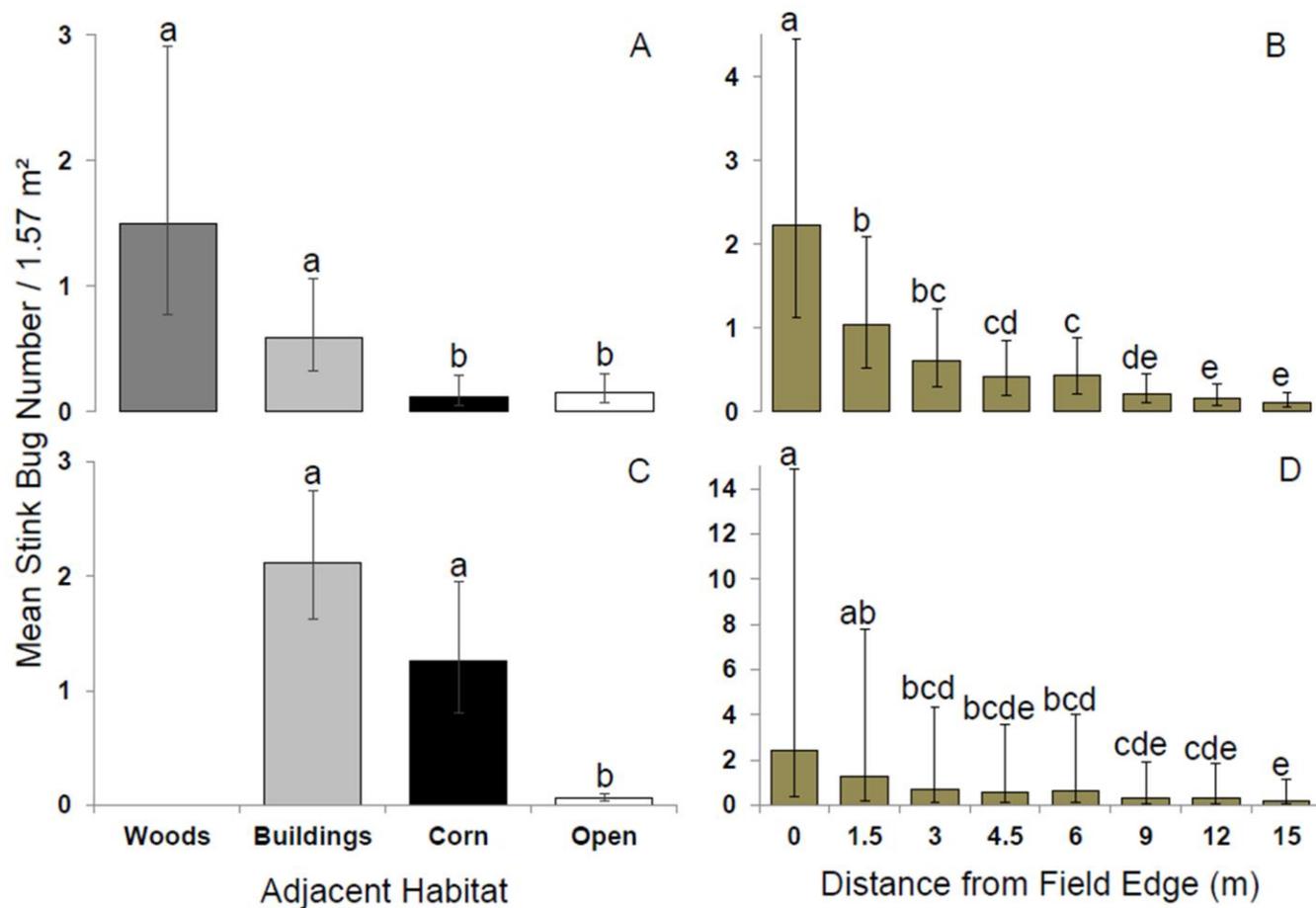
Corn and soybean seed damage

For field corn, results from the quasi-poisson GLM showed a significant positive association between % stink bug damaged kernels and mean stink bug density (y = 0.57 + 0.15x, n = 252, P < 0.001, pseudo R^2 = 0.47). A poisson GLM showed that the % collapsed kernels was not significantly associated with mean stink bug density (y = - 6.75 + 0.14x, n = 252, P = 0.50, pseudo R^2 = 0.17). For soybean pod development data, regression analysis revealed that the % full pods was negatively influenced by mean stink bug density (y = 5.9 - 0.17x, n = 63, P <0.001, R^2 = 0.51), while % flat pods (square root) was positively influenced (y = 2.18 + 0.26x, n = 63, P <0.001, R^2 = 0.63). Results of LMMs analyzing each seed quality category (Table 1.4) showed a significant positive association between mean stink bug density and purple stained seeds (y = 1.39 - 0.09x), % stink bug damaged seeds (y = 3.41 + 0.07x), % immature, shriveled and moldy seeds (y = 2.59 + 0.09x), and overall % of damaged seeds (y = 4.78 + 0.18x).

A significant negative relationship was observed between stink bug density and overall % normal, undamaged soybean seeds (y = 75.8 − 2.11x), and yield (y = 17.1 - 0.2x). The overall seed damage by stink bugs in both corn and soybean, and their impact on soybean pod development, were highest at immediate field edges and declined gradually towards the field interior (Fig. 1.4). Furthermore, soybean yields were lowest at the immediate field edge, gradually increasing inward into the field and with highest yields at 12 and 15 m from the edge (Fig. 1.4B).

Table 1. 4. Statistical results of LMMs for analyzing the relationship between stink bug density and various soybean seed damage categories and yield.

Dependent variable	Data Transformation	Intercept	Intercept SE	Estimate	SE	DF	Wald t	Pval	psuedo R2
% normal seeds	None	75.8	8.04	-2.11	0.25	145	-8.28	<0.001	0.30
% stink bug damaged seeds	Square Root	3.41	0.5	0.07	0.01	145	4.58	<0.001	0.12
% purple damaged seeds	log	1.39	0.14	0.09	0.01	145	9.99	<0.001	0.44
% moldy + shriveled + immature seeds	Square Root	2.59	0.47	0.09	0.02	148	5.87	<0.001	0.19
% all damaged seeds	Square Root	4.78	0.63	0.18	0.02	145	9.03	<0.001	0.35
Total Yield (grams / 20 plants)	Square Root	17.1	1.04	-0.20	0.04	140	-4.67	<0.001	0.13

Figure 1. 4. Patterns of kernel damage in field corn (A), soybean yield (B), soybean seed damage by category (C), and soybean pod development (D) in relation to mean stink bug density at different distance from field edge. The proportions of soybean seeds in each seed quality category (stink bug damaged, purple damaged, and normal seeds) and pod types (flat and full) are also provided. The dashed lines represent mean stink bug abundance represented by the second y axis.
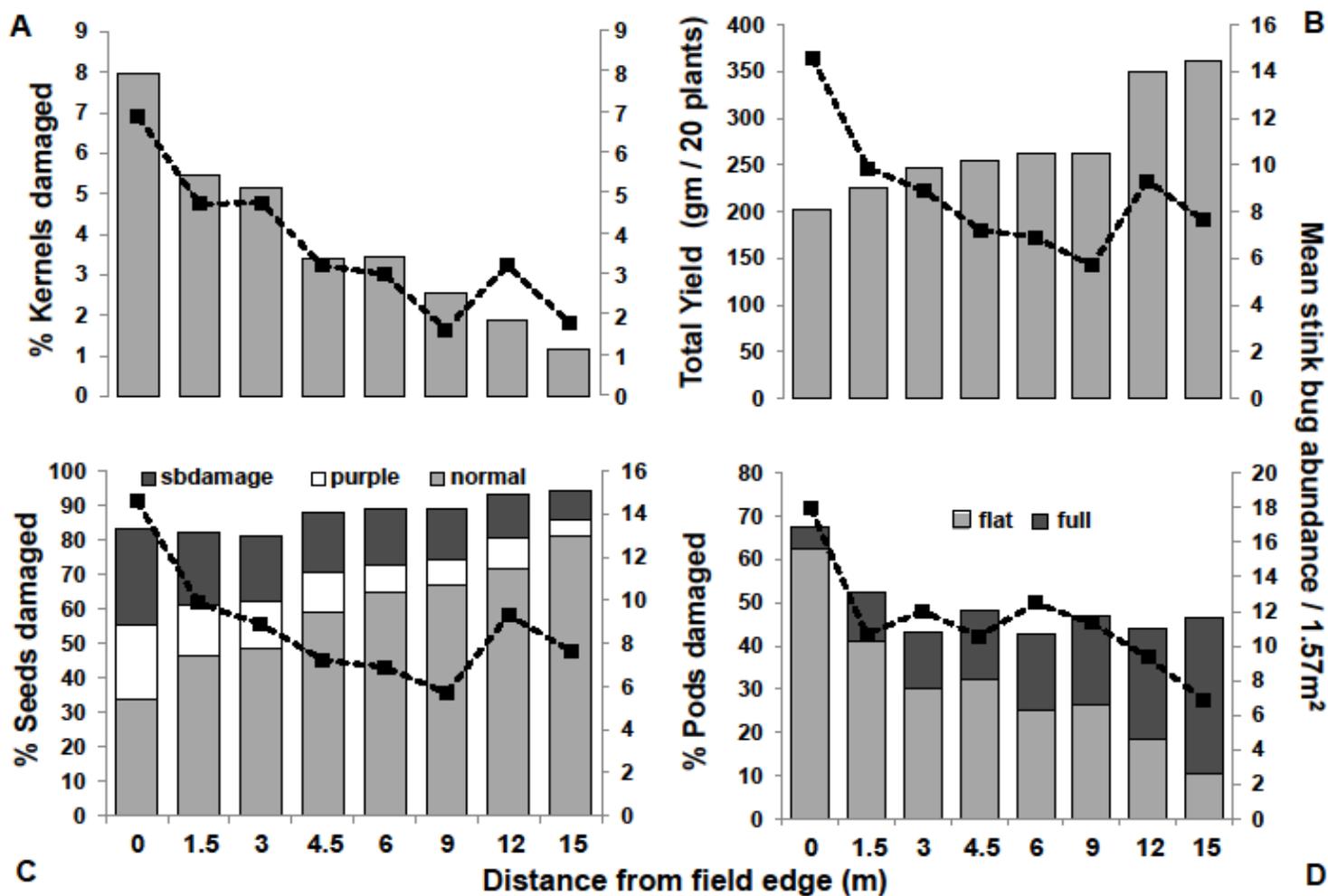
Discussion

This study addressed the influence of adjacent habitats on stink bug density and quantified differences in density at various distances from the field edges in soybean and corn crops. Results showed that adjacent habitats, particularly woods, influenced the abundance of *H. halys* and other stink bugs. In both row crops, fields adjoining woods, pooled over all study sites and distances from field edge, consistently harbored significantly higher numbers of stink bugs than in fields adjacent to open area habitats. Also, stink bug density along woods was consistently higher than in fields next to buildings, mixed crops, and corn fields at various distances, albeit not statistically significant in all cases. These results suggest that wooded habitats play an important role in supporting stink bug populations that colonize crops.

Given the timing of infestations during mid to late July in corn, and then later colonization of soybean fields in August, the majority of *H. halys* adults were offspring of the first generation which occurred on earlier host plants. *H. halys* is known to feed on a wide range of cultivated and wild hosts (up to 170 species) (BMSB IPM Working Group & Northeastern IPM Center, 2013), of which many tree and shrub species were probably present in the wooded habitats. Particularly high density of *H. halys* was observed in soybean fields bordering woods with tree of heaven (*Ailanthus altissima* Swingle), princess tree (*Paulownia tomentosa* Baill.), and black cherry (*Prunus serotina* Ehrhart), all which support high population densities of reproducing *H. halys* (BMSB IPM Working Group & Northeastern IPM Center,

2013; Nielsen & Hamilton, 2009a). The role of wild plant hosts in influencing higher stink bug density has been reported by (Jones & Sullivan, 1982) who found high *C. hilaris* populations in soybean adjacent to wooded borders with black cherry, and elderberry (*Sambucus canadensis* L.). Similarly, cotton fields with adjacent woods containing many oak species (*Quercus sp.*) and black cherry supported higher densities of *E. servus* (Reay-Jones, 2010).

My results present strong evidence that *H. halys* density exhibits a clear edge effect in both field corn and soybean. Across all adjacent habitats, density of *H. halys* and other stink bugs was highest within the first few meters from the edge (0-3m), gradually dropped to 9 m from the edge, and then reached lowest levels between 9-15 m. The strong edge effect exhibited by *H. halys* is similar to the within-field infestation pattern reported for other native stink bug species in U.S. crops (Pease & Zalom, 2010; Reay-Jones, 2010; Reeves *et al.*, 2010; Tillman *et al.*, 2009; Tillman, 2011; Tillman, 2010; Toscano & Stern, 1976).

Overall stink bug density and patterns of infestation in corn and soybean field edges differed among study sites and was influenced by other adjacent habitats. Stink bug density in both row crops at Keedysville was consistently (3 - 5 times) greater than the mean density at the other two study sites, and this was attributed to the higher populations of *H. halys* observed in Western Maryland at this site over the past four years. Other adjacent habitats besides wooded areas, particularly bordering areas with buildings and other crops, served as sources of colonizing adults in row crops. *H. halys* utilize buildings as overwintering sites and thus these managed structures

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would more likely influence stink bug populations earlier in the spring when post-diapuase adults are moving to host plants. At Keedysville, stink bug density was higher in alfalfa adjacent corn and soybean fields adjacent to corn, than in fields adjacent to buildings. However at Clarksville and Beltsville, adjacent crops had a lesser influence on stink bug abundance than buildings.

These results highlight the role of other adjacent cultivated crops as sources of stink bug density and agree with other studies. Adjacent fields of alfalfa, field corn and other cultivated borders has been reported as a sources contributing to higher densities of stink bugs in tomato, cotton, sorghum and peanut fields (Reeves *et al.*, 2010; Tillman, 2011; Toews & Shurley, 2009; Toscano & Stern, 1976). However, differences in the relative influence of adjacent habitats in this study could be related to differing overall stink bug population densities among study sites. For example, adjacent habitats did not significantly influence stink bug density in field corn at Beltsville where *H. halys* populations were lowest. Moreover, the influence of the landscape on stink bug density could extend to larger spatial scales beyond habitats just immediately adjacent to a crop. Since insect population dynamics and distributions are affected by regional landscape context and species traits such as dispersal ability (Tscharntke & Brandl, 2004), distribution and density of *H. halys* may depend on habitat and other environmental characteristics at spatial scales greater than the local agricultural field (Thies *et al.*, 2003; Tscharntke *et al.*, 2005). Differences in landscape structure between my study sites at the regional scale and their influence on local stink bug density could be a possible reason for overall higher

density of stink bugs at Keedysville and the role of adjacent crops as a source of stink bugs in field corn and soybean.

This study related the various corn and soybean damage measurements to stink bug density. As expected, stink bug damage to corn kernels increased with stink bug density. The percentage of damaged kernels reached levels up to 8% at the field edge to less than 3% between 9-15m from field edge, and was positively correlated with stink bug density. The percentage of collapsed kernels was negligible and not significantly influenced by stink bug density. Based on findings by earlier studies (Negrón & Riley, 1987; Ni *et al.*, 2010), neither kernel damage, ear weight or grain weight was affected beyond tasseling stage (VT) from feeding damage by *E. servus* and *N. viridula*. Although *H. halys* density can be high along edges of corn fields, my results suggests that *H. halys* kernel quality loss are restricted to about 10 m from the edge and yield loss may not be significant because the majority of damaged kernels should remain intact during harvesting and contribute to the total yield. However, *H. halys* is known to introduce yeast and other microorganisms into host tissue in the process of feeding; thus, this insect could increase the risks of mycotoxins produced in the ear. Preliminary studies in Virginia have reported that *Fusarium sp.* concentrations were positively correlated with the proportion of kernels with *H. halys* damage (personal communication, A. Herbert).

H. halys populations in soybean had a significant impact on pod development, with the percentage of flat pods significantly increased with increasing stink bug density. Concomitantly, the proportion of fully developed pods significantly

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decreased with increasing stink bug density. Effects on pod development also were greatest at the immediate field edge and least at 15m from edge. Changes in the development and maturation of soybean pods due to *H. halys* feeding have been recently documented (Owens *et al.*, 2013), showing that most severe pod loss occurred at the R4 (full pod) growth stage. Observed effects on pod and seed development with higher stink bug density were similar to damage caused by other stink bug species (Daugherty *et al.*, 1964; Todd & Turnipseed, 1974; McPherson *et al.*, 1979; Brier & Rogers, 1991; McPherson *et al.*, 1993). Results showing increased proportions of moldy and purple stained seeds with higher stink bug density indicate the potential role of *H. halys* in transmitting various pathogens; however, this needs to be further investigated experimentally. My study found a significant, yet weak negative association between soybean yield and stink bug density. In contrast, recent field cage-based research addressing the effects of *H. halys* feeding on soybean growth did not detect a significant relationship between H. *halys* stink bug densities and yield loss (Owens *et al.*, 2013). Ongoing field studies in the Mid-Atlantic region comparing yields of insecticide treated and untreated plots of soybean would better establish the relationship between soybean yields and stink bug density.

Knowledge of how adjacent habitats influence *H. halys* populations and the within-field distribution has several implications in stink bug management. First, results indicate that scouting corn and soybean fields can be more efficient if initially concentrated at field edges bordering wooded habitats where there is a greater likelihood of colonization and higher infestation risk. Secondly, the infestation patterns of stink bug communities dominated by *H. halys* are predominantly edge-

centric, and population densities beyond 15 m are invariably very low and generally non-economic. Based on my results, edge-only treatments of insecticides particularly along woods and border areas with buildings could considerably reduce control costs yet still prevent damage due to stink bugs in field corn and soybean. Preliminary studies show that treating just 12 m into the field prevented further invasion by *H. halys* and other stink bugs (personal communication, A. Herbert). The edge-only treatment also resulted in an 85–95% reduction in insecticide used compared with whole-field treatments (Leskey *et al.*, 2012). Results presented here showing highest stink bug density and associated damage limited to the immediate field edge provide validity for the edge-only treatment. Based on my findings, I suggest that integrated pest management programs for the stink bug complex in field crops should include farmscape-level planning, in terms of crop location with regards to adjacent habitats, and targeted interventions in the form of edge-only treatments to prevent seed quality and yield losses.

Chapter 2: Spatio-temporal dynamics and movement of *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae) in and between adjacent corn and soybean fields.

Introduction

Heterogeneity of available habitats within the agricultural ecosystems influence the dispersal and habitat selection of pest insects, thereby affecting their population dynamics (Carrière *et al.*, 2006, 2012). Most polyphagous insect pests, however, display distinct preferences for particular plant species, cultivars and plant growth stages. These preferences can lead to the concentration of peripatetic insect pest populations in fields that represent the most preferred hosts or habitats (Kennedy & Margolies, 1985; Kennedy & Storer, 2000; Kogan & Turnipseed, 1987). Additionally, crop planting dates, harvest dates, and crop maturation influence host preferences of mobile polyphagous stink bugs, thereby heavily affecting the distribution of pest populations within an agricultural ecosystem (Kennedy & Storer, 2000). Therefore, the seasonal availability and suitability of source and recipient crops in relation to the life stages of the pest influence the dispersal dynamics of pests from sources to recipient crops.

Availability and suitability of crops also impact development and survival of the offspring of invading adults, which may control population increase through subsequent generations. This is heavily influenced by seasonal spatial population dynamics of insect pests within the landscape (examples in Kennedy and Margolies 1985; see review by Kennedy and Storer 2000), and given favorable circumstances,

mobile insect pest populations may build up to high densities and inflict heavy crop damages. Thus, knowledge on insect pest population dynamics vis-à-vis the availability of non-crop and crop hosts at preferred growth stages within dispersal distance in the farmscapes is indispensible for developing effective pest management strategies.

Stink bugs in the family Pentatomidae are major worldwide pests of economically important fruit, vegetable, grain, and agronomic crops (Panizzi, 1997), and are considered important pests in soybean *Glycine max* (L.) Merr. producing areas of the world (Panizzi & Slansky, 1985). Polyphagous stink bugs depend on availability of a sequence of host plants for their survival and disperse between these plant hosts at preferred phenological growth stages (Jones & Sullivan, 1982; Panizzi, 1997; Tillman, 2011; Toscano & Stern, 1976). Many pentatomid species show specific feeding habits in relation to the local sequence of host plants available (Panizzi, 1997). For example, host plant sequence for *Nezara viridula* (L.) in Louisiana differed from that in South Carolina, and consequently the spatial population dynamics were different (Jones & Sullivan, 1982). Prior to colonizing soybean in late summer, stink bug species require other host species such as corn (Tillman, 2010) for feeding during the spring and summer at which time they build up population sizes by producing another generation each year (Leskey *et al.*, 2012; Schumann & Todd, 1982). Quantifying the temporal and spatial dynamics of stink bugs will therefore improve the understanding of its build up in crops and the potential for movement to neighboring crops (Tillman *et al.*, 2009).

Stink bugs were not considered serious pests of crops in mid-Atlantic region until recently. The most common stink bugs in agricultural fields in the mid-Atlantic were *Chinavia hilaris* (Say 1832) and *Euschistus servus* (Say 1832), but these species have had little economic impact in the region (Nielsen *et al.*, 2011). The recent explosion in populations of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål 1855), however, has led to significant economic and ecological impacts. Since the accidental introduction and discovery of this Asian stink bug near Allentown, Pennsylvania, USA, *H. halys* has been detected in 41 states, and local populations and detections from Europe (Switzerland, France, Canada, Germany, Italy and Liechtenstein) have also been reported (CABI, 2014). This polyphagous stink bug has a wide range of host plants including tree fruits, vegetables, field crops, ornamental plants, and native vegetation in its native and invaded ranges. Since 2010, serious economic losses have been reported for tree, fruit, ornamental and row crops including field corn *Zea mays* L., and soybeans in the mid-Atlantic region (Leskey *et al.*, 2012).

Corn and soybean are planted in high acreage throughout the United States (NASS - USDA, 2014) often adjacent to each other, and corn is one of the earlier row crops available to stink bugs in the mid-Atlantic region. Hence, quantifying the spatial population dynamics of stink bugs in corn would help in management of stink bugs in the region (Tillman, 2010). As *H. halys* is considered an economic pest of many legumes (particularly soybean) both in its native and introduced areas (Lee *et al.*, 2013; Leskey *et al.*, 2012), soybean adjacent to corn hosts in the Mid-Atlantic region provides a suitable opportunity for outbreaks. The sequence of crop planting

dates in which soybean is planted later than corn in adjacent fields makes soybean a suitable host (at seed filling stages R5 & R6; (Nielsen *et al.*, 2011; Owens *et al.*, 2013) for *H. halys* to transfer from corn. Studies documenting spatial and temporal dynamics of stink bugs in farmscapes with heterogeneous crops all pertain to the Southern portion of the United States, while the population dynamics of stink bugs in adjacent corn and soybean of the Mid-Atlantic region has rarely been addressed (Nielsen *et al.*, 2011; Owens *et al.*, 2013).

This study quantified the spatiotemporal dynamics of stink bug populations between corn and adjacent soybean, and examined potential role of corn as a source of stink bugs in adjacent soybean. The experimental design addresses the following questions: 1) When is the peak density of *H. halys* in relation to corn and soybean reproductive development? 2) How does *H. halys* age structure differ in corn and soybeans through time? 3) How does density of stink bugs spatially vary through the season, within adjacent corn and soybean fields? 4) How does population density of *H. halys* in corn affect density in soybeans? 5) What is the proportion of soybean fields in mid-Atlantic region adjacent to corn? I hypothesized that initial population buildup in corn would reach peak density during grain development stages (CABI, 2014; Leskey *et al.*, 2012). I expected the typical crop sequence and timings prevalent in the mid-Atlantic region to facilitate the dispersal of *H. halys* from corn to soybean during the seed filling stages of soybean.

Methods

The study was conducted at the USDA Beltsville Agricultural Research Center at Beltsville, MD and University of Maryland Research and Education Center facilities at Beltsville and Keedysville, MD. Stink bug populations were monitored during 2012 and 2013 in a total of seven adjacent corn-soybean fields of varying dimensions, using a sampling grid pattern. At each site, corn (30' row spacing) and full season soybean (7' row spacing) fields were planted within 10 m apart using standard agricultural practices (See Table 2.1 for field details), and shared at least 50 m of boundary interface. Visual counts of stink bugs were recorded at geo-referenced grid points within each field spaced 15 m apart in all directions, except at the corn-soybean interface where samples were taken at each crop boundary interface. The total number of the sampling points in corn and soybean varied among sites (Table 2.1).

Stink bugs were enumerated at each sampling point in corn by carefully examining 10 consecutive plants. For soybean, stink bugs were enumerated in all plants within two semicircular plots of 0.5 m radius each. Data were recorded for adults, small nymphs (2nd and 3rd instars), large nymphs (4th and 5th instars) and egg masses of *H. halys*, and densities were converted to numbers per m^2. The crop growth stage was also recorded based on samples from five corn or soybean plants at each point. Sampling commenced at the onset of silking through kernel development of corn (R1- R6; Hanway 1963) during mid July, and continued till the physiological maturity of soybean seeds (R7; Fehr *et al.* 1971) in late September.

In addition to the grid sampling, five soybean field edges adjacent to corn fields were also monitored for stink bugs using transect sampling (Table 1). At edges of soybean fields adjacent to corn, sampling sites along four transects spaced 15 m apart were marked at distances 0, 1.5, 3, 4.5, 6, 9, 12, and 15 m from the edge to field interior (total of 32 samples). Stink bugs were enumerated in all plants within a semicircular area of 0.5 m radius (1.57 m^2) from mid August – late September coinciding with the seed development stages of soybean (R4-R7), which are associated with high *H. halys* abundance (Nielsen *et al.*, 2011).

Statistical Analyses

The influences of crop phenology on the density of *H. halys* was analyzed by Generalized Linear Mixed Models (GLMMs) based on Laplace approximation, with a Poisson-lognormal error distribution and log link function (Bolker *et al.*, 2009; Elston, Moss, Boulinier, Arrowsmith, & Lambin, 2001). Separate GLMMs for corn and soybean were performed, and each analysis treated density of *H. halys* pooled across all sampled grids as response variable, crop stage as fixed effect, and the sampling point in the grid as a random factor to account for repeated measurement (Pinheiro & Bates, 2000). The significance of the fixed effects was determined by Wald χ^2 tests, and the coefficient of determination (R^2) for the fixed effects was also calculated (Nakagawa & Schielzeth, 2013). Significant differences in the estimated means of stink bug density between the different crop stages were identified through Tukey's HSD pair-wise comparisons.

Seasonal dynamics in *H. halys* population structure in relation to crop phenology was visualized through area charts. Differences in *H. halys* population structure between corn and soybean was investigated through Fisher's Exact Test on overall count data (pooled over sampling dates) for each of the grids sampled. The spatial heterogeneity in *H. halys* density was characterized using Inverse Distance Weighted (IDW) interpolation technique. IDW utilizes values from geo-referenced points to predict densities for unsampled points, and values from the geo-referenced points close to the target point carried larger weight than those farther (Webster & Oliver, 2007). The exponent or power value for the IDW was set to the commonly used value of two (Webster & Oliver, 2007), and a search radius that varied based on input from 12 points was used. The primary rationale for using IDW for the interpolation was that *H. halys* is predominantly distributed at the edges of field crops (Venugopal *et al.*, unpublished data) and IDW is reported to be appropriate for such aggregated data. Previous studies have characterized spatial variation in the density of other aggregated insect species, including stink bugs, using IDW (Beckler, French, & Chandler, 2004; Rhodes, Liburd, & Grunwald, 2011; Tillman *et al.*, 2009). For each grid and sampling date, observed *H. halys* densities were converted to density / m^2 and interpolations were performed with the converted data.

H. halys density in soybean field edges adjacent to corn was compared between Beltsville and Keedysville using GLMM based on Laplace approximation with a Poisson-lognormal error distribution and log link function (Bolker *et al.*, 2009; Elston *et al.*, 2001). GLMM were performed with stink bug density as response, study site as the fixed effect and sampling field as random variable to account for repeated

measurement (Pinheiro & Bates, 2000). The significance of the fixed effects was determined by Wald χ^2 tests. Significant differences in the GLMM estimated means of stink bug density between the study sites were identified through Tukey's HSD pair-wise comparisons.

The proportion of soybean fields that were within 10m from corn fields in the mid-Atlantic states was determined through Near (Analysis toolbox; Proximity toolset) analysis (ArcGIS 10.0; ESRI, 2011) of the spatially explicit crop data layer (CROPSCAPE; Han *et al.* 2012). All statistical analyses were performed in R program (R Development Core Team, 2011) and associated statistical packages. GLMMs were performed with package lme4 (Bates *et al.*, 2013) and Tukey's HSD comparisons of means for GLMMs were computed with package multcomp (Hothorn *et al.*, 2013). Coefficient of determination (pseudo R^2) for the GLMM fixed effects was calculated with package MuMin (Bartoń, 2013). IDW interpolations were performed and visualized using package gstat (Pebesma & Graeler, 2013).

Results

The total number of *H. halys* recorded was 90 and 348 in four adjacent corn and soybean fields that were grid sampled at Beltsville during 2012, respectively. Stinkbug populations were significantly lower at Beltsville in 2013, with only 7 and 6 *H. halys* recorded at all grid sampling points in one adjacent corn and soybean site.

Table 2. 1. Details on the corn and soybean fields used for sampling; and soybean fields for edge sampling in Beltsville and Keedysville, MD during 2012 and 2013.

Study	Site	Year	ID	Location	Crop	Area (Ha)	Points	Planting Date	Planting Density / acre	Variety	Sampling dates	Sampling Freq. (Days)
Corn - Soy Grid	Beltsville	2012	1	39.02 N, 76.87 W	Corn	0.63	28	7-May	28000	Hubner 5582VT3	July 26 - Sep 6	7 - 10
					Soy	0.41	28	6-Jun	150000	Channel 3806	July 26 - Sep 26	7 - 10
			2	39.04 N, 76.89 W	Corn	0.42	28	7-May	28000	Hubner 5582VT3	July 18 - Sep 20	7 - 10
					Soy	0.42	28	6-Jun	150000	Channel 3806	July 18 - Sep 26	7 - 10
			3	39.03 N, 76.82 W	Corn	0.72	32	3-May	28000	Channel 207-13VT3P	July 16 - Sep 6	7 - 10
					Soy	0.66	32	6-Jun	150000	Channel 3806	July 16 - Sep 27	7 - 10
			4	39.00 N, 76.85 W	Corn	0.53	32	27-Apr	28000	Channel 210-61VT3	July 18 - Sep 6	7 - 10
					Soy	0.53	32	7-Jun	150000	Channel 3806	July 18 - Sep 26	7 - 10
		2013	1	39.02 N, 76.87 W	Corn	0.63	28	6-May	28000	Hubner 5582VT3	July 30 - Sep 6	7
					Soy	0.41	28	6-Jun	150000	Channel 3806	July 30 - Sep 6	7
	Keedysville		5	39.50 N, 77.74 W	Corn	0.19	19	24-Apr	26000	Pioneer 5K09AM1	July 26 - Sep 6	7
					Soy	0.43	35	22-May	180000	Seed Consultants	July 26 - Sep 24	7

										SCS9360RR		
			6	39.50 N, 77.72 W	Corn	0.47	28	25-Apr	26000	Doebler's 633HXR	July 26 - Sep 6	7
					Soy	0.48	28	27-May	180000	Seed Consultants SCS9360RR	July 26 - Sep 24	7
Soy edge	Beltsville	2012	1	39.02 N, 76.82 W				8-May	155555	Pioneer 93Y91	Aug 16 - Sep 6	7
	Keedysville		2	39.51 N, 77.73 W				4-Jun	180000	Doebler's 3809RR	Aug 16 - Sep 26	7
			3	39.50 N, 77.73 W				4-Jun	180000	Doebler's 3809RR	Aug 16 - Sep 26	7
	Beltsville	2013	4	39.02 N, 76.83 W				8-May	155555	Pioneer 93Y91	Aug 16 - Sep 16	7
	Keedysville		5	39.51 N, 77.74 W				27-May	180000	Seed Consultants SCS9360RR	Aug 16 - Sep 18	7

At Keedysville during 2013, a total of 1157 and 2154 *H. halys* were recorded in two corn and soybean fields that were grid sampled, respectively. As data from the Beltsville sites were too few for any meaningful analyses, only the 2013 data from Keedysville were used for statistical analyses. However, to depict the general population density trend at the Beltsville gridded fields, interpolated density maps for the entire season were generated for the most abundant field sampled in both 2012 and 2013.

GLMMs relating crop phenology to *H. halys* densities at both Keedysville fields showed significant influence of both corn kernel (Wald $\chi^2 = 123.5$, df = 6, $P < 0.001$, fixed effects $R^2 = 0.48$) and soybean seed developmental stages (Wald $\chi^2 = 397.0$, df = 8, $P < 0.001$, fixed effects $R^2 = 0.43$). Highest *H. halys* density in corn was observed during the milk-dough stage (R3/R4; Fig. 2.1A), and generally higher density of *H. halys* was observed during earlier stages of corn kernel development (R2 blister - R3/R4 milk/dough), than the later maturity stages (R4 dough - R6 physiological maturity). In soybean, highest density was observed at begin-full seed (R5/R6; Fig. 2.1B) stages, and higher stink bug densities were observed during seed filling stages (R4-R6) than the begin pod (R3) or physiological maturity (R7) stages.

The seasonal dynamics in the density and age structure of *H. halys* differed between corn and soybean. In corn portion of Field 5 and 6 at Keedysville, proportions of small nymphs and adults was greater than that of large nymphs (Fig 2.2A and 2.3A, respectively). Also, there was a steep decline in total number of stink bugs observed in both fields beyond the dough stage of corn (Figs. 2.2A and 2.3A). This decrease coincided with corresponding increase in observed stink bug density in soybean, particularly at the full pod to early seed development stages (R4 –

R5). Also, higher proportion of large nymphs than small nymphs or adults was observed in soybean (Figs. 2B & 3B). The difference in age structure of *H. halys* between corn and soybean with respect to the relative proportions of large nymphs to small nymphs was statistically significant for both Fields 5 and 6 in Keedysville ($P < 0.001$, Fisher's Exact Test).

Visual inspection of the interpolated density of *H. halys* in Field 5 at Keedysville showed initial distribution and buildup of population restricted to corn (Fig. 2.4; 26 July) and higher densities in corn (15-20/m^2) along the corn-soy interface (31 July & 7 Aug). After Aug 7, densities in corn diminished and stink bugs were observed in soybean adjacent to corn (20 Aug – 12 Sep) and at the other end of the field adjacent to woods (5-10/ m^2), while not at the center of the soybean field. Also, nymphs comprised a high proportion of stink bugs in soybean adjacent to corn on Sep. 6 (6 Sep Nymphs; 3-5/m^2). Spatial pattern of density in Field 6 at Keedysville was similar to that of Field 5, with high density in corn along corn-soy interface (31 July – 07 Aug; 10-12/ m^2) gradually diminishing to show increasing density in adjacent soybean (14 Aug – Sep 6; Fig. 2.5). In Beltsville, however, very few stink bugs were observed overall and there was no buildup of populations in corn in both years at Field 1 (Fig. 2.6). The highest density of stink bugs was observed later in the season, in soybean (20 Aug – 30 Aug 2012; 8/ m^2 and 29 Aug 2013; 8/ m^2). In Beltsville, corn was not a source of *H. halys* population dispersing into soybean and the highest density of stink bug was observed directly in soybean edges bordering woods (Fig. 5; 20 – 31 Aug 2012 and 29 Aug 2013) during the R5-R6 stage.

Results comparing densities at soybean field edges adjacent to corn were similar to the site level differences in the stink bug spatial dynamics as observed from the interpolated maps. GLMM and Tukey's HSD showed significant difference between Beltsville and Keedysville

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(Fig. 2.7) in the density of *H. halys* observed in soybean edges adjacent to corn ($\chi^2 = 33.3$, df = 1, $P < 0.001$), with significantly less *H. halys* density in Beltsville. In the mid-Atlantic region, soybean fields are planted adjacent to corn in very high proportions, especially in PA (83%), DE (73%) and MD (70%; Table 2.2).

Discussion

This study quantified the spatial distribution of *H. halys* in adjacent corn-soybean fields and identified the role of crop phenology on its population dynamics across the growing season. It represents the first effort to examine the influence of corn kernel growth stages on the density of stink bugs in the mid-Atlantic region. Similarly, population dynamics and growth stages differences between adjacent crops for the invasive economic pest *H. halys* has not been quantified. Results showed that, while crop growth stages influenced stink bug population densities, the role of adjacent corn as a source of *H. halys* invading soybean varied with site.

In soybean, highest stink bug density was observed during the seed development stages (particularly R5-R6), which confirmed results from other reports of *H. halys* (Nielsen *et al.* 2011, Leskey *et al.* 2012, Owens *et al.* 2013, CABI 2014) and other stink species including *N. viridula*, *C. hilaris*, and *E. servus* (Bundy & McPherson, 2000; Herbert & Toews, 2011; Herbert & Toews, 2012; Jones & Sullivan, 1982; Kogan & Turnipseed, 1987; McPherson *et al.*, 1993; Olson *et al.*, 2011; Panizzi & Slansky, 1985; Schumann & Todd, 1982; Todd, 1989; Turnipseed & Kogan, 1976).

Figure 2. 1. GLMM comparisons of *Halyomorpha halys* densities at different phenological stages of field corn (A) and soybean (B) at Keedysville, Maryland during 2013. The vertical lines represent 95% confidence interval, hence not symmetrical around the mean. Means with the same letter above bars are not significantly different (α = 0.05, Tukey's HSD).
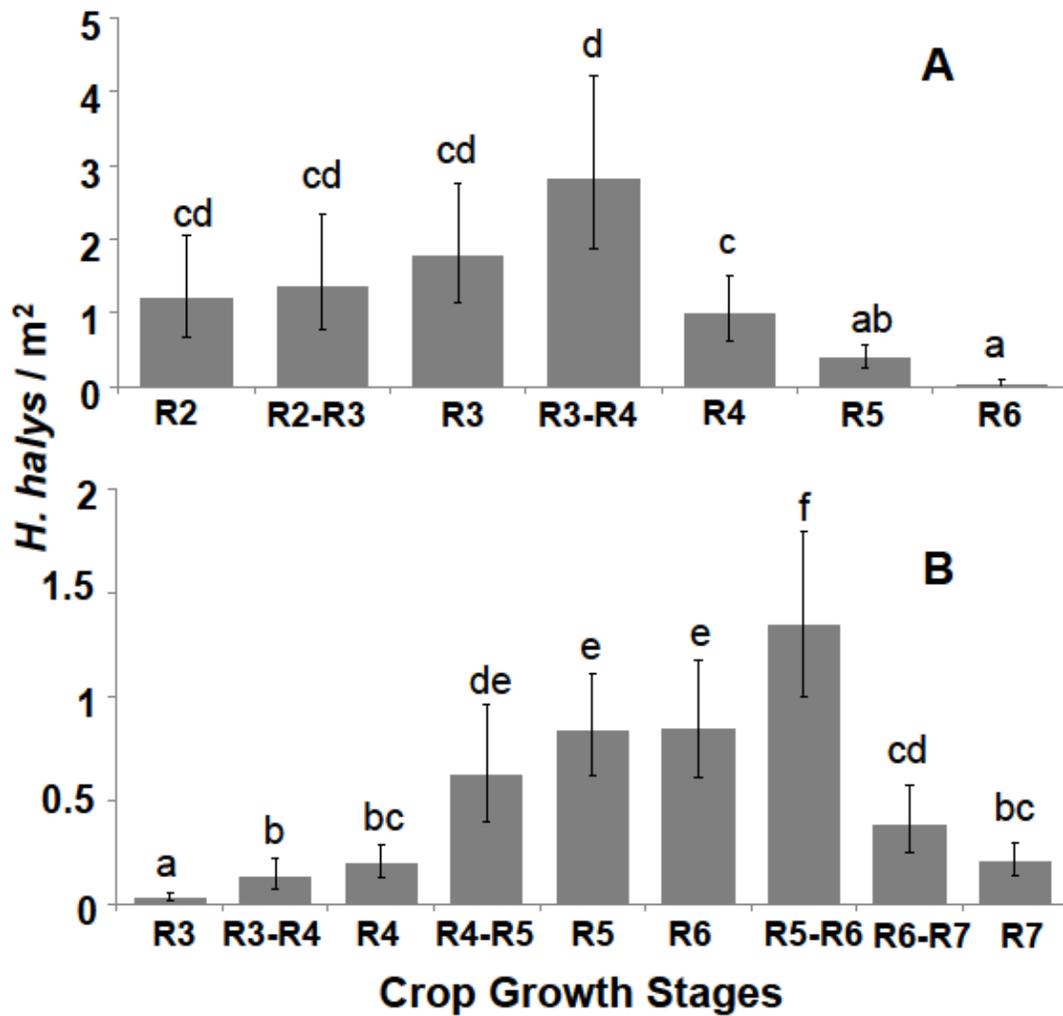
Figure 2. 2. Seasonal dynamics and life stage densities of *Halyomorpha halys* in relation to growth stages of adjacent corn (A) and soybean (B) in Field 6 at Keedysville, MD during 2013.
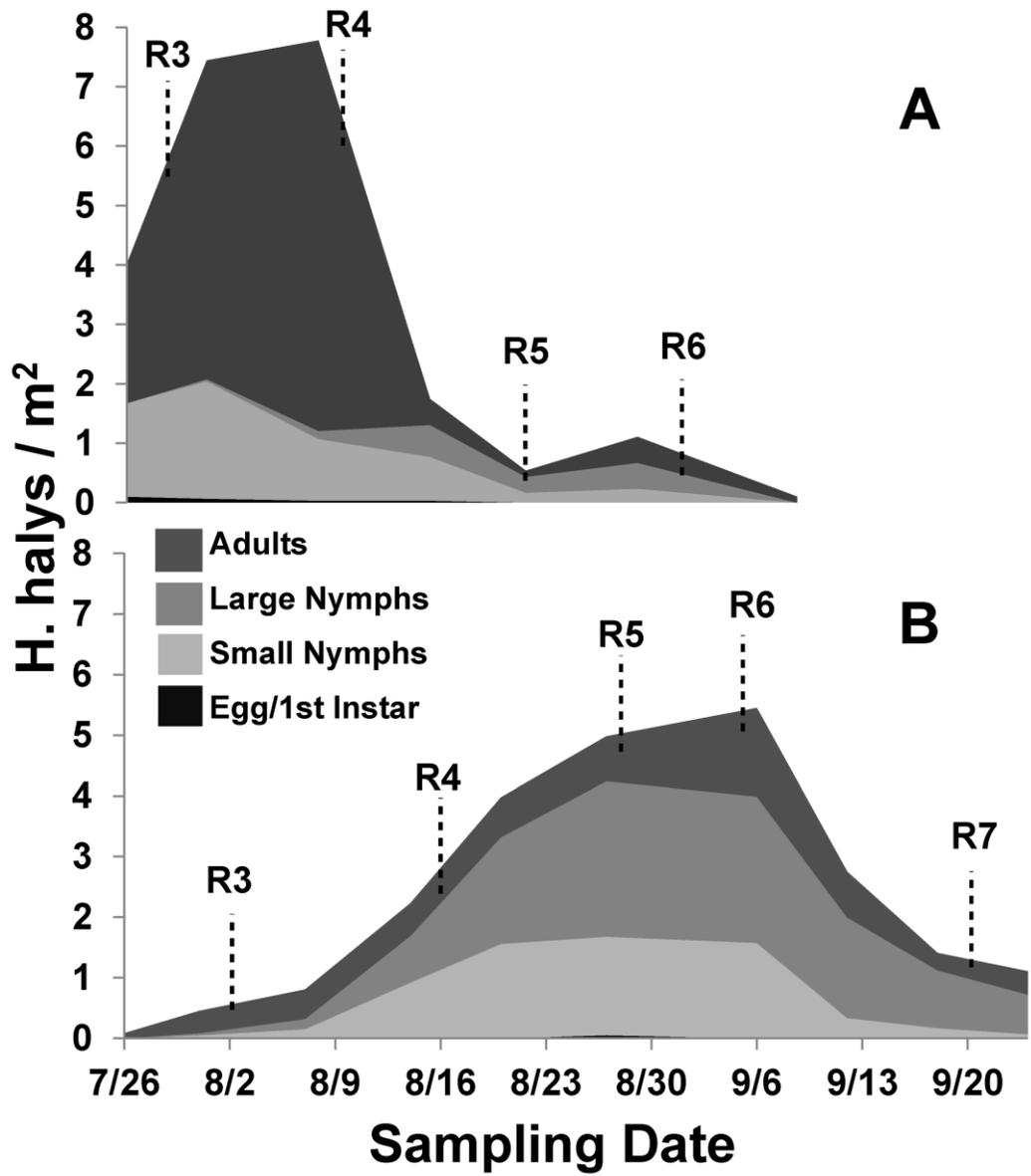
Figure 2. 3. Seasonal dynamics and life stage densities of *Halyomorpha halys* in relation to growth stages of adjacent field corn (A) and soybean (B) in Field 5 at Keedsyville, MD during 2013.
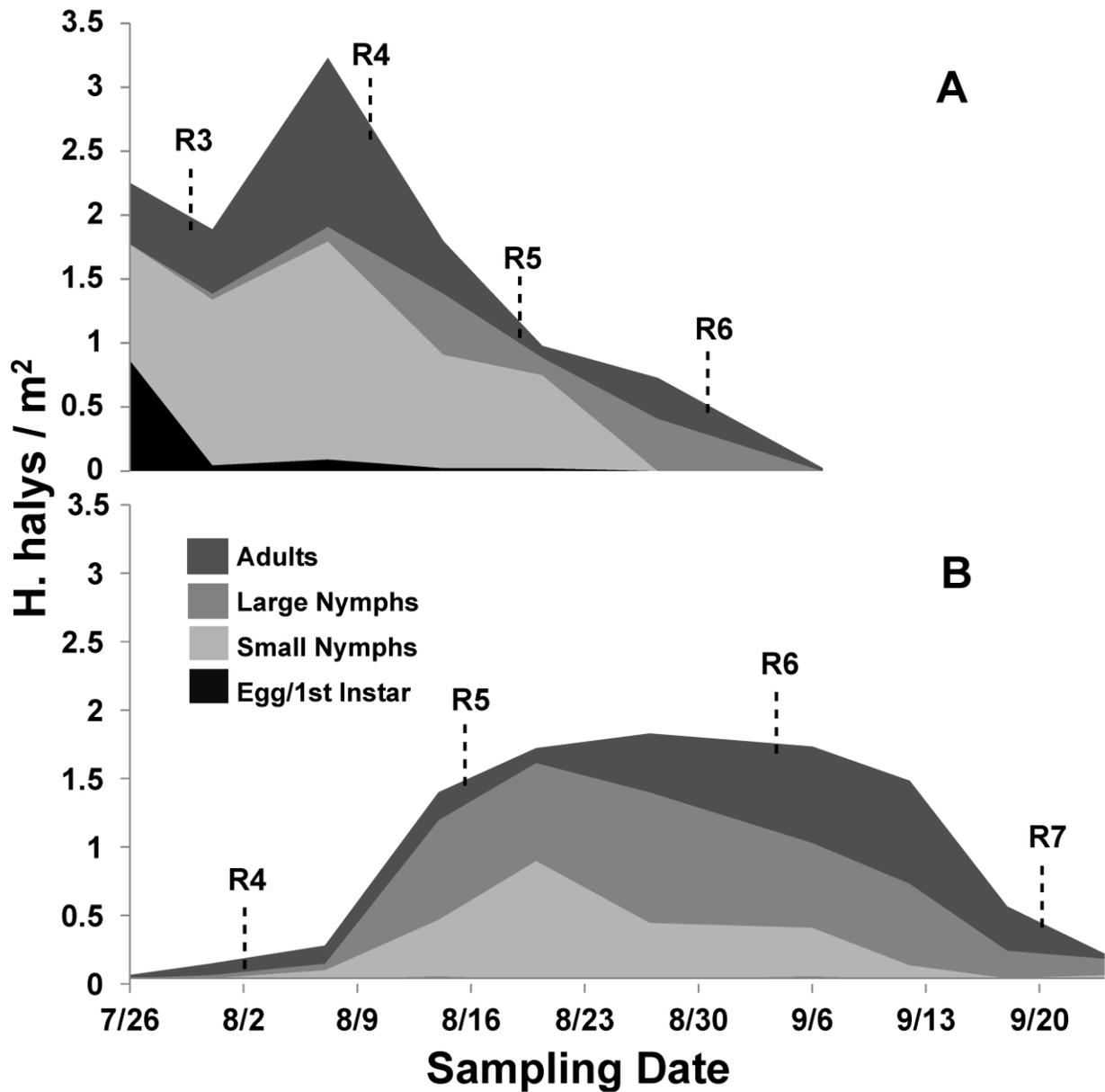
Figure 2. 4. Spatial interpolation of *Halyomorpha halys* densities (per m^2) in adjacent corn (denoted by C) and soybean (S) across the 2013 growing season at Field 5 in Keedysville, MD. Extent of corn and soybean sampled is demarcated by black lines while the black circles represent the location of sample points.
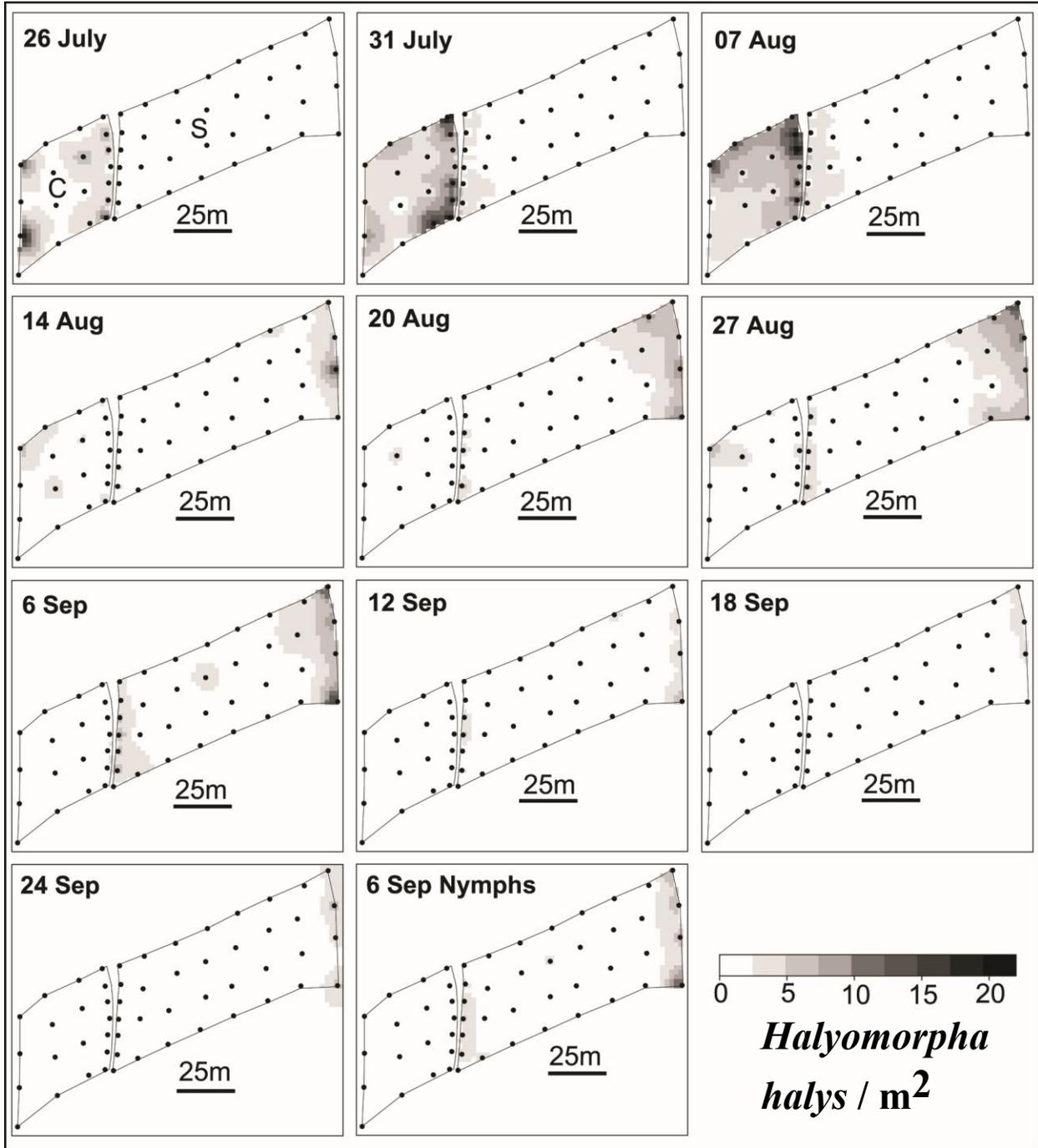
Figure 2. 5. Spatial interpolation of *Halyomorpha halys* densities (per m^2) in adjacent corn (denoted by C) and soybean (S) across the 2013 growing season at Field 6 in Keedysville, MD. Extent of the corn and soybean sampled is demarcated by black lines while the black circles represent the location of sample points.
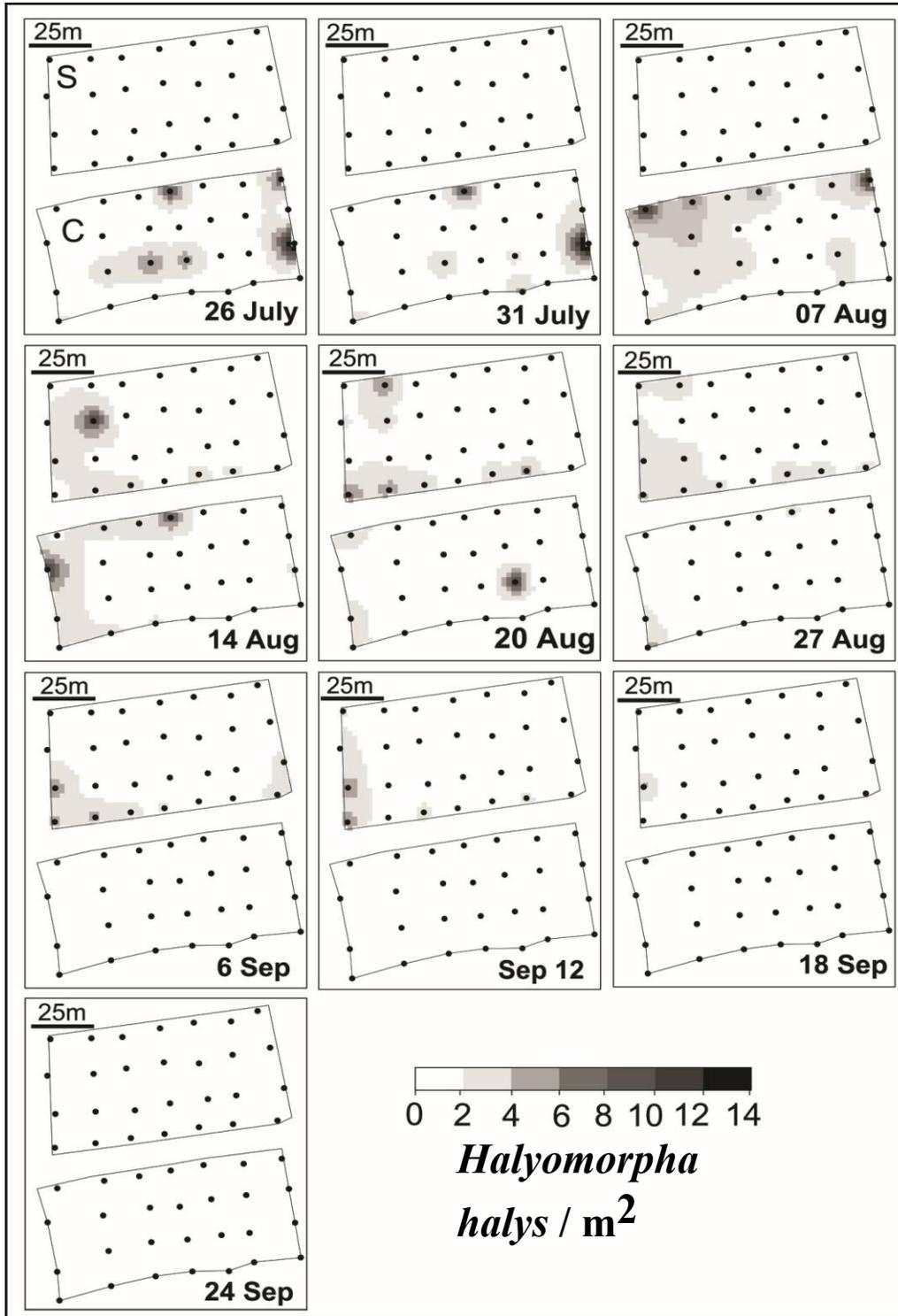
Figure 2. 6. Spatial interpolation of *Halyomorpha halys* densities (per m^2) in adjacent corn (denoted by C) and soybean (S) across the 2012 and 2013 growing seasons at Field 1 in Beltsville, MD. Extent of the corn and soybean sampled is demarcated by black lines while the black circles represent the location of sample points.
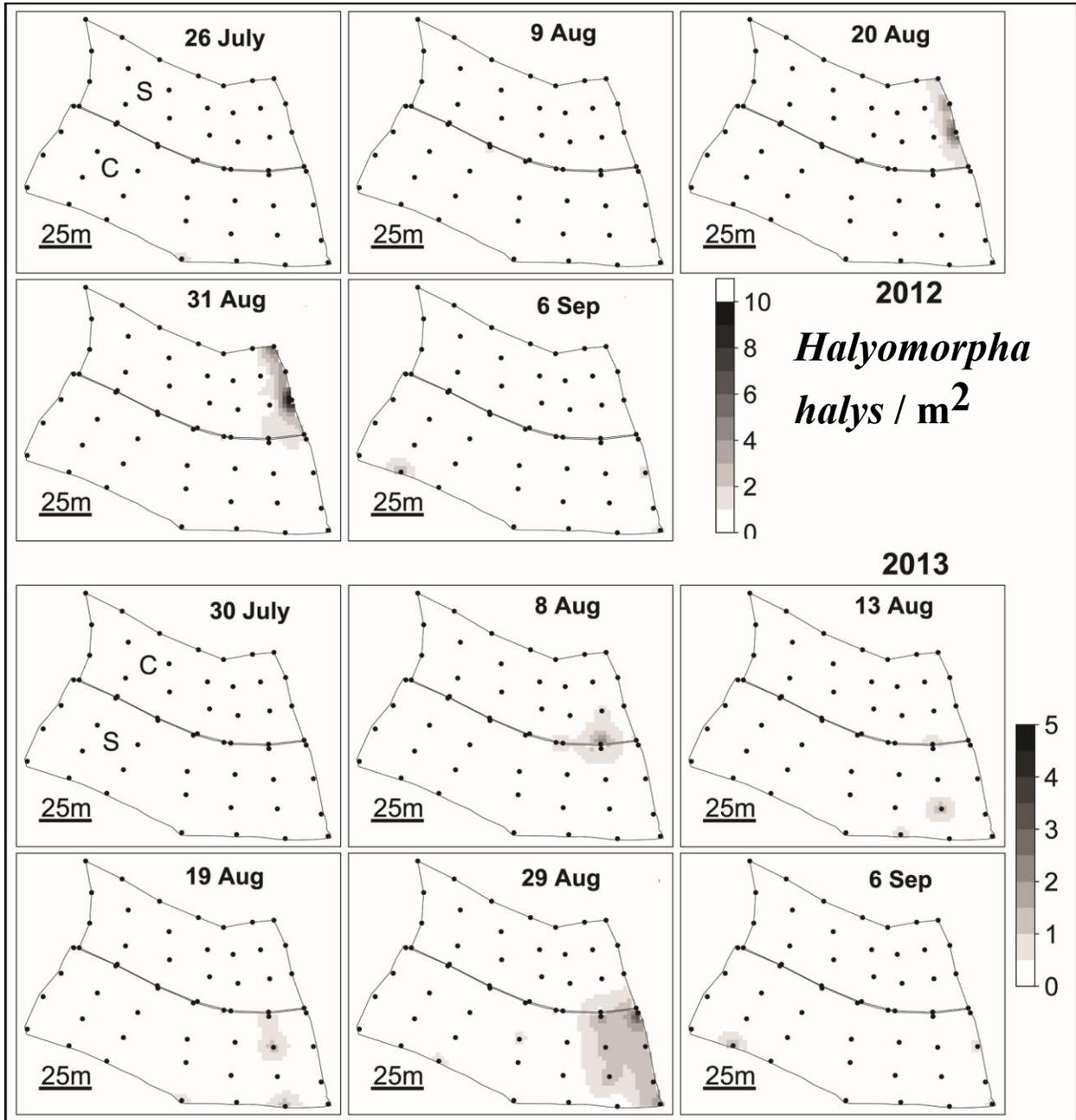
Figure 2. 7. GLMM estimated difference between sampling sites in *Halyomorpha halys* density at edges of soybean fields adjacent to field corn in Maryland during 2012 and 2013. The vertical lines represent 95% confidence interval and the statistical significance ($P < 0.001$; $\alpha = 0.05$) based on Tukey's HSD are denoted by the asterisks.
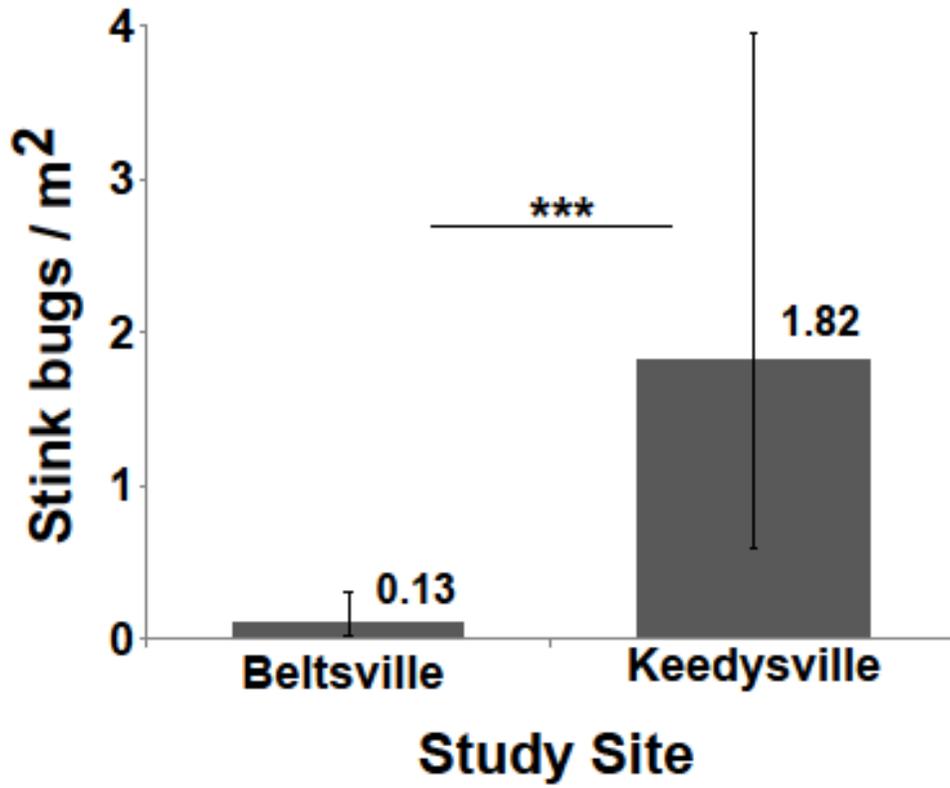
Table 2. 2. Area of corn and soybean plantings in the Mid-Atlantic States of USA during 2013 (NASS - USDA 2014) and proportion of soybean fields adjacent to corn.

State	Corn Area (1,000 acre)	Soybean Area (1,000 acre)	Fields in proximity (%)
Delaware	95	160	72.7
Maryland	490	470	69.5
New Jersey	90	96	48.0
Pennsylvania	1500	560	83.4
Virginia	510	590	42.6
West Virginia	50	22	51.1

H. halys adults and older nymphs feed primarily on developing corn ears by penetrating the husk leaves with their feeding stylets to remove pre-digested tissue from the developing kernels (personal observation, D. Venugopal). They also feed on the developing seeds in soybean pods in a similar way. The nutritional quality of developing corn kernels and soybean seeds likely explains the high density of H. halys during these stages of crop growth. The moisture and sugar content in corn grain peaks just around the blister stage (Ingle, Beitz, & Hageman, 1965; Ritchie, Hanway, & Benson, 1993). The various nitrogenous materials including protein, soluble nitrogen, amino acid, RNA, DNA, and soluble nucleotides increase steadily during milk stage (Ingle *et al.*, 1965). While the sugar content continues to decrease after blister, amino acid content, soluble nucleotides and RNA all which peak around the dough stage, also begin to decline steeply as the grain hardens and matures (Ingle *et al.*, 1965).

In soybean, seed weight increases rapidly during the pod filling stages (R4-R6), to 90% of total by R6, providing continuous consumable food resources for stink bugs. Peak abundance of stink bugs were observed between R5- R6 stages which represent the stages with increasing seed dry weight, protein, oil, and sugar content (Dornbos & McDonald, 1986; Kim *et al.*, 2006; Rubel, Rinne, & Canvin, 1972). Overall free sugar content, particularly sucrose, raffinose and stachyose, increased sharply between R5- R6 during which the fatty acid content, especially oleic and linoleic acids also accumulated rapidly (Dornbos & McDonald, 1986; Kim *et al.*, 2006). In both corn and soybean, the high density of stink bugs observed was associated with the nutritional quality of the fruiting bodies at these stages. Corn blister to dough stages and soybean seed filling stages represent the period of availability of both carbonaceous and nitrogenous material in high proportions for the stink bugs.

The duration of fruiting bodies at preferred stages available for the stink bugs vary between corn and soybean. The longer period for which high density of stink bugs was observed in soybean than in corn could be attributed to the duration of kernel and seed growth stages preferred by stink bugs in each crop. Beyond the dough stage, maturity of corn proceeds rapidly with grain hardening to maturity within two weeks. However, the seed enlargement period in soybean occurs over an entire month. At Keedysville after the initial buildup of population in corn, the steep decline in *H. halys* density during the dent stage corresponded to the steep increase in soybean during the pod filling stages. Also, interpolation maps revealed high densities in soybean edge bordering corn (during Aug 9 – Sep 6) illustrating the potential dispersal of stink bugs from corn into soybean. The preference and dispersal of stink bugs into soybean during the reproductive stages has been well documented by earlier studies (Bundy & McPherson, 2000; Herbert & Toews, 2012; Jones & Sullivan, 1982; Kennedy & Storer, 2000; Kogan & Turnipseed, 1987; McPherson *et al.*, 1993; Olson *et al.*, 2011; Panizzi & Slansky, 1985; Schumann & Todd, 1982; Todd, 1989; Turnipseed & Kogan, 1976; Velasco & Walter, 1992).

Additionally, the age structure of *H. halys* within each crop was significantly different. Disproportionately higher numbers of small nymphs and adults compared to large nymphs were recorded in corn, whereas the relative proportions of these stages were reversed in soybean. This suggests potential dispersal of large nymphs from corn into soybean at the interface of these crops, particularly during the dent stage in corn. Previous studies have documented fewer number of large nymphs in comparison to adults of *N. viridula* and *E. servus* in corn (Herbert & Toews, 2011; Herbert & Toews, 2012; Reisig, Roe, & Dhammi, 2013). Like the adults, large nymphs of *H. halys* are capable of movement and dispersal and observed to move between

habitats at the rate of 5 m / hr (personal communication, D-H Lee). Taken together, the spatial

population dynamics and age structure within each crop at the Keedysville sites implies that the

sequential movement of *H. halys* (particularly adults and large nymphs) between corn and

soybean fields is strongly influenced by the availability of the preferred phenological growth

stages. Such movement and aggregation of nymphs at the interface of peanut-cotton systems has

been reported for *N. viridula* and *E. servus* (Tillman, 2011). Shifting between host plants as the

preferred phenological stages become available in other hosts at is a prevalent behavioral

characteristic of stink bugs (Jones & Sullivan, 1982; Olson *et al.*, 2011; Panizzi, 1997; Reay-

Jones, 2010; Reisig, 2011; Tillman *et al.*, 2009; Tillman, 2011; Toscano & Stern, 1976).

Studies quantifying spatial population dynamics have documented the movement and

build up of stink bugs between corn and other adjacent crops. Similar to my study, adult stink

bugs were observed to move from senescing corn into peanut and cotton (Tillman 2011). High

stink bug densities in corn resulted in adjacent and more attractive cotton fields, and localized

control methods in corn have been recommended to mitigate stink bug invasion in subsequent

crops (Tillman, 2011). Likewise, the findings of this study identify the potential role of corn as

source of stink bugs invading soybean but more research is needed to determine if managing

stinkbugs in corn will reduce the risk of infestations in soybean. The stink bug population density

in late maturing crops such as soybean is heavily influenced by the extent of synchrony between

dispersing adults and large nymphs, and availability of phenological stages of the crop preferred

by stink bugs (Kennedy & Storer, 2000). The seasonal occurrence of preferred soybean crop

stage is largely determined by the planting date, cultivar of choice, and maturity group (Kennedy

& Storer, 2000; Schumann & Todd, 1982). For the corn-soybean sites in this study, there was

observed synchrony between the stink bug stages dispersing from corn and the preferred pod

filling stages of adjacent soybean planted as a full season crop. However, the synchrony between the two crops may be different if the soybean fields were planted later as a double crop after small grains, which is a common practice in the mid-Atlantic region. In fact, reports from crop advisors indicate that the highest stink bug infestations in soybean has varied from year to year with respect to full season or double crop plantings (personal communication, G.P. Dively).

At Beltsville, *H. halys* population build up in corn was not observed, and overall very few stink bugs were observed at all sampled grid points. Furthermore, the spatial pattern of density did not illustrate any dispersal of stink bugs from corn into soybean. These results are similar to an earlier study which did not find any *C. hilaris* in corn but reported higher densities in soybean later in the season (Herbert & Toews, 2012). The density of stink bugs recorded across transects from soybean field edges bordering corn also highlight the differences between sites. These results are consistent with the grid pattern findings, with both data sets from Keedysville showing high densities of stink bugs at sampling points in soybean closest to adjacent corn but this was not observed at Beltsville. These results suggest potential differences in the role of corn as a source of *H. halys* invading soybean, between sites with differing overall *H. halys* population densities.

The different density of stink bug populations between study locations was probably associated with overall lower population density at Beltsville rather than any asynchrony in the availability of preferred crop growth stages when stink bugs were moving among host plants during the mid to late summer. Therefore, the combined results of the study demonstrate the role of corn as a potential source of *H. halys* that disperse (particularly adults and large nymphs) into soybean, when overall stink bug population density is high. This has significant relevance for *H.*

halys management in field crops especially given the high proportion of soybean fields that are planted adjacent to corn. Eight and seven out of ten soybean fields are adjacent to corn in PA and MD, respectively, to just highlight the extent of vulnerability of soybean to dispersal of stink bugs from corn. While the invasion of *H. halys* into soybean from corn is observed only at sites with high overall population density, the ubiquity of adjacent soybean and corn plantings in the mid-Atlantic region does warrant attention with regards to managing *H. halys* in field crops.

Overall, this study provides evidence that *H. halys* is a generalist feeder that exhibits edge-mediated dispersal from corn into soybean at locations with higher initial population in corn and that the timing of movement is highly dependent on the presence of preferred crop growth stages. This preference for fruiting bodies and edge-centric behavior are similar to that of many other stink bug species (Jones & Sullivan, 1982; Kennedy & Storer, 2000; Panizzi & Slansky, 1985; Reay-Jones, 2010; Reeves *et al.*, 2010; Tillman *et al.*, 2009). Pest management strategies must consider an area-wide manipulation of the phenology, placement, and suitability of a few types of vegetation and/or crops to counteract landscape level processes supporting pest outbreaks (Jonsson, Wratten, Landis, Tompkins, & Cullen, 2010; Kennedy & Storer, 2000; Lamp & Zhao, 1993). Findings of this study have important implications for managing *H. halys* both at the regional and farm levels. Particularly in high density sites, the timing of scouting in corn and soybean should coincide with the onset of preferred growth stages in each crop and focus at least initially on the corn-soybean interfaces of adjacent fields. Consideration of crop arrangement in the farmscapes, planting date, and cultivar, are also possible options to desynchronize the timing for initial stink bug build up in corn and subsequent dispersal into soybean.

Chapter 3: **Temperature and resource availability drive regional patterns in stink bug (Hemiptera: Pentatomidae) pest populations**

Introduction

Understanding patterns over space and time is central to ecology and the assessment of spatial patterns is a fecund paradigm in ecology (Borcard *et al.*, 2004; Jombart *et al.*, 2009; Legendre, 1993). Biological communities and associated biota interact with the physical environment at definite temporal and spatial scales (*sensu* Turner, 1989) resulting in spatial structures (random, aggregated or regular). Therefore assessment and identification of the spatial structures in populations or communities is an important step toward unraveling the ecological processes that structure them (Borcard *et al.*, 2004; Dray *et al.*, 2012; Jombart *et al.*, 2009; Legendre & Fortin, 1989). Spatially correlated patterns (spatial dependence) of species distribution and abundance, or of communities, are influenced by exogenous factors such as environmental and habitat variables which are also spatially structured. Such an association is generally referred to as environment induced spatial dependence (Borcard *et al.*, 2004; Jombart *et al.*, 2009; Legendre, 1993; Wagner & Fortin, 2005). Besides environmental influences, endogenous, biotic processes such as dispersal, intra- and inter specific interactions and their own population dynamics result in species distribution or abundance exhibiting spatial dependence, known as pure spatial dependence or spatial autocorrelation (Borcard *et al.*, 2004; Dray *et al.*, 2012; Legendre & Legendre, 2012; Legendre, 1993; Peres-Neto & Legendre, 2010; Wagner, 2003).

Insects can be randomly distributed in the landscape, with no spatial structure. For example, inferring from damage on lodgepole pine, *Pinus contorta* Bol., Schroff, Lindgren, &

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Gillingham (2006) found that *Hylobius warren* Wood, Warren root collar weevil, was randomly distributed. When spatial structures are present those produced through environment induced spatial dependence are expected predominantly to occur at broad spatial scales (Legendre & Legendre, 2012; Legendre, 1993; Wiens, 1989). For example, broad scale spatial patterns in Carabid beetle communities was associated with topoclimatic differentiation (Judas, Dornieden, & Strothmann, 2002) and broad scale spatial structures in Oribatid mite communities were primarily related to the density of shrub cover (Borcard *et al.*, 2004; Jombart *et al.*, 2009). Alternately, spatial structures arising due to pure spatial dependence / spatial autocorrelation, due to biotic processes, are expected to occur at medium to fine spatial scales (Legendre & Legendre, 2012; Legendre, 1993; Wagner & Fortin, 2005; Wiens, 1989). For example, Moravie, Borer, & Bacher (2006) found that the stem-boring weevil, *Apion onopordi* infested thistle, *Cirsium arvense* (L.) Scop., were aggregated at fine scales in relation to the limited dispersal capability of the weevil.

Assumption of such dichotomy could be an oversimplification and indeed a combination of several ecological processes occurring at different spatial scales could lead to an empirically observed spatial pattern (Borcard *et al.*, 2004; Dray *et al.*, 2012; Jombart *et al.*, 2009, 2009; Wagner & Fortin, 2005). Aukema *et al.* (2006) found that fine scale spatial pattern of outbreaks in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, was primarily associated with dispersal. However, temperature which varied at broad spatial scales influenced dispersal behavior. Testing for spatial pattern at multiple scales and identifying the scale of occurrence, therefore, has significant implications for hypotheses about the ecological processes – environmental, biotic or in combination - structuring them (Dray *et al.*, 2012).

Concepts in spatial ecology are relevant for developing management strategies for controlling insect pest species (Tscharntke *et al.*, 2005) as insect population densities are typically spatially heterogeneous (Liebhold *et al.*, 1993; van Helden, 2010). Knowledge of spatial patterns in pest insect abundance could help us deduce ecological processes driving pest outbreaks and inform pest monitoring planning (Taylor, 1984), predict abundances (Liebhold *et al.*, 1993) or future outbreaks (de Valpine, Scranton, & Ohmart, 2010), and prioritize areas for appropriate management interventions (Aukema *et al.*, 2006; Cocu *et al.*, 2005; Eber, 2004; Rodeghiero & Battisti, 2000). For example, spatially explicit information within a field is the core component of site-specific insect pest management (review by Park, Krell, and Carroll 2007) or precision agriculture for agricultural management in general (Oliver, 2010).

Throughout the world, stink bugs are major pests of economically important crops (Panizzi, 1997). Stink bugs in the family Pentatomidae are considered to be an important pest in soybean *Glycine max* (L.) Merr. producing areas in various parts of the world (Panizzi & Slansky, 1985; McPherson & McPherson, 2000). The most common stink bug pests in agricultural fields of mid-Atlantic United States are the green stink bug, *Chinavia hilaris* (Say) and the brown stink bug, *Euschistus servus* (Say 1832), both pests of economic importance in a variety of commodities including cotton (*Gossypium hirsutum* L.), soybeans, tomatoes (*Solanum lycopersicum* L.), and peaches *Prunus persica* (L.) Batsch and other trees crops (Kamminga, Koppel, Herbert, & Kuhar, 2012; McPherson & McPherson, 2000). The recent explosion in populations of the invasive brown marmorated stink bug, *Halyomorpha halys* (Stål 1855) however, has led to significant economic and ecological impacts.

Since the accidental introduction from its native Asia, *H. halys* since late 1990s (Hoebeke & Carter, 2003), has spread to 41 states in the USA and has become a severe agricultural and nuisance pest in the mid-Atlantic region (Leskey *et al.*, 2012). They also have been introduced into Ontario in Canada (Fogain & Graff, 2011; Gariepy, Haye, Fraser, & Zhang, 2014) and in many parts of Europe including Switzerland (Wermelinger, Wyniger, & Forster, 2008), Liechtenstein, Germany (Gariepy *et al.*, 2014), France (Callot & Brua, 2013) and Italy (Haye, Abdallah, Gariepy, & Wyniger, 2014). This polyphagous stink bug has a wide range of host plants including tree fruits, vegetables, field crops, ornamental plants, and native vegetation in its native and invaded ranges (BMSB IPM Working Group & Northeastern IPM Center, 2013). Since 2010, serious crop losses have been reported for apples (*Malus domestica* Baumg.), peaches, sweet corn (*Zea mays* L.), peppers (*Capsicum annuum* L.), tomatoes and row crops such as field corn and soybeans in the mid-Atlantic region and *H. halys* is also a nuisance pest entering homes for overwintering (Leskey *et al.*, 2012).

In this context, assessment of spatial structures in stink bug population dynamics, particularly for the invasive *H. halys*, and the ecological processes controlling them, could help elucidate factors influencing pest invasion (With, 2002). The effect of landscape configuration and composition on the spread or containment of exotic pests informs how spatial patterns of resource distributions affect the various stages of the invasion process (With, 2002). An assessment of the spatial distribution and influence of resources and other landscape features on the populations of exotic pests may aid prediction and management of the spread of invasive species such as *H. halys*. Also, the spatial scale of association between insect densities and landscape might vary with the focal scale addressed (Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tscharntke, 2002; Tscharntke *et al.*, 2012). Hence explicitly analyzing spatial structure

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in species abundance across multiple spatial scales, in relation to landscape variables at different spatial scales may enable accurate quantification of pest insect population dynamics and landscape association. Additionally, the ability of farmers to manipulate pests such as *H. halys* requires knowledge of its pattern of distribution and abundance within fields and across large landscapes and of how prevailing environmental and landscape factors may inhibit or support pest outbreaks. This is important for developing effecting management strategies and may aid prediction and prevention of the spread of this invasive insect. However, other than climate related distributional range (Musolin, 2007) and predictive distribution models (Zhu *et al.*, 2012), detailed assessment on spatial structures in stink bug populations across large study area and the underlying ecological process, are currently not available. The only available, but spatially implicit study relating *H. halys* population dynamics in the wild with temperature found that in its original range, the proportion of surviving adult *H. halys* may be higher when temperatures in early spring (March and April) are lower (Funayama, 2013).

I examined the spatial structure, spatial dependence and spatial autocorrelation in stink bug abundance to infer the underlying ecological processes. I followed the thematic recommendations by McIntire & Fajardo (2009), and its methodological exegesis by Dray *et al.*, (2012) and employed 'space as a surrogate' explanatory variable to heuristically discern the ecological processes underlying the spatial structures in stink bug populations. The 'space as a surrogate' method is a deductive procedure that combines statistical models and mechanisms for inferring ecological processes from spatial patterns. In this approach, ecological theories and/or knowledge are used for developing hypotheses about the spatial pattern the relevant ecological processes may create, and using precise spatial analysis these hypotheses are tested (McIntire & Fajardo, 2009). 'Space as a surrogate' approach is valid for understanding factors influencing the

spatial structuring of invasive pests like *H. halys*. Existing information on the biology of this stink bug both from its native and introduced ranges (Funayama, 2013; Haye *et al.*, 2014 in press; Lee *et al.*, 2013; Nielsen, Hamilton, & Matadha, 2008; Niva & Takeda, 2003; Taylor, Coffey, DeLay, & Dively, 2014) could be used to formulate and test various hypotheses on ecological processes that drive its spatial structuring in its introduced range where no such information currently exists. This would help us gain valuable insight into potential ecological factors that influence stink bug populations in introduced range, and thereby help devise management strategies for this invasive agricultural pest and contribute to broader understanding of invasion processes.

I formulated various such hypotheses as follows - 1) spatial structures might not be present and stink bug population dynamics might be randomly distributed, representing null hypothesis; 2) spatial structuring at very broad scales primarily in relation to climatic conditions since temperature profoundly influences development, growth, survival and abundance (Funayama, 2013; Haye *et al.*, 2014 in press; Nielsen *et al.*, 2008; Niva & Takeda, 2003); 3) trees represent the primary hosts for stink bugs upon reemergence from overwintering (Lee *et al.*, 2013). Also, habitats adjacent to the crop field influence stink bug abundance and high level of infestations in crops along wooded regions and buildings are reported (Leskey *et al.*, 2012). Hence, presence of host plant species, including forested areas, may influence stink bug abundance at multiple spatial scales (dependent on the scale they themselves vary over the landscape) including broad, medium to fine spatial scales; 4) Intraspecific interactions such as semio-chemically mediated aggregations could influence dispersal and abundance (Toyama, Ihara, & Yaginuma, 2006). Bacterial gut symbiont *Pantoea agglomerans* that are indispensible for *H. halys* survival and abundance, and smeared on the eggs by the *H. halys* female, could be

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affected by micro-climatic conditions (Taylor *et al.*, 2014). Hence intraspecific interactions or a combination of inter-specific interaction with microclimate could influence spatial structuring at fine spatial scales; and 5) Exogenous factors such as climate and resource availability could combine with endogenous factors like dispersal and species interactions, and produce patterns at broad and fine spatial scales.

Utilizing data from a regional network of soybean sampling fields, I tested these hypotheses for *H. halys* and such similar hypotheses for *C. hilaris* and *E. servus*. In this study which represents first such effort addressing large scale patterns in stink bugs, I followed the methodology put forth by (Dray *et al.*, 2012) and addressed the specific questions - a) at which spatial scale is the abundance of stink bug species in the mid-Atlantic region structured?; b) what are the environmental and multi-scale landscape factors associated with stink bug abundance and at which spatial scales do they influence stink bug abundance?; and c) do the spatial structures persist after the environmental influences have been accounted for, and at which spatial scales? Finally, I also separately tested the influence of adjacent habitat influence on within field population abundance, as a measure of fine-scale spatial structure.

Methods

Study area and stink bug sampling

The study area covered a large portion of mid-Atlantic USA (38.0° - 39.7° N and 75.5° – 79.0° W) including New Castle County in Delaware; Carroll, Frederick, Montgomery, and Washington Counties in Maryland; Augusta, Clarke, Culpeper, Frederick, Loudoun, Orange, Shenandoah and Spotsylvania counties in Virginia; and Jefferson County in West Virginia (Fig.

3.1). It encompasses a range of topographical, bioclimatic conditions and heterogeneous

landscapes, and also experienced high stink bug density over the past three years, particularly *H.*

halys, which were serious agricultural pests (Leskey *et al.*, 2012). Sampling was conducted in

soybean as focal crop system, which is a preferred host of stink bugs (Panizzi & Slansky, 1985),

and constitutes a very high proportion of Northeastern US (8 % or 665,709 Ha) and overall US

crop area (23%; NASS - USDA, 2014). Soybean also suffers quality and yield loss due to stink

bug feeding and stay-green syndrome (Leskey *et al.*, 2012).

Field sampling was carried out between Aug 25 - Sep 16 of 2012 and 2013, during seed

growth stages of soybean which is associated with highest abundances of *H. halys* and other

stink bugs in the mid-Atlantic region (Nielsen *et al.*, 2011). Only full season soybean fields (full

pod stage and older) in the study area, devoid of any insecticidal applications, were sampled to

avoid biases in abundance due to soybean maturity differences. Stink bug abundance was

determined by sweep net (38 cm diameter) sampling in the soybean canopy within the first few

meters from field edge, where stink bug densities were expected to be the highest (Leskey *et al.*,

2012). A set of 25 sweeps was taken at each of three sides of each field. Sweep net procedures

(sweeping height, speed and sweep net arc length) were maintained similar across the field crew

members (O'Neill, Larson, & Kemp, 2002). The growth stages, species and counts of stink bugs

observed in the sweep net samples were either field identified or collected for later identification.

The adjacent habitat at each of three sides of the field was noted along with the spatial

coordinates of the field at one location for the entire field. Adjacent habitats were classified into

9 categories – Buildings, Buildings&Crop, Buildings&Open, Buildings&Woods, Crop,

Crop&Open, Crops&Woods, Open, Woods and Woods&Open. A total of 208 soybean fields, 89

during 2012 and 119 during 2013 were sampled. Counties in Maryland and West Virginia were

sampled during 2012 and 2013, while Loudoun County in Virginia was sampled only during 2012 and rest of Virginia counties and Delaware were sampled only during 2013.

Explanatory variables

Topography, temperature related variables, quantitative measures of landscape composition (proportional abundance of each landscape class and landscape diversity), and landscape configuration (perimeter-area ratio of patches), all were used as predictors of stink bug abundance across the study area (Table 3.1). Topography of the sampled fields was characterized by altitude, slope and aspect (directionality of slope) derived with digital elevation models from National Elevation Dataset (Gesch *et al.*, 2002) with a spatial resolution of 1/3 arc-seconds (~10m). Aspect values were further transformed by trigonometric functions (sine and cosine) to identify 'Eastern' and 'Northern' exposure respectively (4 topography variables in total).

Daily minimum and maximum temperature data during the 2012 and 2013 stink bug reproductive seasons (May 15 – Sept 30) were procured for all the available weather stations in the study area (Climate Data Online (CDO) - NCDC, 2014). Daily min and max temperature values for each of the sampled fields were then derived through inverse distance weighted interpolations (exponent or power value of 2 and 12 neighboring points; (Webster & Oliver, 2007) daily temperature data from weather stations in the region. A suite of temperature related variables (8 in total) were calculated for each sampling field including: average monthly minimum and average maximum for Jun, July, and August; number of days with maximum temperature above the upper *H. halys* temperature threshold (35°C) and number of days with minimum temperature below the lower *H. halys* minimum temperature threshold (14.15°C; Nielsen & Hamilton, 2009a; Table 3.1).

Figure 3.1. Location of soybean fields sampled (black circles) for stink bugs during 2012 and 2013 in mid-Atlantic USA. Inset depicts the landscape composition (developed areas in black, crop areas in dark grey, forest areas in grey and others in white) around each sampled field quantified at four different spatial scales (100m, 500m, 1 Km and 5 Km concentric circles).
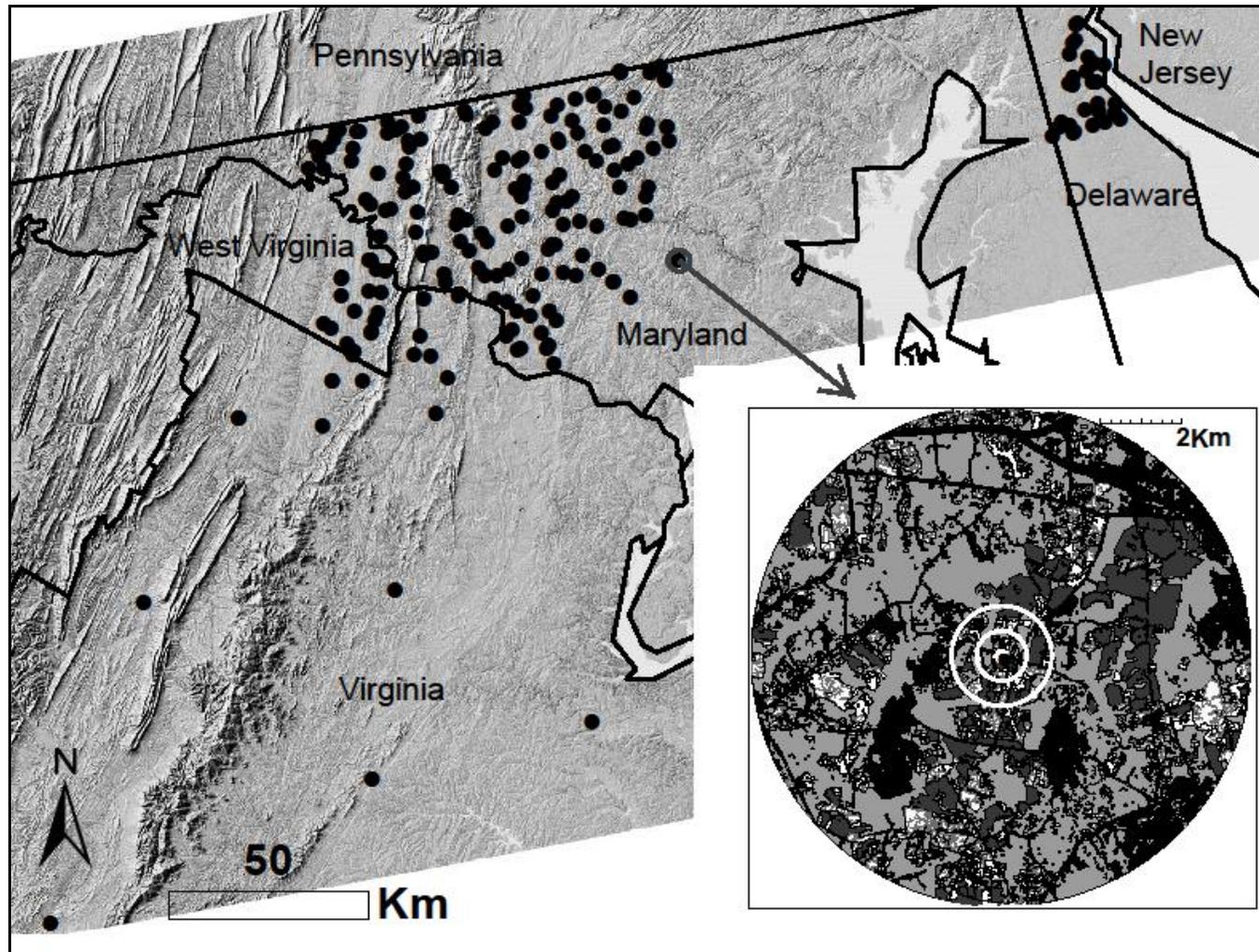
Data on land-use surrounding the sampled fields were generated by overlaying and clipping buffers at four different spatial scales (100m, 500m, 1000m, 5000m radii centered in sampled fields; Fig. 3.1) from CropScape. This online dataset is a 56-m resolution, remotely sensed land cover map available from the USDA National Agricultural Statistics Service for 2012 (Boryan, Yang, Mueller, & Craig, 2011; Han *et al.*, 2012; Han, Yang, Di, Yagci, & Han, 2014). For each spatial scale, the following landscape composition variables were generated (Table 3.2): % overall crop area (all cultivated land types), % overall forest area (all natural habitat types); % developed area (categorized into open and developed areas with low, medium, and high intensities); Shannon-Wiener landscape diversity index (Magurran, 2013); and perimeter- area ratio for each habitat types averaged for the entire landscape as a measure of landscape configuration. A total of 32 land-use variables were thence calculated (8 X 4 spatial scales). Finally, Euclidean distance of each sampled field to the location of the original *H. halys* source population (Allentown, Pennsylvania; (Hoebeke & Carter, 2003) was also calculated. All GIS data manipulations and compilations for the landscape, topography and climatic variables were performed in ArcGIS 10.0 (ESRI, 2011).

Statistical Analyses

Analyses were performed as two parts of the regional stink bug abundance data. Firstly, the spatial structure in stink bug abundance data was analyzed for induced spatial dependence (associations with environmental factors, and the landscape at multiple spatial scales) and spatial autocorrelation (residual spatial structure) for stink bug abundance were then analyzed. Then, the very fine scale landscape influences of adjacent habitat on within field stink bug abundance were analyzed and compared with and without accounting for differences between sampled fields.

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Model comparisons with and without sampling year as a random effect (not reported here), while other parameters were held similar, showed that the random year effect did not significantly improve model. For each species separately, analyses were hence performed on data pooled over sampling years (2012 and 2013), and across different growth stages.

Environmental and multi-scale landscape influence

The multi-scale landscape and environmental influences on the abundance of each stink bug species were analyzed through individual generalized linear models (GLMs) with a quasipoisson error distribution and log link function (Ver Hoef & Boveng, 2007). In all of the GLMs, the total number of each stink bug species enumerated at a sampled field (data pooled over all the 3 sides of a field) was the response variable (208 fields in total). In the GLM for *H. halys* all the 45 multi-scale landscape, topography and temperature related variables were used as predictors, while in the GLM for *C. hilaris* and *E. servus*, day counts of temperature below and above the *H. halys* developmental threshold, and distance from Allentown were excluded. Model selection and validation for the quasipoisson GLMs followed (Zuur *et al.*, 2009) and relevant variables were selected by running a full model (with all explanatory variables) and then a step wise backward selection to eliminate insignificant terms. At every step single insignificant term ($P > 0.05$), as identified by a likelihood ratio test between models with and without the term, was dropped sequentially till all terms retained in the model were significant. Plots of the response residuals (observed values subtracted from fitted values), Pearson residuals, scaled Pearson residuals (accounting for overdispersion) and the deviance residuals for the chosen quasi-Poisson model were inspected for patterns or lack thereof; with a lack of pattern validating the model. Pseudo R^2 values, as measures of variance explained were also computed for the GLMs (McFadden, 1973; Nagelkerke, 1991).

Spatial structure, dependence and residual patterns

The procedures employed here for analyzing multi-scale spatial structure, dependence and autocorrelation in stink bug abundance broadly follow that of the worked example in (S. Dray *et al.*, 2012). While this example elaborated the methodological framework for such an analysis primarily for multivariate, community data, the same is applied here for univariate species abundance data. Using the spatial coordinates of the sampled fields, the spatial component was quantified through Moran's Eigenvector Maps (MEMs; Borcard *et al.*, 2004; Borcard & Legendre, 2002) based on Gabriel graph as spatial weighting matrix (Legendre & Legendre, 2012): 836 -838). The spatial eigenfunctions of MEMs reflect patterns in the spatial distribution of sampled fields since they are orthogonal maps that decompose the spatial relationships among the sampled fields, based on a given spatial weighting matrix and arranged along broadest to finest spatial scales (Dray *et al.*, 2012; Griffith & Peres-Neto, 2006). As MEMs are orthogonal decomposition of spatial relationships between sampled fields, the spatial eigenfunctions reflect independent information about spatial pattern ranging from broad to fine spatial scales thereby enabling easier interpretation of the spatial pattern and its relevant scale (Dray *et al.*, 2012; Griffith & Peres-Neto, 2006; Gutzwiller, 2013).

MEMs based on Gabriel graph were used to estimate and test the multi-scale components of spatial structures in stink bug abundance (original field data), model approximations (fitted values from regression model with the selected explanatory variables) and, the residual variance once the influence of the explanatory variables was factored out (Dray *et al.*, 2012; McIntire & Fajardo, 2009). For each stink bugs species, individual scalograms were computed by projecting each of the three data (raw abundance, model estimations, residuals) onto the spatial component

generated by the MEMs (n-1; 207 in total), thereby partitioning the respective variances into spatial scales ranked from broadest to the finest. On ground, the very broad scale corresponds to the entire study area and very fine scale to a few sampled fields. Scalograms were smoothed into 9 spatial components each with 23 successive MEMs (Munoz, 2009; Dray *et al.*, 2012), representing a gradient of very broad to very fine spatial scales respectively. When spatial structure is absent, the individual scalogram R^2 values (amount of variation in each data explained by a given spatial scale) are expected to be uniformly distributed (Ollier, Couteron, & Chessel, 2006). As demonstrated by Dray *et al.* (2012), a permutation procedure with 999 repetitions was used to test if the maximum observed R^2 (R^2 max; corresponding to the smoothed MEM at which the ecological pattern in mainly structured) is significantly higher than the values determined in the absence of a spatial pattern. Finally, maps of the spatial structure in the residual data were examined to understand the sampled fields that contribute to the patterns in the unexplained variance.

Table 3.1. Description and summary statistics (Mean values and standard deviation in parentheses) of the topographic and temperature variables used for predicting stink bug abundance in mid-Atlantic US.

Variable Type	Variable name	Description	Mean (SD)
Distance	Distance from Allentown	Euclidean distance of sampled fields from original source of *Halyomorpha halys* (Hoebeke & Carter, 2003); km)	202.6 (44.8)
Topography	Altitude	Altitude of sampled fields (m)	152.5 (77.7)
	Slope	% slope gradient at sampled points	3.8 (3.5)
	Sine (Aspect)	Sine of aspect value as a measure of 'Northness'. Values range between - 1 and 1 indicating South to North	0.1 (0.8)
	Cosine (Aspect)	Cosine of aspect value as a measure of 'Eastness'. Values range between - 1 and 1 indicating West to East	0.0 (0.6)
Temperature	Days above *H. halys* upper threshold	Count of days between Jun-Sept during which the maximum temperature was above 35 °C, the maximum temperature threshold (Nielsen & Hamilton, 2009a)	2.0 (1.8)
	Days below *H. halys* lower threshold	Count of days between Jun-Sept during which the minimum temperature was below 14.15 °C, the minimum temperature threshold (Nielsen & Hamilton, 2009a)	34.1 (8.9)
	Monthly Average Minimum Temperature (°C)	Minimum temperatures for June	16.0 (1.1)
		Minimum temperatures for July	19.8 (0.9)
		Minimum temperatures for August	17.3 (0.9)
	Monthly Average Maximum Temperature (°C)	Maximum temperatures for June	27.3 (0.5)
		Maximum temperatures for July	30.3 (0.9)
		Maximum temperatures for August	28.0 (1.0)

Table 3. 2. Description and summary statistics of (Mean values and standard deviation of percentage areas in parentheses) the landscapes variables at different spatial scales used for predicting stink bug abundance in mid-Atlantic US.

Variable name	Description	Scale			
		100m	500m	1 Km	5 Km
% Crop area	% area of all cultivated landuse types	50.7 (24.2)	45.0 (18.8)	37.2 (15.3)	25.4 (10.6)
% Forest area	% area of all natural habitat types	5.8 (10.2)	16.7 (13.1)	22.9 (13.6)	34.3 (13.5)
% Developed - High Intensity area	Highly developed residential / work areas with impervious surfaces < 80 % of total area. Examples include apartment complexes, row houses and commercial/industrial.	0.1 (0.8)	0.1 (0.5)	0.2 (0.8)	0.3 (0.6)
% Developed - Medium Intensity area	Mix of constructed materials and vegetation. Impervious surfaces 50 - 79 % of total cover. Commonly single-family housing units	0.3 (1.5)	0.5 (1.7)	0.6 (1.7)	1.0 (1.7)
% Developed - Low Intensity area	Mix of constructed materials and vegetation. Impervious surfaces 20 - 49 % of total cover. Commonly single-family housing units	6.4 (10.9)	3.0 (5.2)	3.0 (4.8)	3.7 (4.1)
% Developed - Open area	Some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces < 20 % of total cover. Commonly include large-lot single-family housing units, vegetation planted in developed settings	16.5 (13.1)	7.9 (6.0)	7.1 (4.5)	8.6 (4.5)
Index of landscape diversity	Shannon-Weiner index of landscape diversity	2.2 (0.2)	2.3 (0.2)	2.5 (0.2)	1.7 (0.4)
Perimeter-Area ratio	A measure of geographical complexity of a polygon, with a high ratio denoting complex polygon. Calculated for each patch and averaged for the entire landscape	0.1 (0.0)	0.2 (0.2)	0.2 (0.3)	0.2 (0.1)

Adjacent habitat influence

For *H. halys* and *C. hilaris*, the influence of adjacent habitat on the abundance of each species was tested by two separate lognormal-Poisson generalized linear mixed models (GLMM) each with an observation-level random effect in the model to account for overdispersion (Bolker *et al.*, 2009; Elston *et al.*, 2001). For each model, the response (stink bug abundance along each side of the sampled field; 208 fields * 3 sides each, 624 data points) and the fixed effect (adjacent habitat) were held constant. However, one of the models contained the sampled field as a random effect term, to account for differences in stink bug abundance between sampled fields. Significance of the fixed effect (adjacent habitat) was determined through Type II Wald χ^2 tests. The models were compared through calculations of relative log-likelihood based on Akaike information criteria (AIC) and Bayesian information criteria (BIC), hypothesis tests, and coefficient of determination (R^2) for GLMMs (Nakagawa & Schielzeth, 2013). For each model, significant differences in the estimated means of stink bug abundance in soybean between the adjacent habitat types were identified through Tukey's HSD pair-wise comparisons. For *E. servus*, the adjacent habitat influence on the abundance was tested by a generalized linear model (GLM) with a quasipoisson error distribution and log link function.

All statistical analyses were performed in R program (R Development Core Team, 2011) with associated packages. GLMMs were performed with package lme4 (Bates *et al.*, 2013, p. 4) and Tukey's HSD for GLMMs were performed with multcomp (Hothorn *et al.*, 2013). The relative log-likelihoods for GLMMs were calculated with package LMERConvenienceFunctions (Tremblay & Ransijn, 2013). GLMM estimated coefficients were extracted and plotted using package effects (Fox *et al.*, 2013) and coefficient of determination for the GLMMs were

calculated with package MuMin (Bartoń, 2013). Packages sp (Pebesma, Bivand, Rowlingson, & Gomez-Rubio, 2013), spdep (Bivand *et al.*, 2014) and spacemakeR (Dray, 2011) were used to generate the MEMs based on Gabriel graph. The scalograms were derived by modifying the R codes provided by (Dray *et al.*, 2012) and permutations for the scalograms were performed with package ade4 (Dray *et al.*, 2013).

Results

An overall total of 8702 stink bugs were observed in 624 sweep nets samples from 208 fields during 2012 and 2013 of which *H. halys* and *C. hilaris* constituted 88% and 8%, respectively.

Multi-scale landscape and environmental influence

GLM results for *H. halys* identified six main explanatory variables out of the 45 variables used as predictors (Table 3.3), accounting for 26% - 31 % of the variance (based on pseudo R^2 measures). Temperature variables were the most important predictors, with negative association between *H. halys* abundance and average minimum temperatures in July, and positive association with average minimum temperature in both June and August. *H. halys* abundance was also positively associated with % high density developed areas at 500 m and % open developed areas at 1 km scale. Also, North facing slopes were associated with higher abundances of *H. halys*. Distance from Allentown, PA, the putative source population, was not a significant predictor of *H. halys*, and neither were % forest and crop area variables. *C. hilaris* was associated primarily with altitude and landscape variables at large spatial scales (5 km scale), with higher abundance at higher altitudes and fields surrounded by high % forest area and % crop area (Table

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3.3). *C. hilaris* abundance was negatively associated with landscape diversity at 5 Km scale. *E. servus* abundance increased along with the % forest area at 500m scale and decreased with high % of low intensity developed area at 5 km scale (Table 3.3).

Spatial structure, dependence and residual pattern

Projection of *H. halys* abundance onto the spatial component showed a scalogram with significant variance accumulation in the very broad scale spatial component (R^2 Max = 0.15, P = 0.001; Fig. 3.2A) identifying the non-random, very broad scale spatial structuring of *H. halys* abundance. For *C. hilaris*, the scalogram revealed patterns similar to that of *H. halys*, with significant variance accumulation at the very broad and broad scales (R^2 Max = 0.11, P = 0.014 and R^2 = 0.11, P = 0.010, respectively; Fig 3.2D). Scalogram for *E. servus* data (Fig 3.2G) showed significant variance accumulation in the very broad (R^2 Max = 0.10, P = 0.019) and broad spatial scales (R^2 = 0.10, P = 0.032) with non-random spatial structuring.

Scalograms of the GLM model for *H. halys* data approximated with the environmental and landscape variables showed significant variance accumulation at the very broad scale component (R^2 Max = 0.32, P = 0.001; Fig. 3.2B). Expectedly, this reflected the very broad spatial scales at which the environmental factors (temperature and aspect) included in the GLM varied in my study area. *C. hilaris* scalogram showed skewed distribution of spatial variance accumulation at the very broad spatial scales (R^2 Max = 0.30, P = 0.001 and R^2 = 0.25, P = 0.001 respectively; Fig. 3.2E) corresponding again to the very broad scales at which the predictor variables (altitude, % forest area at 5 km scale, % crop area at 5 km scale) varied in my study area.

Table 3.3. Results of Generalized linear models analyzing the influence of multi-scale landscape and environmental influences on the abundance of stink bug species in soybean fields of mid-Atlantic USA. The model estimated values (β; in log-link function), its standard error (β s.e), t-value and p-value are provided for each independent variable in models corresponding to each species, along with pseudo R^2 measures. Non-significant predictors were excluded from the final model by stepwise backward-selection (P<0.05) and likelihood ratio tests.

Species	Variables	β	β s.e	t-val	p-val	Nagalk-erke's Pseudo R^2	McFad-den's Pseudo R^2
Halyomorpha halys	Average Minimum Temperature in July	-1.15	0.22	-5.22	<0.001	0.31	0.26
	Average Minimum Temperature in June	0.57	0.12	4.90	<0.001		
	Average Minimum Temperature in August	0.48	0.17	2.89	0.004		
	% Developed Area - High Intensity at 500m scale	0.31	0.12	2.61	0.010		
	% Developed Area - Open at 1 Km scale	0.04	0.01	2.50	0.013		
	Sine (Aspect)	0.23	0.10	2.29	0.023		
Chinavia hilaris	% Forest Area at 5 Km Scale	0.04	0.01	5.05	<0.001	0.14	0.23
	Altitude	0.00	0.00	3.80	<0.001		
	% Crop Area at 5 Km Scale	0.06	0.02	3.54	<0.001		
	% Developed Area - High Intensity at 5 Km scale	0.08	0.03	2.48	0.014		
	Shannon-Weiner Index of Landscape Diversity at 5 Km scale	-1.78	0.77	-2.30	0.023		
Euschistus servus	% Forest Area at 500m Scale	0.03	0.01	4.16	<0.001	0.11	0.19
	% Developed Area - Low Intensity at 5 Km scale	-0.13	0.04	-3.19	0.002		
	% Forest Area at 5 Km Scale	-0.02	0.01	-2.61	0.010		
	Average Minimum Temperature in August	-0.25	0.10	-2.45	0.015		
	Average Minimum Temperature in June	0.21	0.09	2.34	0.020		

Scalogram for GLM model approximations of *E. servus* abundance showed significant non-random spatial components at the very fine (R^2 Max = 0.17, P = 0.007) and very broad (R^2 = 0.09, P = 0.041) spatial scales (Fig. 3.2H) corresponding to the very broad (temperature variables) and very fine scale (% forest area at 500m) at which the predictor variables varied in my study area.

Scalogram for *H. halys* residual data showed significant accumulation of the spatial variance in the very broad scale spatial component (R^2 Max = 0.13, P = 0.004) and a non-significant, yet important variance accumulation at the very broad to broad scale component (R^2 = 0.07, P = 0.059; Fig 3.2C). Scalograms for *E. servus* residuals also showed similar results with significant variance accumulation at the broad spatial scale (R^2 = 0.09, P = 0.016; Fig 3.2I). Scalograms for *C. hilaris* residuals, however, did not reveal any significant spatial structures at any spatial scale (Fig. 3.2F).

Adjacent habitat influences

GLMMs testing influence of adjacent habitat on *H. halys* abundance, with and without sampled field as random effect, both showed significant effects (Wald χ^2 = 66.19, df = 9, P < 0.001 and Wald χ^2 = 98.89, df = 9, P <0.001 for GLMM without and with sampled field as random effect, respectively). In both models, highest mean abundance of stink bug was found in fields adjacent to wooded regions, while lowest mean abundance was observed in fields adjacent to open areas.

Figure 3. 2. Smoothed scalograms (207 MEMs assembled in 9 groups) indicating the portion of variance (R2) explained by each spatial scale for stink bug abundance data from soybean fields of mid-Atlantic USA. The spatial scales are denoted by the letters VB – Very Broad, B – Broad, M – Medium, F – Fine, and VF – Very fine. Scalograms for *Halyomorpha halys* abundance, its approximation with environmental variables and the residual data are provided (A – C respectively). Similarly, scalograms for *Chinavia hilaris* (D - F) and *Euschistus servus* (G - I) are also provided. For each scalogram, the scale corresponding to the highest R^2 (in dark grey) is tested using 999 permutations of the observed values (p-values are given). The dotted line with (+) symbols represent the 95% confidence limit.
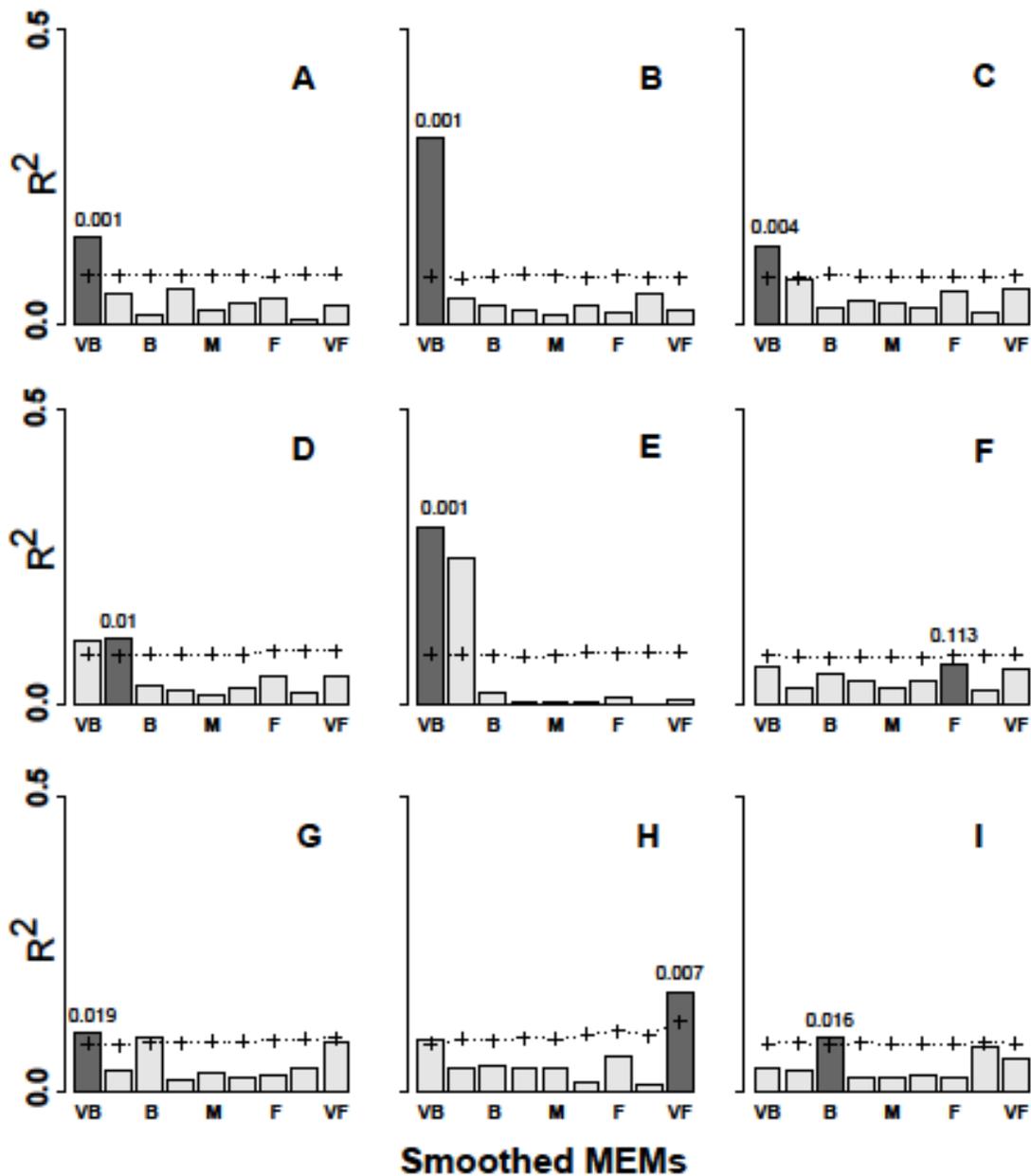
Figure 3.3. Abundance of *Halyomorpha halys* in the sampled plots across the mid-Atlantic region in relation to minimum temperature (°C) on a random July day.
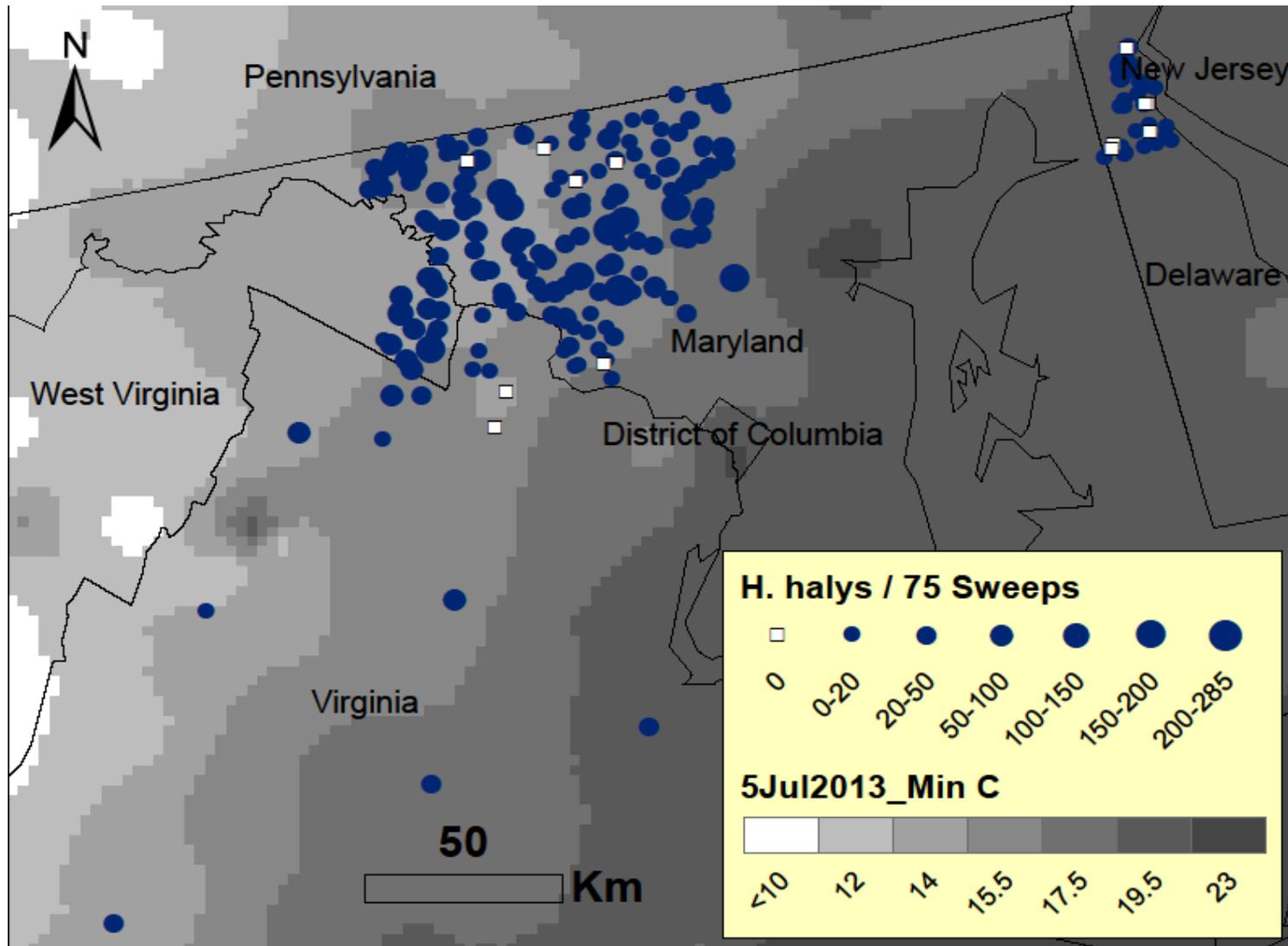
Figure 3. 4. Abundance of *Chinavia hilaris* in the sampled fields across the mid-Atlantic region.
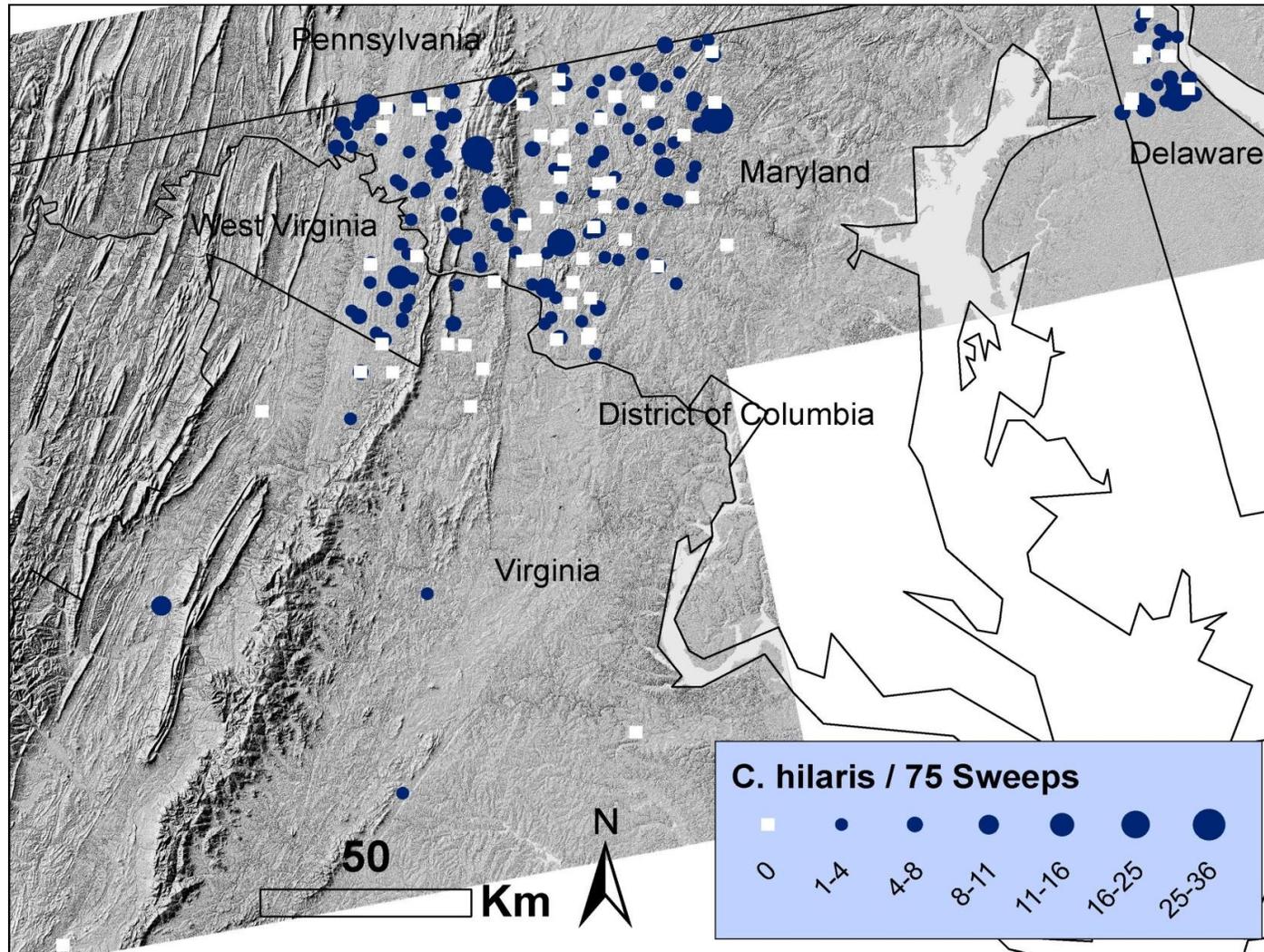
Figure 3. 5. Abundance of *Euschistus servus* in the sampled fields across the mid-Atlantic region.
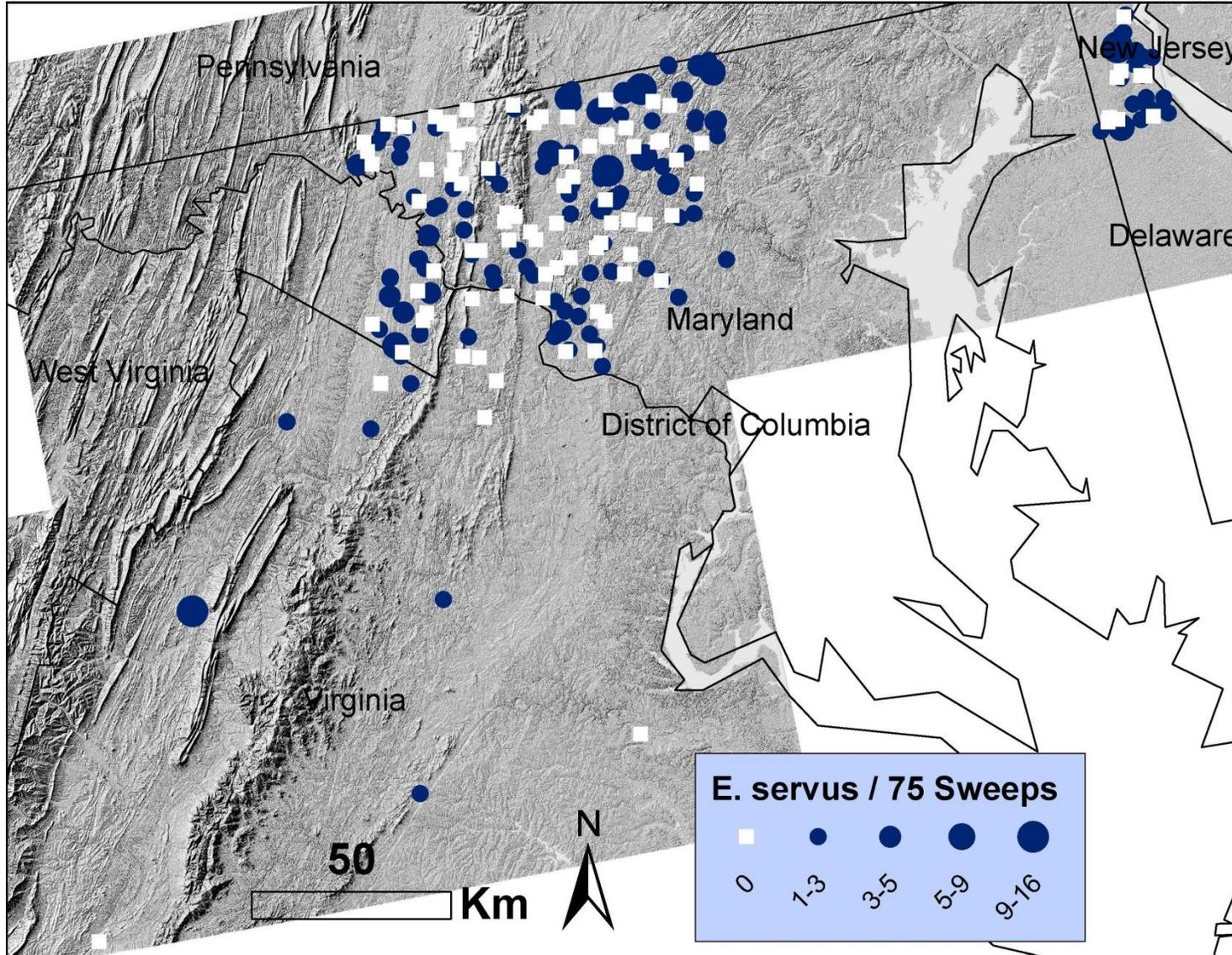
The model with the sampled field as a random effect was identified as better fit based on model relative log-likelihood calculations using AIC and BIC values (Table 3.4). In both models, highest abundance of stink bugs was observed adjacent to the woods and buildings. Multiple means comparisons as obtained from each of these models showed more significant differences between adjacent habitats in the model with sampling field as random effect (Figs. 3.6A & 3.6B). Particularly, differences between crops and other adjacent habitats that were insignificant in the model without sampled field as a random term, were identified as significant.

For *C. hilaris* abundance data GLMMs testing the influence of adjacent habitat with and without sampled field as a random effect, both showed significant effects (Wald $\chi^2 = 28.94$, df = 9, P <0.001 and Wald $\chi^2 = 33.12$, df = 9, P <0.001 for GLMM without and with sampled field as random effect, respectively). Similar to *H. halys* results, comparisons of the *C. hilaris* GLMMs revealed that the model with the random effect was better based on comparative log-likelihood calculations using AIC and BIC values for each model (Table 3.4; Fig. 3.7A & 3.7B). Results of the GLM showed that *E. servus* abundance was not significantly influenced by adjacent habitat (Wald $\chi^2 = 12.47$, df = 9, *P* = 0.13) and multiple comparison of means were not performed.

Table 3.4. Comparison of GLMMs analyzing the influence of adjacent habitat on abundance of stink bug species in soybean fields of mid-Atlantic USA. For each of the models, the fixed effect remained constant while the random model terms varied.

Species	Model random terms	AIC	BIC	logLik	relLikAIC	relLikBIC	Fixed effects R^2
Halyomorpha halys	Observation	2319	2363	-1150			0.095
	Sampled field and observation	2165	2214	-1071	3.13E+33	3.40E+32	0.117
Chinavia hilaris	Observation	1053	1098	-517			0.223
	Sampled field and observation	1032	1081	-505	4422.63	9731.62	0.231

Figure 3.6. Mean number of *Halyomorpha halys* in soybean fields of mid-Atlantic USA along different adjacent habitats. Means were estimated by GLMMs with (A) and without (B) sampled field as random effect and the vertical lines represent 95% confidence interval. Abundance values with the same letter above them are not statistically different ($\alpha = 0.05$; Tukey's HSD).
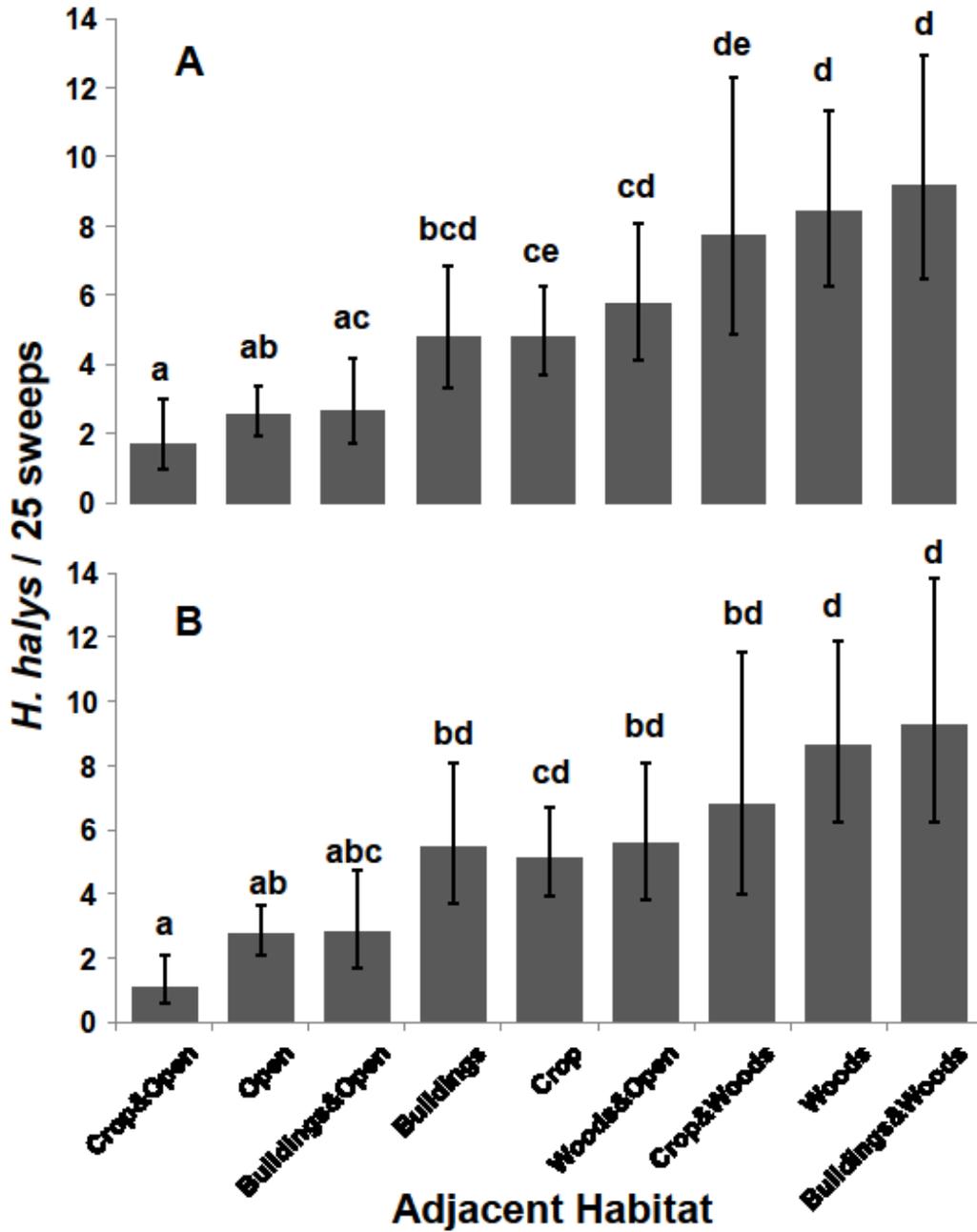
Figure 3.7. Mean number of *Chinavia hilaris* in soybean fields of mid-Atlantic USA along different adjacent habitats. Means were estimated by GLMMs with (A) and without (B) sampled field as random effect and the vertical lines represent 95% confidence interval. Abundance values with the same letter above them are not statistically different ($\alpha = 0.05$; Tukey's HSD).
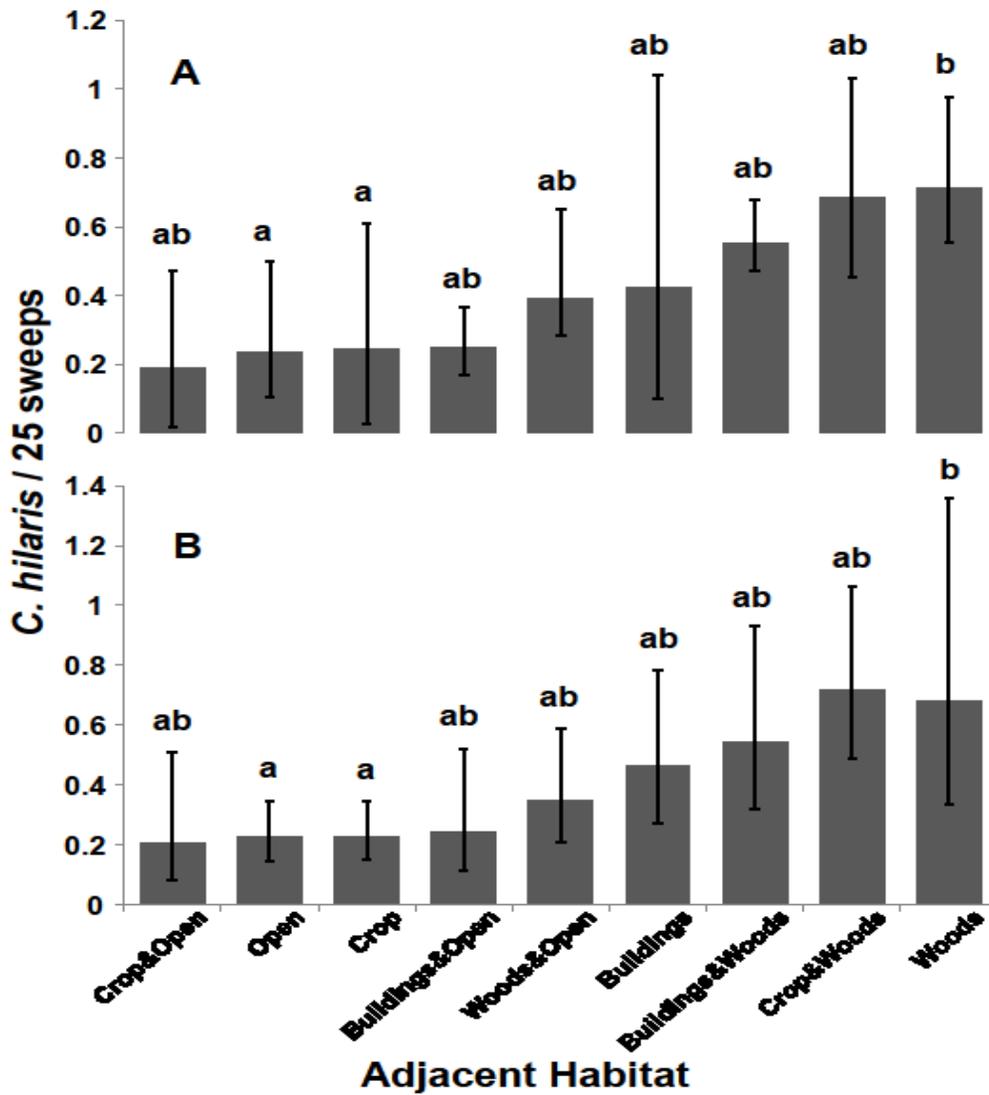
Discussion

This study quantified the multi-scale spatial pattern in regional stink bug abundance and identified the environmental and multi-scale landscape factors associated with them. *H. halys* abundance was primarily structured at broad spatial scales in association with temperature and developed area proportion, while the broad scale spatial pattern in *C. hilaris* abundance was related to altitude, forest and crop area; and broad scale structure in *E. servus* was associated with temperature and forest area. Based on the results, the null hypotheses of random distribution of stink bug abundance can be rejected. Very broad scale spatial pattern observed for all stink bug species studied, primarily in relation to climate (temperature) and resource availability, elucidates the predominant role of environmental processes, rather than biotic processes, in structuring regional stink bug populations (Dray *et al*., 2012; Jombart *et al.*, 2009; Legendre, 1993; Wiens, 1989).

Temperature is the most important abiotic factor that affects herbivorous insects such as stink bugs by directly influencing their development, survival, distributional range and abundance (Bale *et al.*, 2002). Average monthly minimum temperatures (Jun-Aug) during the reproductive season were the most important predictors of *H. halys* abundance and temperature also influenced *E. servus* abundance. *H. halys* abundance increased with average minimum temperature during June and August corresponding to the initial oviposition period (May) of stink bugs upon emergence from overwintering and the period of its first generation. My results are in direct alignment with findings from lab experiments that have clearly

demonstrated the critical role of temperature on development, survival and growth of *H. halys* in their native range as well as the introduced ranges in US and Europe. In Asia, at minimum temperature thresholds, the degree days required for development decreased from 630 at 11°C to 471 at 13.9°C (Lee *et al.*, 2013). In introduced populations of the US and Switzerland, no development to adults at 15°C and 35°C, < 2 % and < 5 % survival at 17°C and 33°C respectively, and steep decline in growth rates above 30°C were observed (Nielsen & Hamilton 2009; Haye *et al.* 2014 in press). Additionally, higher survival of post-overwintering adults in early spring in Japan have been reported in relation to lower temperature during March and April (Funayama, 2013). Thus the differences in temperature conditions between sampled fields could lead to varied rates of growth, survival and development, and thereby the observed differences in abundance.

Aspect of the landscape is another factor related to temperature effect that influenced *H. halys* abundance, with higher populations in eastern facing than western facing slopes. This is similar to previous reports on the influence of aspect on insect population dynamics (Jeffries, Marquis, & Forkner, 2006; Marquis & Le Corff, 1997), with fewer forest insect herbivores on sunny south- and west-facing slopes than on shaded north- and east-facing slopes. East facing slopes receive radiation from sun during colder morning hours, whereas west facing slopes receive radiation during warmer afternoon. So the daily maximum temperature is heavily influenced by the topographic exposure (Bolstad, Swift, Collins, & Régnière, 1998; Lookingbill & Urban, 2003). The aspect influence on *H. halys* abundance, with fewer stink bugs in western slopes, is associated with the negative influence of temperature during July.

The average temperature recorded in conterminous US during July 2012 was the warmest on record since national records began in 1895 (http://www.ncdc.noaa.gov/sotc/global/2012/7#temp). While the results identified minimum temperature during July (not maximum) to negatively influence *H. halys* abundance, it still is an indicator of the detrimental influence of the overall high mean temperatures observed in July during my study. In the study area, a gradient of higher to lower values of monthly minimum temperature in July was observed along east-west axis (Fig. 3.2), and the Western portion is also topographically diverse in comparison to eastern portion which has flat terrain. Corresponding to this gradient of temperature and directionality of slope, highest abundance of *H. halys* was observed in the Piedmont Plateau region.

Urbanized regions, namely high density developed areas (>80% constructed land) and open developed areas (typically large-lot single family houses), supported high abundance of *H. halys*. There are many features and mechanisms through which urban areas could support high arthropod abundances (reviews by Raupp, Shrewsbury, & Herms, 2010, 2012), including that of *H. halys.* High density developed areas provide resources in the form of houses and other buildings that are utilized as overwintering sites for *H. halys* (Leskey *et al.*, 2012; Lee *et al.*, 2013). In addition to the overwintering habitat resource, urban regions also contain many landscape trees and other ornamental plants that are hosts of *H. halys* (BMSB IPM Working Group & Northeastern IPM Center, 2013). While *H. halys* has a broad host range, the presence of alien plants such as *Paulownia tomentosa* (Thunb.) Steud. and

Ailanthus altisimma (Mill.) Swingle, which are originally from the same endemic range as *H. halys*, could also help support high population abundance.

Urbanized areas could also support higher abundance of *H. halys* in lower than optimal temperature regions by acting as 'heat islands' that provide refuge, as cities tend to be warmer than surrounding natural areas and affect population dynamics of various arthropod pests (Raupp *et al.*, 2010, 2012). Similar to herbivorous arthropods with short generational time such as aphids, adelgids, scales, psyllids, and mites all which are reported to occur at higher abundances in urbanized regions (Raupp *et al.*, 2012), for *H. halys* warmer cities could reduce mortality and increase developmental rates particularly for eggs and first instars that are vulnerable to temperatures closer to lower threshold.

Surprisingly, temperature variables used in my analysis did not significantly influence *C. hilaris* abundance patterns although the detrimental influence of temperature at the upper and lower thresholds on egg development has been reported previously (no development at 15°C and 36°C; Simmons & Yeargan, 1988). However, *C. hilaris* increased with altitude. A globally consistent negative association between altitude and temperature (termed lapse rate), particularly within the troposphere, is well established (Stone & Carlson, 1979). Altitude is the most commonly used surrogate for temperature in ecological research (Körner, 2007) and altitude influence on stink bug could be interpreted as that of temperature. Percent forest area at 5 km and 500 m scales was the most important predictor for both *C. hilaris* and *E. servus*, respectively. Both species have a wide host range, including

woody hosts in the wild (Jones & Sullivan, 1981; Kamminga *et al.*, 2012; Panizzi, 1997; Reay-Jones, 2010). Alternative host plants are important for stink bug development and can be essential for population buildup before dispersing to agricultural crops (Panizzi, 1997). Association of *E. servus* and *C. hilaris* with forest area is also consistent with reports of their overwintering habits in deciduous forests and open areas (Jones & Sullivan, 1981). *C. hilaris* increased with % crop area at 5 km, which comprised predominantly of soybean. This is consistent with earlier reports of *C. hilaris*, particularly the latter generation remaining in the cropping system (Miner, 1966), and its preference for soybean (Kamminga *et al.*, 2012).

The role of adjacent habitats in influencing stink bug abundance has been well documented (Toscano & Stern 1976, Pease & Zalom 2010, Reay-Jones 2010, Reeves *et al.* 2010, Tillman 2011) and is associated with the dispersal of stink bugs between preferred plant hosts (Stinner *et al.*, 1983). The highest abundance of both *H. halys* and *C. hilaris* in sampled fields adjacent to woods is related to their dispersal from wild hosts into soybean during the seed filling stages of soybean (Kogan & Turnipseed, 1987). Thus within field pattern of abundance of stink bugs was influenced primarily by dispersal, in combination with resource availability. However, the adjacent habitat types differed in the magnitude of their influence on abundance, especially if differences between fields were accounted for.

The improved performance of the GLMM model accounting for differences in abundance between sampled fields suggests that landscape and environmental factors occurring at spatial scales larger than the adjacent habitat are important drivers of

patterns in both *H. halys* and *C. hilaris* populations. As stink bug abundance was mainly structured at broad spatial scales by climate and resource availability, adjacent habitat influence associated with dispersal is a localized effect influencing within field abundance patterns. These results are consistent with earlier reports of community structure, species distribution and abundance, and biotic interactions dependent on climatic and habitat characteristics at spatial scales greater than the local habitat patch (Thies *et al.*, 2003; Tscharntke *et al.*, 2005). Finally, the spatial scale of association with landscape variables may be related to the relative body size of each stink bug species as a determinant of their dispersal capacity (Steffan-Dewenter *et al.*, 2002; Zaller, Moser, Drapela, Schmöger, & Frank, 2008). For example, the smallest species, *E. servus*, was associated with forest cover at 500 m, the intermediate sized *H. halys* with developed areas at 500 m - 1 km, and the larger bodied *C. hilaris* with landscapes at 5 km scale.

The scalogram for *H. halys* residuals showed that a significant very broad scale spatial pattern remained in the data after the influence of temperature, % developed areas, and aspect was factored out. Similarly for *E. servus*, a significant broad scale structure persisted after forest cover and temperature effects had been removed. A multitude of others factors could have influenced stink bug abundance among sampling fields including cropping patterns, rotations, planting dates, row spacing, variety maturation date, land preparation patterns, and cultivation systems, to name a few (Kogan & Turnipseed, 1987). Nevertheless, a significant portion of the variance in stink bug abundance across a large study region was explained by the variables identified (~ 40 % each for *H. halys* and *C. hilaris*). The detection of

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significant residual spatial structures at very broad - broad scales indicates that there are other broad scale drivers in the study system that could be environmental, historical or biotic, that influence abundance of these two species. The residual variance in abundance may be the product of species responses to environmental drivers that are unmeasured in the study, other biotic processes or random stochasticity (Dray *et al.*, 2012). Relative humidity which was not included as a predictor is important for insect egg emergence, dispersal (Buxton, 1932; Hirose, Panizzi, & Cattelan, 2006), and abundance (Raghu, Drew, & Clarke, 2004). Also, temperature during the previous winter and early spring (April and May; Funayama, 2013), could influence abundance. These variables could be included in future studies.

Overall, my results identify environmental factors (temperature, altitude, aspect, landscape composition) as the prominent drivers of broad spatial patterns in stink bug populations in the mid-Atlantic region, and the role of dispersal related processes to be limited to within-field scale. The study also highlights how native and invasive species differ in their responses to the environment, particularly the landscape. Invasive *H. halys* was primarily associated with developed areas, while both native stink bugs were associated with forest cover and the spatial scale of association with the landscape varied among the stink bug species. Such difference in environment association and its spatial scale has been observed between the invasive argentine ant *Linepithema humile* (Mayr) and other native ant species (Menke, Fisher, Jetz, & Holway, 2007). These results have important implications for managing the invasive *H. halys* in mid-Atlantic crops through both area-wide and field level

management strategies. Based on findings of higher *H. halys* associated with developed areas at very broad spatial scales, scouting and control efforts could be targeted towards crops in proximity (< 2 km) to urban areas.

High abundance of *H. halys* was associated with the presence of woods as adjacent habitats, and efforts to control or prevent invasion through insecticide application could focus only on field edges bordering woods.

Research Summary and implications for managing *H. halys* in field crops

Since its introduction into the United States near Allentown, PA during late 1990s, the brown marmorated stink bug *H. halys* has steadily expanded in population number and distributional range. While at present they are just a nuisance in many states, the recent explosion in *H. halys* populations has led to significant economic impacts as agricultural pests. *H. halys* caused unprecedented crop damage and economic losses particularly in the Northeast U. S. since 2009-2010 across a broad range of cropping systems (fruit, grain, vegetable, field and tree) in the Mid-Atlantic region (Nielsen *et al.* 2011). *H. halys* outbreak has also disrupted the existing IPM practices that are in place in many of these systems. The unequivocal response by farmers to *H. halys* outbreaks across many of these cropping systems in the Northeast (particularly mid-Atlantic) has been the regular and repeated use of broad spectrum insecticides (e.g. pyrethroids) through the growing season. Consequently, costs associated with pest control have risen along with concerns on food safety and negative impacts on beneficial insects.

The research/extension community has responded swiftly to the *H. halys* outbreak and over the past 3 years efforts to understand *H. halys* invasion and develop management strategies have increased with multi-institutional and multi-investigator collaborations and funding availability also has increased. However, these efforts primarily focus on specialty crops (e.g. $5.7 M USDA NIFA Specialty Crop Research Initiative Grant), and research and extension efforts in field crops, which are not within the purview of such grant initiatives, remains sparse. Particularly, despite field crops constituting very high proportion of overall crop area

studies concentrating on developing strategies for *H. halys* are few. My dissertation research filled this lacuna in information by quantifying the heterogeneity in *H. halys* population at multiple spatial scales and relating it to the multi-scale landscape and environmental influences.

Species Composition and Abundance

Species composition and abundance of the stink bugs was largely skewed with *H. halys* as the most abundant stink bug observed. Based on data from corn and soybean field edges (Chapter 1) and grid sampling of adjacent corn-soybean fields (Chapter 2), *H. halys* accounted for ~95% of all species recorded during 2012 and 2013. For the large scale surveys (Chapter 3) during both sampling years, *H. halys* was also numerically the most abundant species constituting ~90% of all stink bugs observed. Although there were differences among sites in the density and proportion of *H. halys*, results clearly identified *H. halys* as the most dominant stink bug in the region. The species composition is similar to that of existing reports (Nielsen *et al.*, 2011) of *H. halys* accounting for 70% of all stink bugs in mid-Atlantic region. Invasive species often are better competitors than native species in the invaded ecosystems, resulting in rapid community-level changes (Sanders, Gotelli, Heller, & Gordon, 2003). A similar pentatomid stink bug *Nezara viridula* (L.) with a cosmopolitan distribution (McPherson & McPherson, 2000) replaced the native *N. antennata* Scott, within a span of 20 years at many areas of sympatric distribution in Japan (Musolin, 2007). Since *H. halys* has rapidly become the most dominant and

numerically abundant stink bug species in agricultural systems of the mid-Atlantic

region, it could outcompete and eventually replace the native species in the landscape.

Patterns and factors influencing stink bug population dynamics

High density of *H. halys* was concentrated at the edge of fields, and density

beyond 15 m from the field edge was minimal. This was consistently observed at the

corn and soybean field edges (Chapter 1), particularly edges adjacent to woods, and

also at the corn-soybean interface of adjacent corn-soybean fields (Chapter 2). Results

clearly indicated the edge-centric behavior of *H. halys*, similar to many other stink

bug species, and that the density and distribution patterns were influenced by the

adjacent habitat. The consistent finding across all studies was that the highest

densities of stink bugs were observed in fields adjacent to woods, despite site level

differences in overall stink bug density. Trees represent the primary hosts for stink

bugs upon reemergence from overwintering. Hence forested areas with many host

plant species provide a continuous supply of food to support the first generation of *H.

halys* (BMSB IPM Working Group & Northeastern IPM Center, 2013), which can

result in high abundance of F1 adults that invade corn and then move later in the

season to soybean. Results of other studies have shown that the movement of adults

off trees generally occurs during mid to late July.

While fields adjacent to wooded areas consistently harbored high density of

stink bugs, density of stink bugs in fields adjacent to other crops varied between sites.

All studies reported here identified site level differences in the influence of adjacent

crops on density of observed stink bugs. In Chapter 1, densities of stink bugs at

soybean field edges adjacent to corn were not significantly different from those adjacent to woods in Keedysville, but were significantly lower at Beltsville. In the Chapter 3, potential dispersal of stink bugs from corn into soybean was observed only at Keedysville and not at Beltsville. Also, Keedysville had higher density of *H. halys* in soybean field edges adjacent to corn than Beltsville. Similarly, once differences between sampled fields were accounted for in the large scale study (Chapter 3), significant differences between crops and other adjacent habitats were identified. These results all point to the fact that the role of adjacent crops as source of stink bugs invading soybean is largely dependent on the regional population dynamics that operate beyond single field or field edge. Site level variation dictates initial build up of populations in crops or non-crop areas and subsequent invasion into adjacent crops. High site level variations in stink bug densities could be due the localized influence of adjacent habitats but factors operating at larger spatial scales as drivers of stink bug population dynamics.

The large scale study (Chapter 3) identified temperature as the most important factor structuring regional patterns in *H. halys* population dynamics. In terms of landscape factors, high abundance of *H. halys* was observed in soybean fields in proximity (1 km scale) to developed areas, and adjacent habitats also influence local abundance patterns. Landscape features are important predictors of stink bug abundance at smaller spatial scales, but are not the primary drivers of *H. halys* patterns at the regional scale.

Field and farm level stink bug management

While intensive management for stink bugs might not be required in low stink bug population areas like Beltsville and the Delmarva Peninsula, scouting efforts are still needed, because high stink bug densities could occur in field portions adjacent to tree of heaven (*Ailanthus altissima* Swingle), princess tree (*Paulownia tomentosa* Baill.), and black cherry (*Prunus serotina* Ehrhart). The field and farm level management strategies can be predominantly applicable to corn and soybean fields in the high stink bug density areas of the mid-Atlantic mainly in the Piedmont Plateau region. Placement and arrangement of fields in the farm could avoid incurring heavy damage and yield losses. Planting corn and soybean fields adjacent to wooded areas and buildings can be avoided if possible.

Planting corn and soybean as repeated strips for soil conservation purposes is currently practiced in the western portion of Maryland. In high stink bug density areas, such an arrangement of host crops could facilitate the subsequent dispersal of *H. halys* into soybean from many sides, upon initial colonization in corn. Thus, strip planting of corn and soybean as a cultural practice associated with farm topography may represents a poor strategy for placement and arrangement of crops in the farm in terms of stink bug management tactics and should be avoided if possible. In high stink bug population density areas, reducing the extent of boundary shared between corn and soybean would reduce damage and yield loss in soybean. Also, in high stink bug population areas, repeated scouting of field corn to assess stink bug density levels, particularly from blister stage onwards, could inform decisions on

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management interventions for preventing or mitigating *H. halys* colonization into soybean. The synchrony between corn maturity and adjacent soybean reaching seed filling stages could be broken by planting an early maturing variety of soybean that reaches the less attractive seed filling stages (R6) before stink bugs move off trees or out of corn; conversely, using late soybean varieties with delayed maturation might avoid the greatest movement of stink bugs in mid to late July.

Presently, insecticidal applications are currently the primary option for controlling *H. halys* in both corn and soybean. The current management strategy is to apply perimeter treatments where an increasing infestation of stink bugs is observed along the field edge. Cage studies of manually introduced infestation levels have shown that 1 to 2 stink bugs per foot row of soybean plants can result in losses of yield and quality (Owens *et al.*, 2013). Threshold results relate stink bug density to yield losses in wide row plantings which are easier to sample and delineate plots for research purposes. Since most soybean fields are drilled in narrow rows, further research is on-going to develop decision rules for triggering perimeter treatments based on yield loss relationships under actual field situations. Although the sampling and decision-making guidelines for managing *H. halys* in field crops have not yet been fully developed, soybean fields with high stink bug infestations are being treated with insecticides. For example, crop advisors and commercial pest control operators reported an estimated 75, 60, and 100% of the soybean acreage in 2010-11 was either perimeter or whole field treated in northern VA, Western MD (Washington and Frederick Counties), and central MD (Carroll, Montgomery, Howard Counties), respectively. Also, about 50% of the infested fields were whole-field treated,

particularly the smaller fields, and some fields were treated twice. Even among the fields that were perimeter treated, commercial applicators used high clearance sprayers to apply one or two 90 foot swaths around the edge along all sides of the field.

Findings of this study support the current recommendation that a reduced, site-specific treatment just along the perimeter will be sufficient for efficient *H. halys* control without jeopardizing yield and quality. Results from the edge and grid pattern studies (Chapters 1 and 2) clearly identify the edge-mediated distribution of stink bugs including *H. halys* and density beyond 50 feet is low for causing seed injury and losses. Hence, perimeter only treatment of insecticides will largely control *H. halys* and prevent reinvasion. Experimental trials in VA during 2011-2013 growing seasons have established that perimeter treatments (45 feet from edge) control 90-95 % of *H. halys* and out of 24 fields trials only one field had re-colonization (personal communication, A Herbert). So, applying 90 foot swaths from the field edge is probably not required in most infested field situations for control of *H. halys* in soybean. It may be possible to effectively treat less than the current spray swath width (90 in total; 45 feet on both sides) and avoid the yield loss due to sprayer wheel tracks. One swath of 45 feet treatment from the field edge will ensure adequate control of stink bugs. If field conditions prevent movement of the sprayer at the field edge, the first few rows (which typically yield less than rows further infield) could be trampled and 45 foot from the edge could be treated. Also *H. halys* abundances are the highest along perimeters adjacent to woods, corn and buildings and lowest in perimeters adjacent to open areas. Hence, insecticide applications may be restricted to

field edges along woods, corn and buildings and not applied in field edges bordering open areas. While the strategies mentioned thus far pertain to soybean, insecticidal application in field corn poses a problem. Effectively treating infested corn fields to achieve adequate spray coverage can be challenging because of the canopy height of mid- to late-season corn plants and the amount of foliage between the top of the plants and the ear.

Area wide management implications

All the field level management strategies discussed above could be applied across the mid-Atlantic region regional scale particularly in the Piedmont Plateau. In these high stink bug population areas, timely scouting in both corn and soybean, placement of fields in farms to avoid invasion, and perimeter only treatment could be a regional management strategy applicable to counties in MD, WV, and VA along the Piedmont Plateau. Soybean fields around developed areas, primarily residential, contained high abundances of *H. halys* (Chapter 3). Based on this, scouting and control efforts could be targeted towards crops in proximity (< 2 km) to urban areas. Also, creating better awareness to home owners could help in keeping *H. halys* out of residential areas during late fall to reduce overwintering survival of adults, and thus lower densities in the fields in subsequent crop season.

The Delmarva Peninsula with the highest acreage of corn and soybean in the MD and DE had very low stink bug population density over the past 4 years. Based on results from Chapter 3, this could be explained by high temperatures in July in the Delmarva Peninsula area. Also, unlike in the topographically diverse western portion

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of MD, the flat terrain in Delmarva Peninsula does not provide refuges with cooler temperatures in fields, particularly those situated on north facing slopes. Alternately, the scale of landscape association at the 500 m -1 km indicates the potential dispersal capability of *H. halys* and it might be incapable of a sustained flight across the Chesapeake Bay, with distances typically longer than 1 km. These limiting factors together with the less farmscapes fragmented with wooden area suggest that *H. halys* might not attain high abundances in the Delmarva Peninsula.

Given the influence of temperature during late spring on the abundance of stink bugs observed in the sampled soybean fields, the North Central region of the United States which has the highest acreage of corn and soybean, might also not attain very high population densities. For example the monthly minimum average temperature at Baltimore, Maryland during May – June (based on data from 1971 – 2010; (Climate Data Online (CDO) - NCDC, 2014) was 13.8°C – 19.4 °C ranging from just lower than minimum temperature threshold of *H. halys* (14.1 °C; Nielsen *et al.*, 2008) to 5 °C above it. In contrast, temperatures at Des Moines, Iowa ranged 11.1°C – 16.6 °C, mostly below the minimum temperature threshold of *H. halys*. Minimum temperatures during May – June across the North Central region typically fall in ranges not suitable for growth and development of eggs to 1st instar nymphal stages of *H. halys* that are particularly vulnerable to low temperatures close to minimum threshold. Moreover, agricultural landscapes in the region consist of more open areas of continuous fields with less fragmented areas of trees for early season recruitment of stink bugs and less developed areas with dwellings for overwintering

The dissertation has characterized stink bug abundance at multiple scales (field edge, entire field, across mid-Atlantic region) and elucidated the aggregated pattern in the density of stink bugs. The role of various landscape factors and environmental variables associated with stink bugs were also identified. Specifically, the study provides strong evidence that wooded regions influenced high densities of stink bugs in the corn and soybean edges, and demonstrated the differences between sites in terms of adjacent habitat influence. The trend of high density at immediate field edge corresponded to the pattern of damage to corn kernel and soybean seeds. Field corn planted close to soybean could be a source of *H. halys* dispersing into soybean at regions with high overall population density. While landscape features are important at the field level, their influence is limited in scale and temperature during the reproductive season was the primary driver of *H. halys* patterns across the mid-Atlantic region. These results have major implications for both field level and area wide management of this invasive insect pest.

References

Akin, S., All, J., Allen, C., Boerma, R., Buntin, D., Cardinal, A., … Way, M. (2011). *A Strategy for Prioritizing Research Goals and Outreach Plans to Reduce Soybean Production Losses Caused by Stink Bugs and Related Insect Pests.* Retrieved from http://soybase.org/StinkBugStratPlan//StkBgWhtPpStratPlan4May2011Final.pdf

Aukema, B. H., Carroll, A. L., Zhu, J., Raffa, K. F., Sickley, T. A., & Taylor, S. W. (2006). Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography*, *29*(3), 427–441. doi:10.1111/j.2006.0906-7590.04445.x

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., … Whittaker, J. B. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, *8*(1), 1–16. doi:10.1046/j.1365-2486.2002.00451.x

Bartoń, K. (2013). MuMIn: Multi-model inference (Version 1.9.13). Retrieved from http://cran.r-project.org/web/packages/MuMIn/index.html

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2013). lme4: Linear mixed-effects models using Eigen and S4 (Version 1.0-5). Retrieved from http://cran.r-project.org/web/packages/lme4/index.html

Beckler, A. A., French, B. W., & Chandler, L. D. (2004). Characterization of western corn rootworm (Coleoptera: Chrysomelidae) population dynamics in relation to landscape attributes. *Agricultural and Forest Entomology*, *6*(2), 129–139. doi:10.1111/j.1461-9563.2004.00213.x

Bianchi, F. J. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1595), 1715–1727. doi:10.1098/rspb.2006.3530

Bivand, R., Altman, M., Anselin, L., Assunção, R., Berke, O., Bernat, A., … Yu, D. (2014). spdep: Spatial dependence: weighting schemes, statistics and models (Version 0.5-71). Retrieved from http://cran.r-project.org/web/packages/spdep/index.html

Blom, P. E., Fleischer, S. J., & Smilowitz, Z. (2002). Spatial and Temporal Dynamics of Colorado Potato Beetle (Coleoptera: Chrysomelidae) in Fields with Perimeter and Spatially Targeted Insecticides. *Environmental Entomology*, *31*(1), 149–159. doi:10.1603/0046-225X-31.1.149

BMSB IPM Working Group & Northeastern IPM Center. (2013, October 7). Host Plants of the Brown Marmorated Stink Bug in the U.S. Retrieved January 2, 2014, from http://www.stopbmsb.org/where-is-bmsb/host-plants/

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. doi:10.1016/j.tree.2008.10.008

Bolstad, P. V., Swift, L., Collins, F., & Régnière, J. (1998). Measured and predicted air temperatures at basin to regional scales in the southern Appalachian mountains. *Agricultural and Forest Meteorology*, *91*(3–4), 161–176. doi:10.1016/S0168-1923(98)00076-8

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, *153*(1–2), 51–68. doi:10.1016/S0304-3800(01)00501-4

Borcard, D., Legendre, P., Avois-Jacquet, C., & Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, *85*(7), 1826–1832. doi:10.1890/03-3111

Boryan, C., Yang, Z., Mueller, R., & Craig, M. (2011). Monitoring US agriculture: the US Department of Agriculture, National Agricultural Statistics Service, Cropland Data Layer Program. *Geocarto International*, *26*(5), 341–358. doi:10.1080/10106049.2011.562309

Brewer, M. J., & Goodell, P. B. (2012). Approaches and Incentives to Implement Integrated Pest Management that Addresses Regional and Environmental Issues. *Annual Review of Entomology*, *57*(1), 41–59. doi:10.1146/annurev-ento-120709-144748

Brier, H. B., & Rogers, D. J. (1991). Susceptibility of Soybeans to Damage by *Nezara viridula* (l.) (hemiptera: Pentatomidae) and *Riptortus serripes* (f.) (Hemiptera: Alydidae) During Three Stages of Pod Development. *Australian Journal of Entomology*, *30*(2), 123–128. doi:10.1111/j.1440-6055.1991.tb00403.x

Bundy, C. S., & McPherson, R. M. (2000). Dynamics and Seasonal Abundance of Stink Bugs (Heteroptera: Pentatomidae) in a Cotton–Soybean Ecosystem. *Journal of Economic Entomology*, *93*(3), 697–706. doi:10.1603/0022-0493-93.3.697

Buxton, P. A. (1932). Terrestrial Insects and the Humidity of the Environment. *Biological Reviews*, *7*(4), 275–320. doi:10.1111/j.1469-185X.1962.tb01044.x

CABI. (2014, February 11). *Halyomorpha halys* [original text by T. C. Leskey, G. C. Hamilton, D. C. Biddinger, M. L. Buffington, C. Dicekhoff, G. P. Dively, H. Fraser, T. D. Gariepy, C. Hedstrom, D. A. Herbert, K. A. Hoelmer, C. R. R. Hooks, D. Inkley, G. Krawczyk, T. P. Kuhar, D.-H. Lee, A. L. Nielsen, D. Pfeiffer, C. Rodriguez-Saona, P. W. Shearer, E. Talamas, E. Tomasino, J. Tooker, P. D. Venugopal, J. Whalen, V. Walton, and N. Wiman]. In: Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc. Retrieved March 19, 2014, from http://www.cabi.org/isc/?compid=5&dsid=27377&loadmodule=datasheet&page=481&site=144

Callot, H., & Brua, C. (2013). *Halyomorpha halys* (Stål,1855), the marmorated stink bug, new species for the fauna of France (Heteroptera Pentatomidae). *L' Entomologiste*, *69*(2), 69–71.

Carrière, Y., Ellsworth, P. C., Dutilleul, P., Ellers-Kirk, C., Barkley, V., & Antilla, L. (2006). A GIS-based approach for areawide pest management: the scales of Lygus hesperus movements to cotton from alfalfa, weeds, and cotton. *Entomologia Experimentalis et Applicata*, *118*(3), 203–210. doi:10.1111/j.1570-7458.2006.00384.x

Carrière, Y., Goodell, P. B., Ellers-Kirk, C., Larocque, G., Dutilleul, P., Naranjo, S. E., & Ellsworth, P. C. (2012). Effects of Local and Landscape Factors on Population Dynamics of a Cotton Pest. *PLoS ONE*, *7*(6), e39862. doi:10.1371/journal.pone.0039862

Clarke, R. G., & Wilde, G. E. (1971). Association of the Green Stink Bugand the Yeast-Spot Disease Organism of Soybeans. III. Effect on Soybean Quality. *Journal of Economic Entomology*, (64), 222–223.

Climate Data Online (CDO) - NCDC. (2014). Climate Data Online (CDO) - National Climatic Data Center (NCDC). Retrieved January 21, 2014, from http://www.ncdc.noaa.gov/cdo-web/

Cocu, N., Harrington, R., Hullé, M., & Rounsevell, M. D. A. (2005). Spatial autocorrelation as a tool for identifying the geographical patterns of aphid annual abundance. *Agricultural and Forest Entomology*, *7*(1), 31–43. doi:10.1111/j.1461-9555.2005.00245.x

Corrêa-Ferreira, B. S., & De Azevedo, J. (2002). Soybean seed damage by different species of stink bugs. *Agricultural and Forest Entomology*, *4*(2), 145–150. doi:10.1046/j.1461-9563.2002.00136.x

Daehler, C. C. (2003). Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 183–211.

Daugherty, D. M., Neustadt, M. H., Gehrke, C. W., Cavanah, L. E., Williams, L. F., & Green, D. E. (1964). An Evaluation of Damage to Soybeans by Brown and Green Stink Bugs. *Journal of Economic Entomology*, *57*, 719–722.

De Valpine, P., Scranton, K., & Ohmart, C. P. (2010). Synchrony of population dynamics of two vineyard arthropods occurs at multiple spatial and temporal scales. *Ecological Applications*, *20*(7), 1926–1935. doi:10.1890/09-0468.1

Den Belder, E., Elderson, J., van den Brink, W. J., & Schelling, G. (2002). Effect of woodlots on thrips density in leek fields: a landscape analysis. *Agriculture, Ecosystems & Environment*, *91*(1–3), 139–145. doi:10.1016/S0167-8809(01)00264-X

Dornbos, D. L., & McDonald, M. B. (1986). Mass and Composition of Developing Soybean Seeds at Five Reproductive Growth Stages. *Crop Science*, *26*(3), 624. doi:10.2135/cropsci1986.0011183X002600030042x

Dray, S. (2011). spacemakeR: Spatial modelling. (Version R package   version 0.0-5/r98). Retrieved from http://R-Forge.R-project.org/projects/sedar/

Dray, S., Dufour, A.-B., Thioulouse, and J., Jombart, with contributions from T., Pavoine, S., Lobry, J. R., … Chessel, and A. S. B. on earlier work by D. (2013). ade4: Analysis of Ecological Data : Exploratory and Euclidean methods in Environmental sciences (Version 1.6-2). Retrieved from http://cran.r-project.org/web/packages/ade4/index.html

Dray, S., Pélissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., … Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, *82*(3), 257–275. doi:10.1890/11-1183.1

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological Processes That Affect Populations in Complex Landscapes. *Oikos*, *65*(1), 169–175. doi:10.2307/3544901

Dutilleul, P., & Legendre, P. (1993). Spatial Heterogeneity against Heteroscedasticity: An Ecological Paradigm versus a Statistical Concept. *Oikos*, *66*(1), 152–171. doi:10.2307/3545210

Eber, S. (2004). Bottom-up density regulation in the holly leaf-miner *Phytomyza ilicis*. *Journal of Animal Ecology*, *73*(5), 948–958. doi:10.1111/j.0021-8790.2004.00867.x

Ekbom, B. S., Erwin, M. E., & Robert, Y. (2000). *Interchanges of Insects Between Agricultural and Surrounding Landscapes*. Springer.

Elston, D. A., Moss, R., Boulinier, T., Arrowsmith, C., & Lambin, X. (2001). Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology*, *122*(05), 563–569. doi:10.1017/S0031182001007740

ESRI. (2011). ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute. (Version Release 10.).

Fehr, W. R., Caviness, C. E., Burmood, D. T., & Pennington, J. S. (1971). Stage of Development Descriptions for Soybeans, *Glycine Max* (L.) Merrill. *Crop Science*, *11*(6), 929. doi:10.2135/cropsci1971.0011183X001100060051x

Fernandez-Cornejo, J., Nehring, R., Sinha, E. N., Grube, A., & Vialou, A. (2009). *Assessing recent trends in pesticide use in US agriculture.* Presented at the Annual Meeting of the Agricultural and Applied Economics Association (AAEA),, Milwaukee, WI. Retrieved from http://purl.umn.edu/49271

Fogain, R., & Graff, S. (2011). First records of the invasive pest, Halyomorpha halys (Hemiptera: Pentatomidae), in Ontario and Quebec. *Journal of the Entomological Society of Ontario*, *142*, 45–48.

Fox, J., Weisberg, S., Friendly, M., Hong, J., Andersen, R., Firth, D., & Taylor, S. (2013). effects: Effect Displays for Linear, Generalized Linear, Multinomial-Logit, Proportional-Odds Logit Models and Mixed-Effects Models (Version 2.3-0). Retrieved from http://cran.r-project.org/web/packages/effects/index.html

Funayama, K. (2013). Effect of Climate Change on Annual Fluctuations in the Population Density of the Brown Marmorated Stink Bug (Hemiptera: Pentatomidae) in Northern Japan. *Journal of Economic Entomology*, *106*(5), 2141–2143. doi:10.1603/EC13240

Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C. D., O'Neal, M., Chacon, J. M., … Heimpel, G. E. (2009). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications*, *19*(1), 143–154. doi:10.1890/07-1265.1

Gariepy, T. D., Haye, T., Fraser, H., & Zhang, J. (2014). Occurrence, genetic diversity, and potential pathways of entry of *Halyomorpha halys* in newly invaded areas of Canada and Switzerland. *Journal of Pest Science*, *87*(1), 17–28. doi:10.1007/s10340-013-0529-3

Gesch, D., Herold, N., Greenlee, S., Nelson, C., Steuck, M., & Tyler, D. (2002). The National Elevation Dataset. *Photogrammetric Engineering and Remote Sensing*, *68*(1), 5–11.

Goodwin, B. J., & Fahrig, L. (2002). Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, Trirhabda borealis. *Canadian Journal of Zoology*, *80*(1), 24–35. doi:10.1139/z01-196

Griffith, D. A., & Peres-Neto, P. R. (2006). Spatial Modeling in Ecology: The Flexibility of Eigenfuntion Spatial Analyses. *Ecology*, *87*(10), 2603–2613. doi:10.1890/0012-9658(2006)87[2603:SMIETF]2.0.CO;2

Gutzwiller, K. J. (2013). Increasing the chance that landscape- and regional-level hypotheses will reflect important spatial patterns. *Landscape Ecology*, *28*(10), 1849–1858.

Han, W., Yang, Z., Di, L., & Mueller, R. (2012). CropScape: A Web service based application for exploring and disseminating US conterminous geospatial cropland data products for decision support. *Computers and Electronics in Agriculture*, *84*, 111–123. doi:10.1016/j.compag.2012.03.005

Han, W., Yang, Z., Di, L., Yagci, A. L., & Han, S. (2014). Making Cropland Data Layer Data Accessible and Actionable in GIS Education. *Journal of Geography*. doi:10.1080/00221341.2013.838286

Hanway, J. J. (1963). Growth Stages of Corn (*Zea mays*, L.). *Agronomy Journal*, *55*(5), 487. doi:10.2134/agronj1963.00021962005500050024x

Harrell, F. E. (2013). rms: Regression Modeling Strategies (Version 4.1-0). Retrieved from http://cran.r-project.org/web/packages/rms/index.html

Haye, T., Abdallah, S., Gariepy, T., & Wyniger, D. (2014). Phenology, life table analysis and temperature requirements of the invasive brown marmorated stink bug, *Halyomorpha halys*, in Europe - Springer. *Journal of Pest Science*. doi:10.1007/s10340-014-0560-z

Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, *97*(3), 393–403. doi:10.1111/j.1365-2745.2009.01480.x

Herbert, J. J., & Toews, M. D. (2011). Seasonal Abundance and Population Structure of Brown Stink Bug (Hemiptera: Pentatomidae) in Farmscapes Containing Corn, Cotton, Peanut, and Soybean. *Annals of the Entomological Society of America*, *104*(5), 909–918. doi:10.1603/AN11060

Herbert, J. J., & Toews, M. D. (2012). Seasonal Abundance and Population Structure of *Chinavia hilaris* and *Nezara viridula* (Hemiptera: Pentatomidae) in Georgia Farmscapes Containing Corn, Cotton, Peanut, and Soybean. *Annals of the Entomological Society of America*, *105*(4), 582–591. doi:10.1603/AN12008

Hirose, E., Panizzi, A. R., & Cattelan, A. J. (2006). Effect of relative humidity on emergence and on dispersal and regrouping of first instar *Nezara viridula* (L.) (Hemiptera: Pentatomidae). *Neotropical Entomology*, *35*(6), 757–761. doi:10.1590/S1519-566X2006000600006

Hoebeke, E. R., & Carter, M. E. (2003). *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): a polyphagous plant pest from Asia newly detected in North America. *Proceedings of the Entomological Society of Washington*, *105*(1), 225–237.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R. M., & Schuetzenmeister, A. (2013). multcomp: Simultaneous Inference in General Parametric Models (Version 1.3-1). Retrieved from http://cran.r-project.org/web/packages/multcomp/index.html

Ingle, J., Beitz, D., & Hageman, R. H. (1965). Changes in Composition during Development and Maturation of Maize Seeds. *Plant Physiology*, *40*(5), 835–839.

Jeffries, J. M., Marquis, R. J., & Forkner, R. E. (2006). Forest Age Influences Oak Insect Herbivore Community Structure, Richness, And Density. *Ecological Applications*, *16*(3), 901–912. doi:10.1890/1051-0761(2006)016[0901:FAIOIH]2.0.CO;2

Jombart, T., Dray, S., & Dufour, A.-B. (2009). Finding essential scales of spatial variation in ecological data: a multivariate approach. *Ecography*, *32*(1), 161–168. doi:10.1111/j.1600-0587.2008.05567.x

Jones, W., A., & Sullivan, M. J. (1981). Overwintering Habitats, Spring Emergence Patterns, and Winter Mortality of Some South Carolina Hemiptera. Retrieved from http://umd.library.ingentaconnect.com/content/esa/envent/1981/00000010/00000003/art00030

Jones, W. A., & Sullivan, M. J. (1982). Role of Host Plants in Population Dynamics of Stink Bug Pests of Soybean in South Carolina. *Environmental Entomology*, *11*(4), 867–875.

Jonsson, M., Wratten, S. D., Landis, D. A., Tompkins, J.-M. L., & Cullen, R. (2010). Habitat manipulation to mitigate the impacts of invasive arthropod pests. *Biological Invasions*, *12*(9), 2933–2945. doi:10.1007/s10530-010-9737-4

Judas, M., Dornieden, K., & Strothmann, U. (2002). Distribution patterns of carabid beetle species at the landscape-level. *Journal of Biogeography*, *29*(4), 491–508. doi:10.1046/j.1365-2699.2002.00697.x

Kamminga, K. L., Koppel, A. L., Herbert, D. A., & Kuhar, T. P. (2012). Biology and Management of the Green Stink Bug. *Journal of Integrated Pest Management*, *3*(3), C1–C8. doi:10.1603/IPM12006

Kareiva, P., Mullen, A., & Southwood, R. (1990). Population Dynamics in Spatially Complex Environments: Theory and Data [and Discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *330*(1257), 175–190. doi:10.1098/rstb.1990.0191

Kennedy, G. G., & Margolies, D. C. (1985). Mobile Arthropod Pests: Management in Diversified Agroecosystems. *Bulletin of the Entomological Society of America*, *31*(3), 21–35.

Kennedy, G. G., & Storer, N. P. (2000). Life Systems of Polyphagous Arthropod Pests in Temporally Unstable Cropping Systems. *Annual Review of Entomology*, *45*(1), 467–493. doi:10.1146/annurev.ento.45.1.467

Kim, S.-L., Berhow, M. A., Kim, J.-T., Chi, H.-Y., Lee, S.-J., & Chung, I.-M. (2006). Evaluation of Soyasaponin, Isoflavone, Protein, Lipid, and Free Sugar Accumulation in Developing Soybean Seeds. *Journal of Agricultural and Food Chemistry*, *54*(26), 10003–10010. doi:10.1021/jf062275p

Kogan, M. (1998). Integrated Pest Management: Historical Perspectives and Contemporary Developments. *Annual Review of Entomology*, *43*(1), 243–270. doi:10.1146/annurev.ento.43.1.243

Kogan, M., & Turnipseed, S. G. (1987). Ecology and Management of Soybean Arthropods. *Annual Review of Entomology*, *32*(1), 507–538. doi:10.1146/annurev.en.32.010187.002451

Körner, C. (2007). The use of "altitude" in ecological research. *Trends in Ecology & Evolution*, *22*(11), 569–574. doi:10.1016/j.tree.2007.09.006

Kruess, A., & Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science*, *264*(5165), 1581–1584.

Kuhn, M., Weston, contributions from S., Wing, J., & Thaler, J. F. and T. (2013). contrast: A collection of contrast methods (Version 0.19). Retrieved from http://cran.r-project.org/web/packages/contrast/index.html

Lamp, W. O., & Zhao, L. (1993). Prediction and manipulation of movement by polyphagous, highly mobile pests. *Journal of Agricultural Entomology*, *10*(4), 267 – 281.

Landis, D. A., Gardiner, M. M., Werf, W. van der, & Swinton, S. M. (2008). Increasing corn for biofuel production reduces biocontrol services in

agricultural landscapes. *Proceedings of the National Academy of Sciences*, *105*(51), 20552–20557. doi:10.1073/pnas.0804951106

Lee, D.-H., Short, B. D., Joseph, S. V., Bergh, J. C., & Leskey, T. C. (2013). Review of the Biology, Ecology, and Management of *Halyomorpha halys* (Hemiptera: Pentatomidae) in China, Japan, and the Republic of Korea. *Environmental Entomology*, *42*(4), 627–641. doi:10.1603/EN13006

Legendre, P. (1993). Spatial Autocorrelation: Trouble or New Paradigm? *Ecology*, *74*(6), 1659–1673. doi:10.2307/1939924

Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, *80*(2), 107–138. doi:10.1007/BF00048036

Legendre, P., & Legendre, L. (2012). *Numerical Ecology*. Elsevier.

Leskey, T. C., Hamilton, G. C., Nielsen, A. L., Polk, D. F., Rodriguez-Saona, C., Bergh, J. C., … Wright, S. E. (2012). Pest Status of the Brown Marmorated Stink Bug, *Halyomorpha halys* in the USA. *Outlooks on Pest Management*, *23*(5), 218–226. doi:10.1564/23oct07

Liebhold, A. M., Rossi, R. E., & Kemp, W. P. (1993). Geostatistics and Geographic Information Systems in Applied Insect Ecology. *Annual Review of Entomology*, *38*(1), 303–327. doi:10.1146/annurev.en.38.010193.001511

Lookingbill, T. R., & Urban, D. L. (2003). Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology*, *114*(3–4), 141–151. doi:10.1016/S0168-1923(02)00196-X

Magurran, A. E. (2013). *Measuring Biological Diversity*. John Wiley & Sons.

Margosian, M. L., Garrett, K. A., Hutchinson, J. M. S., & With, K. A. (2009). Connectivity of the American Agricultural Landscape: Assessing the National Risk of Crop Pest and Disease Spread. *BioScience*, *59*(2), 141–151. doi:10.1525/bio.2009.59.2.7

Marquis, R. J., & Le Corff, J. (1997). Estimating pretreatment variation in the oak leaf-chewing insect fauna of the Missouri Ozark Forest Ecosystem Project (MOFEP). In B. Brookshire & S. Shifley (Eds.), *Proceedings of the Missouri Ozark forest ecosystem project symposium.* (pp. 332–346). St. Paul, Minnesota, USA. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station.

Matern, A., Drees, C., Kleinwächter, M., & Assmann, T. (2007). Habitat modelling for the conservation of the rare ground beetle species *Carabus variolosus*

(Coleoptera, Carabidae) in the riparian zones of headwaters. *Biological Conservation*, *136*(4), 618–627. doi:10.1016/j.biocon.2007.01.006

McFadden, D. (1973). Conditional logit analysis of qualitative choice behavior. In P. Zarembka (Ed.), *Frontiers in Econometrics* (pp. 105−142). New York: Academic Press. Retrieved from http://elsa.berkeley.edu/reprints/mcfadden/zarembka.pdf

McIntire, E. J. B., & Fajardo, A. (2009). Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology*, *90*(1), 46–56. doi:10.1890/07-2096.1

McPherson, J. E., & McPherson, R. (2000). *Stink Bugs of Economic Importance in America North of Mexico*. CRC Press.

McPherson, R. M., Douce, G. K., & Hudson, R. D. (1993). Annual variation in stink bug (Heteroptera: Pentatomidae) seasonal abundance and species composition in Georgia soybean and its impact on yield and quality. *Journal of Entomological Science*, *28*(1), 61–72.

McPherson, R. M., Newsom, L. D., & Farthing, B. F. (1979). Evaluation of Four Stink Bug Species From Three Genera Affecting Soybean Yield and Quality in Louisiana. *Journal of Economic Entomology*, *72*(2), 188–194.

Medrano, E. G., Esquivel, J., Bell, A., Greene, J., Roberts, P., Bacheler, J., … Lopez, J. (2009). Potential for *Nezara viridula* (Hemiptera: Pentatomidae) to Transmit Bacterial and Fungal Pathogens into Cotton Bolls. *Current Microbiology*, *59*(4), 405–412. doi:10.1007/s00284-009-9452-5

Menke, S. B., Fisher, R. N., Jetz, W., & Holway, D. A. (2007). Biotic and abiotic controls of argentine ant invasion success at local and landscape scales. *Ecology*, *88*(12), 3164–3173. doi:10.1890/07-0122.1

Miner, F. D. (1966). Biology and control of stink bugs on soybeans. *Arkansas Agricultural Experiment Station Bulletin*, *708*, 1 − 40.

Mitchell, P. L. (2004). Heteroptera as vectors of plant pathogens. *Neotropical Entomology*, *33*(5), 519–545. doi:10.1590/S1519-566X2004000500001

Moravie, M.-A., Borer, M., & Bacher, S. (2006). Neighbourhood of host plants influences oviposition decisions of a stem-boring weevil. *Basic and Applied Ecology*, *7*(6), 545–554. doi:10.1016/j.baae.2005.12.005

Munoz, F. (2009). Distance-based eigenvector maps (DBEM) to analyse metapopulation structure with irregular sampling. *Ecological Modelling*, *220*(20), 2683–2689. doi:10.1016/j.ecolmodel.2009.07.008

Musolin, D. L. (2007). Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Global Change Biology*, *13*(8), 1565–1585. doi:10.1111/j.1365-2486.2007.01395.x

Musser, F., & Catchot, A. (2008). Mississippi Soybean Insect Losses. *Midsouth Entomologist*, *1*(1), 29–36.

Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, *78*(3), 691–692. doi:10.1093/biomet/78.3.691

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. doi:10.1111/j.2041-210x.2012.00261.x

NASS - USDA. (2014). *Crop Production*. Retrieved from http://usda01.library.cornell.edu/usda/current/CropProd/CropProd-01-10-2014.pdf

Negrón, J. F., & Riley, T. J. (1987). Southern Green Stink Bug,*Nezara viridula* (Heteroptera: Pentatomidae), Feeding in Corn. *Journal of Economic Entomology*, *80*(3), 666–669.

Nestel, D., Carvalho, J., & Nemny-Lavy, E. (2004). The Spatial Dimension in the Ecology of Insect Pests and Its Relevance to Pest Management. In P. D. A. R. Horowitz & P. D. I. Ishaaya (Eds.), *Insect Pest Management* (pp. 45–63). Springer Berlin Heidelberg.

Ni, X., Da, K., Buntin, G. D., Cottrell, T. E., Tillman, P. G., Olson, D. M., … Scully, B. T. (2010). Impact of Brown Stink Bug (Heteroptera: Pentatomidae) Feeding on Corn Grain Yield Components and Quality. *Journal of Economic Entomology*, *103*(6), 2072–2079. doi:10.1603/EC09301

Nielsen, A. L., & Hamilton, G. C. (2009a). Life History of the Invasive Species *Halyomorpha halys* (Hemiptera: Pentatomidae) in Northeastern United States. *Annals of the Entomological Society of America*, *102*(4), 608–616. doi:10.1603/008.102.0405

Nielsen, A. L., & Hamilton, G. C. (2009b). Seasonal Occurrence and Impact of *Halyomorpha halys* (Hemiptera: Pentatomidae) in Tree Fruit. *Journal of Economic Entomology*, *102*(3), 1133–1140. doi:10.1603/029.102.0335

Nielsen, A. L., Hamilton, G. C., & Matadha, D. (2008). Developmental Rate Estimation and Life Table Analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae). *Environmental Entomology*, *37*(2), 348–355. doi:10.1603/0046-225X(2008)37[348:DREALT]2.0.CO;2

Nielsen, A. L., Hamilton, G. C., & Shearer, P. W. (2011). Seasonal Phenology and Monitoring of the Non-Native *Halyomorpha halys* (Hemiptera: Pentatomidae) in Soybean. *Environmental Entomology*, *40*(2), 231–238. doi:10.1603/EN10187

Niva, C. C., & Takeda, M. (2003). Effects of Photoperiod, Temperature and Melatonin on Nymphal Development, Polyphenism and Reproduction in *Halyomorpha halys* (Heteroptera: Pentatomidae). *Zoological Science*, *20*(8), 963–970. doi:10.2108/zsj.20.963

O'Neill, K., M., Larson, D., P., & Kemp, W. P. (2002). Sweep sampling technique affects estimates of relative abundance and community composition of grasshoppers (Orthoptera: Acrididae). *Journal of Agricultural and Urban Entomology*, *19*, 125–131.

O'Rourke, M. E., Rienzo-Stack, K., & Power, A. G. (2010). A multi-scale, landscape approach to predicting insect populations in agroecosystems. *Ecological Applications*, *21*(5), 1782–1791. doi:10.1890/10-0241.1

Oliver, M. A. (2010). *Geostatistical Applications for Precision Agriculture*. Springer.

Ollier, S., Couteron, P., & Chessel, D. (2006). Orthonormal Transform to Decompose the Variance of a Life-History Trait across a Phylogenetic Tree. *Biometrics*, *62*(2), 471–477. doi:10.1111/j.1541-0420.2005.00497.x

Olson, D. M., Ruberson, J. R., Zeilinger, A. R., & Andow, D. A. (2011). Colonization preference of *Euschistus servus* and *Nezara viridula* in transgenic cotton varieties, peanut, and soybean. *Entomologia Experimentalis et Applicata*, *139*(2), 161–169. doi:10.1111/j.1570-7458.2011.01116.x

Outward, R., Sorenson, C. E., & Bradley, J. R. (2008). Effects of Vegetated Field Borders on Arthropods in Cotton Fields in Eastern North Carolina. *Journal of Insect Science*, *8*. doi:10.1673/031.008.0901

Owens, D. R., Herbert, J., D. A., Dively, G. P., Reisig, D. D., & Kuhar, T. P. (2013). Does Feeding by *Halyomorpha halys* (Hemiptera: Pentatomidae) Reduce Soybean Seed Quality and Yield? *Journal of Economic Entomology*, *106*(3), 1317–1323. doi:10.1603/EC12488

Panizzi, A. R. (1997). Wild Hosts Of Pentatomids:Ecological Significance and Role in Their Pest Status on Crops. *Annual Review of Entomology*, *42*(1), 99–122. doi:10.1146/annurev.ento.42.1.99

Panizzi, A. R., & Slansky, F. (1985). Review of Phytophagous Pentatomids (Hemiptera: Pentatomidae) Associated with Soybean in the Americas. *Florida Entomologist*, *68*(1), 184–214.

Park, Y.-L., Krell, R. K., & Carroll, M. (2007). Theory, Technology, and Practice of Site-Specific Insect Pest Management. *Journal of Asia-Pacific Entomology*, *10*(2), 89–101. doi:10.1016/S1226-8615(08)60337-4

Park, Y.-L., Perring, T. M., Farrar, C. A., & Gispert, C. (2006). Spatial and temporal distributions of two sympatric *Homalodisca spp*. (Hemiptera: Cicadellidae): Implications for areawide pest management. *Agriculture, Ecosystems & Environment*, *113*(1–4), 168–174. doi:10.1016/j.agee.2005.09.011

Parker, H. S. (2002). *Agricultural Bioterrorism: A Federal Strategy to Meet the Threat*. Institute for National Strategic Studies, National Defense University.

Pease, C. G., & Zalom, F. G. (2010). Influence of non-crop plants on stink bug (Hemiptera: Pentatomidae) and natural enemy abundance in tomatoes. *Journal of Applied Entomology*, *134*(8), 626–636. doi:10.1111/j.1439-0418.2009.01452.x

Pebesma, E., Bivand, R., Rowlingson, B., & Gomez-Rubio, V. (2013). sp: classes and methods for spatial data (Version 1.0-14). Retrieved from http://cran.r-project.org/web/packages/sp/index.html

Pebesma, E., & Graeler, B. (2013). gstat: spatial and spatio-temporal geostatistical modelling, prediction and simulation (Version 1.0-18). Retrieved from http://cran.r-project.org/web/packages/gstat/index.html

Peres-Neto, P. R., & Legendre, P. (2010). Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography*, *19*(2), 174–184. doi:10.1111/j.1466-8238.2009.00506.x

Pimentel, D., Acquay, H., Biltonen, M., Rice, P., Silva, M., Nelson, J., … D'Amore, M. (1992). Environmental and Economic Costs of Pesticide Use. *BioScience*, *42*(10), 750–760. doi:10.2307/1311994

Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2000). Environmental and Economic Costs of Nonindigenous Species in the United States. *BioScience*, *50*(1), 53–65. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3), 273–288. doi:10.1016/j.ecolecon.2004.10.002

Pinheiro, J., Bates, D. M., Debroy, S., Sarkar, D., EISPACK authors, & R-core. (2013). nlme: Linear and Nonlinear Mixed Effects Models (Version 3.1-113). Retrieved from http://cran.r-project.org/web/packages/nlme/index.html

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed Effects Models in S and S-Plus*. Springer.

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annual Review of Ecology and Systematics*, *28*(1), 289–316. doi:10.1146/annurev.ecolsys.28.1.289

R Development Core Team. (2011). *R: A Language and Environment for Statistical Computing. The R Foundation for Statistical Computing, Vienna, Austria*. Retrieved from http://www.R-project.org/

Raghu, S., Drew, R. A. I., & Clarke, A. R. (2004). Influence of Host Plant Structure and Microclimate on the Abundance and Behavior of a Tephritid Fly. *Journal of Insect Behavior*, *17*(2), 179–190. doi:10.1023/B:JOIR.0000028568.90719.2a

Raupp, M. J., Shrewsbury, P. M., & Herms, D. A. (2010). Ecology of Herbivorous Arthropods in Urban Landscapes. *Annual Review of Entomology*, *55*(1), 19–38. doi:10.1146/annurev-ento-112408-085351

Raupp, M. J., Shrewsbury, P. M., & Herms, D. A. (2012). Disasters by Design: Outbreaks along Urban Gradients. In P. Barbosa, D. K. Letourneau, & A. A. Agrawal (Eds.), *Insect Outbreaks Revisited* (pp. 311–340). John Wiley & Sons, Ltd. Retrieved from http://onlinelibrary.wiley.com/doi/10.1002/9781118295205.ch15/summary

Reay-Jones, F. P. F. (2010). Spatial and Temporal Patterns of Stink Bugs (Hemiptera: Pentatomidae) in Wheat. *Environmental Entomology*, *39*(3), 944–955. doi:10.1603/EN09274

Reeves, R. B., Greene, J. K., Reay-Jones, F. P. F., Toews, M. D., & Gerard, P. D. (2010). Effects of Adjacent Habitat on Populations of Stink Bugs (Heteroptera: Pentatomidae) in Cotton as Part of a Variable Agricultural Landscape in South Carolina. *Environmental Entomology*, *39*(5), 1420–1427. doi:10.1603/EN09194

Reisig, D. D. (2011). Insecticidal Management and Movement of the Brown Stink Bug, *Euschistus servus*, in Corn. *Journal of Insect Science*, *11*, Article 168. doi:10.1673/031.011.16801

Reisig, D. D., Roe, M., & Dhammi, A. (2013). Dispersal Pattern and Dispersion of Adult and Nymph Stink Bugs (Hemiptera: Pentatomidae) in Wheat and Corn. *Environmental Entomology*, *42*(6), 1184–1192. doi:10.1603/EN13166

Rhodes, E. M., Liburd, O. E., & Grunwald, S. (2011). Examining the spatial distribution of flower thrips in southern highbush blueberries by utilizing geostatistical methods. *Environmental Entomology*, *40*(4), 893–903. doi:10.1603/EN10312

Ritchie, S. W., Hanway, J. J., & Benson, G. O. (1993). *How a Corn Plant Grows* (No. 48). Ames, IA: Iowa State University Extension. Retrieved from http://www.biologie.uni-hamburg.de/b-online/library/maize/www.ag.iastate.edu/departments/agronomy/corngrows.html#r2

Rodeghiero, M., & Battisti, A. (2000). Inter-tree distribution of the spruce web-spinning sawfly, *Cephalcia abietis*, at endemic density. *Agricultural and Forest Entomology*, *2*(4), 291–296. doi:10.1046/j.1461-9563.2000.00078.x

Rosindell, J., Wong, Y., & Etienne, R. S. (2008). A coalescence approach to spatial neutral ecology. *Ecological Informatics*, *3*(3), 259–271. doi:10.1016/j.ecoinf.2008.05.001

Rubel, A., Rinne, R. W., & Canvin, D. T. (1972). Protein, Oil, and Fatty Acid in Developing Soybean Seeds. *Crop Science*, *12*(6), 739. doi:10.2135/cropsci1972.0011183X001200060006x

Samalens, J.-C., & Rossi, J.-P. (2011). Does landscape composition alter the spatiotemporal distribution of the pine processionary moth in a pine plantation forest? *Population Ecology*, *53*(2), 287–296. doi:10.1007/s10144-010-0227-4

Sanders, N. J., Gotelli, N. J., Heller, N. E., & Gordon, D. M. (2003). Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences*, *100*(5), 2474–2477. doi:10.1073/pnas.0437913100

Schroff, A. Z., Lindgren, B. S., & Gillingham, M. P. (2006). Random acts of weevil: A spatial analysis of Hylobius warreni attack on Pinus contorta var. latifolia in the sub-boreal spruce zone of Northern British Columbia. *Forest Ecology and Management*, *227*(1–2), 42–49. doi:10.1016/j.foreco.2006.02.007

Schumann, F. W., & Todd, J. W. (1982). Population Dynamics of the Southern Green Stink Bug (Heteroptera: Pentatomidae) In Relation to Soybean Phenology. *Journal of Economic Entomology*, *75*, 748–753.

Sharov, A. A., Leonard, D., Liebhold, A. M., & Clemens, N. S. (2002). Evaluation of Preventive Treatments in Low-Density Gypsy Moth Populations Using Pheromone Traps. *Journal of Economic Entomology*, *95*(6), 1205–1215. doi:10.1603/0022-0493-95.6.1205

Simmons, A., M., & Yeargan, K., V. (1988). Development and Survivorship of the Green Stink Bug, *Acrosternum hilare* (Hemiptera: Pentatomidae) on Soybean. *Environmental Entomology*, *17*(3), 527–532.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent Effects of Landscape Context on Three Pollinator Guilds. *Ecology*, *83*(5), 1421–1432. doi:10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Stinner, R. E., Barfield, C. S., Stimac, J. L., & Dohse, L. (1983). Dispersal and Movement of Insect Pests. *Annual Review of Entomology*, *28*(1), 319–335. doi:10.1146/annurev.en.28.010183.001535

Stone, P. H., & Carlson, J. H. (1979). Atmospheric Lapse Rate Regimes and Their Parameterization. *Journal of the Atmospheric Sciences*, *36*(3), 415–423. doi:10.1175/1520-0469(1979)036<0415:ALRRAT>2.0.CO;2

Taylor, C. M., Coffey, P. L., DeLay, B. D., & Dively, G. P. (2014). The Importance of Gut Symbionts in the Development of the Brown Marmorated Stink Bug, *Halyomorpha halys* (Stål). *PLoS ONE*, *9*(3), e90312. doi:10.1371/journal.pone.0090312

Taylor, L. R. (1984). Assessing and Interpreting the Spatial Distributions of Insect Populations. *Annual Review of Entomology*, *29*(1), 321–357. doi:10.1146/annurev.en.29.010184.001541

Taylor, L. R. (1986). Synoptic dynamics, migration and the Rothamsted insect survey: presidential address to the British ecological society, December 1984. *Journal of Animal Ecology*, *55*(1), 1–38.

Thies, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, *101*(1), 18–25. doi:10.1034/j.1600-0706.2003.12567.x

Thies, C., & Tscharntke, T. (1999). Landscape Structure and Biological Control in Agroecosystems. *Science*, *285*(5429), 893–895. doi:10.1126/science.285.5429.893

Tillman, P. G. (2010). Composition and Abundance of Stink Bugs (Heteroptera: Pentatomidae) in Corn. *Environmental Entomology*, *39*(6), 1765–1774. doi:10.1603/EN09281

Tillman, P. G. (2011). Influence of Corn on Stink Bugs (Heteroptera: Pentatomidae) in Subsequent Crops. *Environmental Entomology*, *40*(5), 1159–1176. doi:10.1603/EN10243

Tillman, P. G., Northfield, T. D., Mizell, R. F., & Riddle, T. C. (2009). Spatiotemporal Patterns and Dispersal of Stink Bugs (Heteroptera: Pentatomidae) in Peanut-Cotton Farmscapes. *Environmental Entomology*, *38*(4), 1038–1052. doi:10.1603/022.038.0411

Tischendorf, L., & Fahrig, L. (2000). How should we measure landscape connectivity? *Landscape Ecology*, *15*(7), 633–641. doi:10.1023/A:1008177324187

Todd, J. W. (1989). Ecology and behavior of Nezara viridula. *Annual Review of Entomology*, *34*(1), 273–292.

Todd, J. W., & Turnipseed, S. G. (1974). Effects of Southern Green Stink Bug Damage on Yield and Quality of Soybeans. *Journal of Economic Entomology*, (67), 421–426.

Toews, M. D., & Shurley, W. D. (2009). Crop Juxtaposition Affects Cotton Fiber Quality in Georgia Farmscapes. *Journal of Economic Entomology*, *102*(4), 1515–1522. doi:10.1603/029.102.0416

Toscano, N. C., & Stern, V. M. (1976). Dispersal of *Euschistus conspersus* from Alfalfa Grown for Seed to Adjacent Crops. *Journal of Economic Entomology*, *69*(1), 96–98.

Toyama, M., Ihara, F., & Yaginuma, K. (2006). Formation of aggregations in adults of the brown marmorated stink bug, *Halyomorpha halys* (Stal) (Heteroptera: Pentatomidae) : The role of antennae in short-range locations. *Applied Entomology and Zoology*, *41*(2), 309–315. doi:10.1303/aez.2006.309

Tremblay, A., & Ransijn, J. (2013). LMERConvenienceFunctions: A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions (Version 2.5). Retrieved from http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html

Tscharntke, T., & Brandl, R. (2004). Plant-Insect Interactions in Fragmented Landscapes. *Annual Review of Entomology*, *49*(1), 405–430. doi:10.1146/annurev.ento.49.061802.123339

Tscharntke, T., Rand, T. A., & Bianchi, F. (2005). The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Annales Zoologici Fennici*, *42*, 421–432.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., & Thies, C. (2002). Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research*, *17*(2), 229–239. doi:10.1046/j.1440-1703.2002.00482.x

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., … Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, *87*(3), 661–685. doi:10.1111/j.1469-185X.2011.00216.x

Turner, M. G. (1989). Landscape Ecology: The Effect of Pattern on Process. *Annual Review of Ecology and Systematics*, *20*(1), 171–197. doi:10.1146/annurev.es.20.110189.001131

Turnipseed, S. G., & Kogan, M. (1976). Soybean Entomology. *Annual Review of Entomology*, *21*(1), 247–282. doi:10.1146/annurev.en.21.010176.001335

Van Helden, M. (2010). Spatial and Temporal Dynamics of ArthropodsArthropods in Arable Fields. In E.-C. Oerke, R. Gerhards, G. Menz, & R. A. Sikora (Eds.), *Precision Crop Protection - the Challenge and Use of Heterogeneity* (pp. 51–64). Springer Netherlands. Retrieved from http://link.springer.com/chapter/10.1007/978-90-481-9277-9_4

Vargas, R. I., Peck, S. L., McQuate, G. T., Jackson, C. G., Stark, J. D., & Armstrong, J. W. (2001). Potential for Areawide Integrated Management of Mediterranean Fruit Fly (Diptera: Tephritidae) with a Braconid Parasitoid and a Novel Bait Spray. *Journal of Economic Entomology*, *94*(4), 817–825. doi:10.1603/0022-0493-94.4.817

Velasco, L. R. I., & Walter, G. H. (1992). Availability of different host plant species and changing abundance of the polyphagous bug *Nezara viridula* (Hemiptera: Pentatomidae). *Environmental Entomology*, *21*(4), 751–759.

Ver Hoef, J. M., & Boveng, P. L. (2007). Quasi-Poisson Vs. negative binomial regression: How should we model overdispersed count data? *Ecology*, *88*(11), 2766–2772. doi:10.1890/07-0043.1

Vinatier, F., Tixier, P., Duyck, P.-F., & Lescourret, F. (2011). Factors and mechanisms explaining spatial heterogeneity: a review of methods for insect populations. *Methods in Ecology and Evolution*, *2*(1), 11–22. doi:10.1111/j.2041-210X.2010.00059.x

Wagner, H. H. (2003). Spatial covariance in plant communities: integrating ordination, geostatistics, and variance testing. *Ecology*, *84*(4), 1045–1057. doi:10.1890/0012-9658(2003)084[1045:SCIPCI]2.0.CO;2

Wagner, H. H., & Fortin, M.-J. (2005). Spatial Analysis of landscapes: Concepts and Statistics. *Ecology*, *86*(8), 1975–1987. doi:10.1890/04-0914

Walters, H. J. (1980). Soybean leaf blight caused by *Cercospora kikuchii*. *Plant Disease*, *64*(10), 961–962. doi:10.1094/PD-64-961

Webster, R., & Oliver, M. A. (2007). *Geostatistics for Environmental Scientists*. John Wiley & Sons.

Wermelinger, B., Wyniger, D., & Forster, B. (2008). First records of an invasive bug in Europe: *Halyomorpha halys* Stål (Heteroptera: Pentatomidae), a new pest on woody ornamentals and fruit trees? *Mitteilungen Der Schweizerischen Entomologischen Gesellschaft*, *81*(1/2), 1–8.

Wiens, J., A. (1989). Spatial scaling in ecology. *Functional Ecology*, *3*(4), 385–397.

Winder, L., Perry, J. n., & Holland, J. m. (1999). The spatial and temporal distribution of the grain aphid Sitobion avenae in winter wheat. *Entomologia Experimentalis et Applicata*, *93*(3), 275–288. doi:10.1046/j.1570-7458.1999.00588.x

With, K. A. (2002). The Landscape Ecology of Invasive Spread. *Conservation Biology*, *16*(5), 1192–1203. doi:10.1046/j.1523-1739.2002.01064.x

With, K. A., Gardner, R. H., & Turner, M. G. (1997). Landscape Connectivity and Population Distributions in Heterogeneous Environments. *Oikos*, *78*(1), 151–169. doi:10.2307/3545811

Work, T. T., McCullough, D. G., Cavey, J. F., & Komsa, R. (2005). Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biological Invasions*, *7*(2), 323–332. doi:10.1007/s10530-004-1663-x

Zaller, J. G., Moser, D., Drapela, T., Schmöger, C., & Frank, T. (2008). Insect pests in winter oilseed rape affected by field and landscape characteristics. *Basic and Applied Ecology*, *9*(6), 682–690. doi:10.1016/j.baae.2007.10.004

Zhu, G., Bu, W., Gao, Y., & Liu, G. (2012). Potential Geographic Distribution of Brown Marmorated Stink Bug Invasion (*Halyomorpha halys*). *PLoS ONE*, *7*(2), e31246. doi:10.1371/journal.pone.0031246

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer.