Impact of the Invasive Brown Marmorated Stink Bug in North America and Europe: History, Biology, Ecology, and Management

Tracy C. Leskey[1,*] and Anne L. Nielsen[2]

[1]USDA-ARS, Appalachian Fruit Research Station, Kearneysville, West Virginia 25430, USA; email: tracy.leskey@ars.usda.gov

[2]Department of Entomology, Rutgers University, Bridgeton, New Jersey 08302, USA; email: nielsen@aesop.rutgers.edu

*Corresponding author

Keywords

stink bug, invasive, *Halyomorpha halys*, IPM, biological control, pheromone

Abstract

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål), is an invasive pentatomid introduced from Asia into the United States, Canada, multiple European countries, and Chile. In 2010, BMSB populations in the mid-Atlantic United States reached outbreak levels and subsequent feeding severely damaged tree fruit as well as other crops. Significant nuisance issues from adults overwintering inside homes were common. BMSB is a highly polyphagous species with a strong dispersal capacity and high reproductive output, potentially enabling its spread and success in invaded regions. A greater understanding of BMSB biology and ecology and its natural enemies, the identification of the male-produced aggregation pheromone, and the recognition that BMSB disperses into crops from adjacent wooded habitats have led to the development of behavior-based integrated pest management (IPM) tactics. Much is still unknown about BMSB, and continued long-term collaborative studies are necessary to refine crop-specific IPM programs and enhance biological control across invaded landscapes.

1. INTRODUCTION

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål), is an invasive pentatomid introduced into the United States from Asia in the mid-1990s. First detected in eastern Pennsylvania (56), BMSB has spread throughout much of the United States, as well as into Canada (38). In Europe, BMSB was first detected in 2007 in Zurich, Switzerland (153), and has now spread to additional countries (detailed below). BMSB has a broad host range that includes over 170 plants, many of agricultural importance, including various fruit, vegetables, row crops, and ornamentals. In addition to being polyphagous, BMSB is capable of long-distance flight (72, 156) and walking dispersal (73) and frequently moves among crops and wild host plants as they mature during the growing season. Since its introduction into the United States, BMSB feeding has resulted in severe problems in the mid-Atlantic region. Within this region in 2010, *H. halys* caused US$37 million in losses to the apple crop, and many other specialty and row crops, including peaches, nectarines, tomatoes, peppers, sweet corn, and soybeans, incurred severe damage. Homeowners and businesses throughout its range endure serious nuisance pest problems from BMSB in the fall due to its aggregatory behaviors. In Europe, some of the most severe agricultural (15) and nuisance pest problems (89) have been recorded in Italy.

Since the large BMSB outbreak in the United States in 2010 and increasing problems in Europe, studies of its biology, ecology, behavior, and management have increased dramatically. Over 100 journal articles and scientific reports on BMSB from China, Japan, and the Republic of Korea were summarized in a review article (75). As BMSB has continued to spread and establish in new regions, the collaborative BMSB IPM Working Group has documented key advances and research questions. Several large national research projects in the United States (**http://www.stopbmsb.org/**, **https://eorganic.info/brown-marmorated-stink-bug-organic/about**) and collaborative projects in Canada and Europe have generated considerable new information. Here, we examine advances in our understanding of the biology, ecology, and management of this invasive species as well as its spread and impact in the United States and Europe.

2. ORIGIN, SPREAD, AND IMPACT (INCLUDING AGRICULTURE AND NUISANCE)

Large aggregations of stink bugs were found in Allentown, Pennsylvania, in the mid-1990s but were not officially identified as *H. halys* until 2001 (56). Although the method of introduction is unknown, BMSB had been intercepted numerous times at multiple points of entry into the United States and Canada (45, 56). BMSB has an association with human-made structures during the overwintering period, a behavior that enabled its spread across New Jersey to be tracked through homeowner complaints reported to a Rutgers University website (46) that has since been incorporated into a national database (**https://www.eddmaps.org/distribution/uscounty.cfm?sub = 9328**). Beginning in 2008, reports of BMSB became more frequent and widespread owing to rapid geographic spread, greater awareness, or both. In the early stages of the invasion, BMSB spread throughout the mid-Atlantic United States, with small populations in southern and western states. Currently, large populations are present in many eastern states, and populations in the Midwest and on the West Coast are increasing, affecting more than 42 states (46). BMSB was first detected in Switzerland (153) in 2007 and in Canada in 2010 (38). Subsequent detections were reported in Germany (50, 51), France (26), Italy (89), Greece (97), Hungary (148), Romania (88), Spain (34), Georgia, Abkhazia, and Russia (43) and most recently in South America in Chile (37) (**Figure 1**).

A large global distribution of BMSB is projected from climate-matching models (161) and/or inference of the species Pleistocene history from molecular data (162). The introduction pathways and propagule size of an invading population may impact species ecology, including its fitness. Initial genetic analysis identified the putative source of the US population as of 2008 to be from
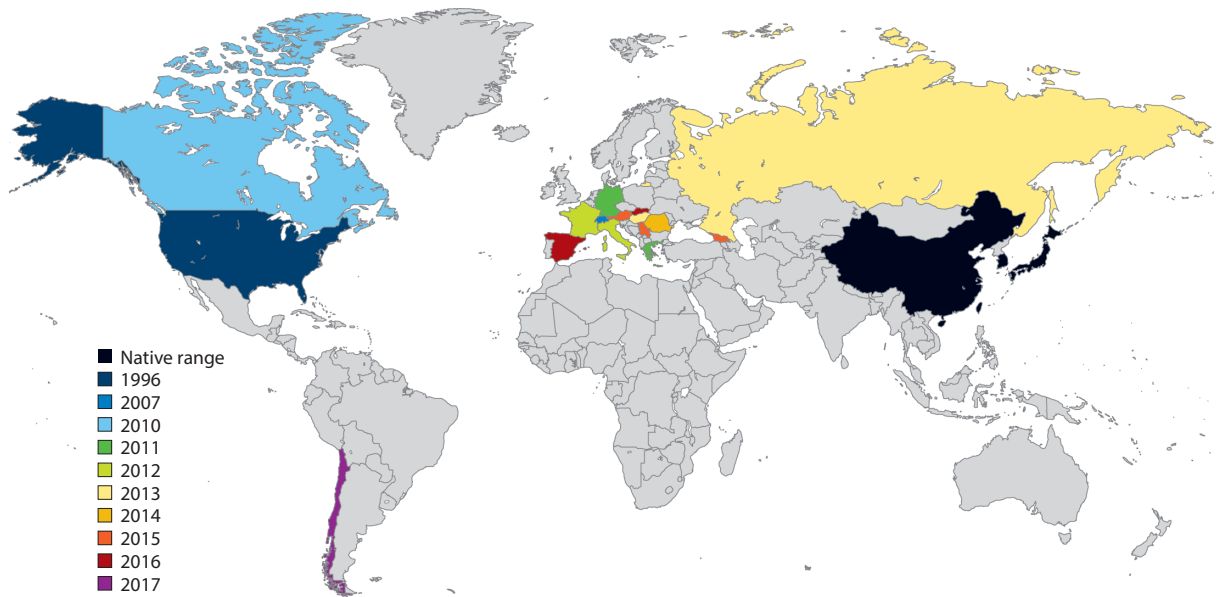
Figure 1

Global distribution of established *Halyomorpha halys* [brown marmorated stink bug (BMSB)] populations in the native range and in the invaded range by year of detection, not of interceptions. Year of detection is based on the earlier of published reports or European and Mediterranean Plant Protection Organization reporting (**https://gd.eppo.int/taxon/HALYHA/distribution**). Detailed information on the distribution of BMSB in the United States is available at **https://www.stopbmsb.org**.

Beijing, China, with an estimated propagule size of 2–18 females (157). This suggests a population bottleneck occurred in the United States (157) and that the population would be expected to experience Allee effects (70, 140), although given BMSB's current distribution and economic injury, this is not the case. Similar analyses performed on the Canadian and European populations also identified reduced haplotypic diversity with a Chinese origin, although high haplotypic diversity was found in Greece and central Europe, suggesting multiple invasion pathways (27, 44). An updated global population analysis using the mitochondrial cytochrome oxidase I (mtCOI) gene confirmed that as of 2016, the eastern US populations were all of the mtCOI H1 haplotype that originated from China and there have been no additional introductions, whereas western US populations have had multiple introductions also from China and represent higher levels of haplotypic diversity (143). European populations originated separately from China, but the population in the Emilia Romagna region of Italy likely originated from the eastern US population—a so-called bridgehead invasion effect (87)—and shares the H1 haplotype (143). On the basis of the 2016 global distribution of BMSB and the incorporation of potential bridgehead invasion effects on population genetics, a revised CLIMEX model was developed that estimated a global distribution of BMSB, in which many horticulturally important regions in the Southern Hemisphere are potential sites for BMSB invasion and establishment (68).

Wherever it has established, BMSB has had significant economic and ecological impacts, particularly in the northeastern United States, where the mtCOI H1 haplotype predominates. Of note, BMSB in Italy, where outbreaks have also resulted in severe agricultural and nuisance pest problems (15, 89), shares this genetic signature (27, 143). Similar to the invasive Argentine ant (*Linepithema humile*), which underwent a genetic bottleneck during range expansion, eastern US BMSB populations, which have a distinctive and reduced haplotype diversity, may have specific

characteristics that make them likely to succeed during invasion processes and enhance their pest status (141). In the United States, BMSB has established as a significant agricultural and nuisance pest (124). Early-season feeding on high-value agricultural crops by BMSB results in high yield loss due to injury during the critical mitotically active plant growth stage, and large late-season-feeding populations cause significant reductions in quality (112). Feeding may occur repeatedly through multiple physiological growth stages of plant development, and effects on quality and quantity may accumulate throughout the growing season. Finally, although indirect effects of BMSB presence and contamination in corn silage fed to lactating dairy cows did not contaminate milk (13), their presence in red wine grape clusters and subsequent release of defensive compounds affected finished wine quality (98).

3. BIOLOGY, ECOLOGY, AND BEHAVIOR

BMSB shares many biological characteristics that make for a successful invader, including a primarily *r*-selected life history and association with human-modified ecosystems. Once established, its high dispersal capacity, polyphagy, and ability to compete with endemic species assist its intercontinental spread (reviewed in 128).

3.1. Life History

BMSB adults overwinter in concealed, sheltered locations, including beneath the bark of dead upright trees, in rocky outcroppings, and in a variety of human-made structures (58, 71, 150). An association with human-made structures has been predicted to enhance overwintering survivorship (65) and perhaps reduce Allee effects (149). As a chill-intolerant species, BMSB acclimates seasonally to lower lethal temperatures. Winter supercooling points averaged $-16.11°C$, although bugs collected in cooler northern US habitats had lower supercooling points than bugs collected in warmer climates (28).

In the mid-Atlantic United States, BMSB begins to emerge from overwintering sites beginning in April, with numbers peaking in late spring (18). Little is known about their behavior at this time, as host plant resources are limited. Where adults go immediately after leaving overwintering sites is unknown, although in Asia, they are reported to utilize arboreal hosts (124). Oviposition begins once critical diapause-terminating cues are met. Females are synovigenic and become reproductively mature after a developmental delay (113, 158) and can continue ovipositing and mating throughout their life span (62, 113), which continues into late summer in Europe (48). Eggs are laid in masses of 28 (median number), predominantly on the underside of leaves. Laboratory studies in the United States found an average of 9.3 egg masses in a lifetime (113), whereas European field studies estimated fecundity to range from 2 to 15 egg masses per female, with higher oviposition rates within the overwintered adult generation (33, 48). During oviposition, females transfer symbionts to the egg chorion surface. This bacterial symbiont, *Pantoea carbekii* (14), is essential for the development and survival of later instars (138). After hatching, first instars remain aggregated on the egg mass to acquire the symbionts (138), and disruption of this behavior significantly reduces survivorship (113, 138).

According to Briere-1 models, the minimum and maximum temperatures for BMSB development in the United States and Europe are $14.14°C$ and $12.97°C$ and $35.76°C$ and $36.5°C$, respectively (48, 113). This equates to 538 DD_{14} and 588 DD_{13} to develop from the egg through the five instars to adult eclosion in the United States and Europe, respectively. A BMSB phenology model predicts the capacity for bivoltinism throughout the United States (108), but population size and structure will be determined by the combination of high-minimum-temperature requirements and critical diapause cues, which are estimated as photoperiods of 12.7–13.5 h in temperate

regions (108, 110, 113). Our current understanding of diapause requirements for BMSB predict that photoperiod, which is hypothesized to be a critical diapause cue, will delay development, especially in the spring of many southern locations prior to female reproductive maturity. Populations build beginning in late spring, with peak populations occurring in August and September in the United States (78, 108). First-generation adults that mature prior to the critical photoperiod during the summer may become reproductive, whereas those that eclose after do not and eventually enter diapause (108, 110). Females enter and leave overwintering sites reproductively immature and unmated (110). In Switzerland, field studies have suggested a univoltine population (48); although in Emilia Romagna, Italy, the population is predicted to be bivoltine (33). Peak movement of adults to potential overwintering sites occurs around or soon after the autumnal equinox in the mid-Atlantic United States (79), with similar patterns reported in Japan (75).

3.2. Host Range, Feeding Behavior, and Nutritional Ecology

BMSB is polyphagous, and its host range in North America includes more than 170 plants belonging to over a dozen families, many of which are arboreal. BMSB utilizes common plant families such as Rosaceae and Sapindaceae, which include wild hosts such as boxelder, big leaf maple, and English hawthorn and cultivated hosts such as apples, peaches, nectarines, pears, and grapes. An electivity analysis identified that BMSB is more commonly found on non-Asian host plants than on Asian host plants in the United States (90). Regardless of host plant, BMSB females oviposit more frequently on crops with long fruiting periods, including some fruiting vegetables (163). BMSB also feeds on small fruit and grapes (131, 154), sweet corn (29), and soybeans (114, 119). Despite the diversity of host plants, some commonalities emerge: (*a*) BMSB requires plants with fruiting structures to complete development (5); (*b*) host plant phenology is strongly related to host quality (5), as is host utilization (29, 111, 114, 163); and (*c*) BMSB prefers some host plants over others (20, 109, 163).

Although BMSB is polyphagous, development and survivorship on particular hosts can vary considerably. For example, nymphs reared on apple alone developed poorly (5, 39), whereas nymphs could complete development on peach alone (5). Multiple host-plant species may be necessary for normal BMSB development (5), a tactic routinely used for laboratory rearing (5, 40, 93). Throughout the growing season, BMSB is present on various wild (12, 111) and cultivated host plants (20, 112) and moves among species (7) as it seeks available fruiting structures based on plant phenology (91, 163). Surveys of woody ornamentals and wild host trees (12, 20) indicate that in North America, BMSB uses angiosperms more commonly than gymnosperms. This is in contrast to the native range, where gymnosperm hosts have been used for population forecasting (42, 75).

Similar to other pentatomids, BMSB secretes a thick, gel saliva from the salivary canal (120) that hardens into a sheath that likely protects and guides the stylets for feeding (24, 25). Proteins composing this saliva are of plant and BMSB origin, whereas the watery saliva injected by the feeding stylets into the plant tissue to break down cells and enable consumption of liquid contents (94) is of BMSB origin only and consists of several typical digestive enzymes, including amylases, proteases, and esterases (120). Maximal feeding by BMSB adults, as estimated by electronically monitored probing studies, likely occurs between 16°C and 17°C (although for shorter periods than longer feeding bouts at warmer temperatures), and ceasing below ∼3–6°C and above ∼26–29°C (155), although similar studies using nymphs have not been conducted.

BMSB feeding results in dry, corky tissue just below the surface of feeding sites on tree fruit (6, 84, 112), small fruit (17, 131, 154), nuts (52), and vegetables (69, 163). Feeding can discolor (6, 154, 163), depress, and distort the surface of fruiting structures (6, 69, 163) and sweet corn kernels (29). In the case of hazelnuts, feeding can result in blank nuts (a shell without a kernel)

(52). The type and severity of injury present on host plants are related to (*a*) the life stage that fed, with injury inflicted by later-instar nymphs and adults being more severe (6); (*b*) the density of individuals (29, 52, 119, 163); and (*c*) the phenology of the host plant (6, 29, 52, 60, 114, 119). BMSB nymphs fed significantly more often on uninjured blueberry fruit than on fruit previously fed upon possibly because of changes in fruit chemistry and quality (160), although similar studies using other host plants have not been conducted.

3.3. Dispersal Capacity and Behavior

The dispersal capacity and behavior of adults and nymphs have been quantified to better understand the potential for invasion into and among crops and spread across landscapes. Techniques include laboratory flight mills and ethological software, field-based mark-recapture studies using immunomarking, fluorescent dusts coupled with modified handheld lasers, and harmonic radar.

Baseline measurements derived from flight mills of tethered adults indicated that at least 85% of all individuals flew up to 5 km within 24 h, although some individuals, termed long-distance fliers, flew >5 km or more (up to 117 km has been recorded) (72, 156). When flight distances of overwintering and foraging BMSB were compared over a full year, the longest monthly flight distances averaged approximately 6 km (72) and coincided with the period of peak dispersal from overwintering sites (18). Under field conditions, BMSB initiates flight at temperatures not lower than 15°C, with wind speeds as low as 0.75 m/s, reducing the likelihood of flight by more than 90% (72). Laboratory measurements of nymph and adult walking behavior revealed that third instars walked significantly greater distances than adults did. In the field, fifth instars walked greater distances than third instars did and as far as 20 m within 4 h (73). Thus, both adults and nymphs can move among or invade crops from wild host habitats, and adults can disperse between farms and across the landscape. Movement of adults and nymphs may be triggered by fruit phenology and nutritional need (7, 91).

Adults disperse from overwintering sites over several months, with peak emergence occurring in late spring in the mid-Atlantic United States (18). However, where adults go and what they do immediately following their exit from overwintering sites are unknown, but new methods using modified handheld lasers in conjunction with adults marked with fluorescent dusts may provide answers, as adults can be spotted over considerable distances, even in high tree canopies (126). Additionally, harmonic radar has been used to track the specific location of individual BMSB adults in the field (74). When tagged individuals were released on various host and nonhost plants, BMSB adults remained six times longer on known hosts than on nonhosts (104). Although dispersal from host plants to overwintering sites in the fall is not well characterized, it is thought to be linked to shortening photoperiod (71, 117), and flight-mill studies have documented longer flights for individuals recovered from host plants late in the growing season (156).

3.4. Landscape Ecology

Research on the influence of landscape features on BMSB abundance in various habitats has been concentrated in the United States, which has the longest history of invasion by BMSB. During the initial spread, the invasion of BMSB throughout New Jersey was tracked using a network of UV black light traps. From 2004 to 2010, the population density increased at a rate of 75% per year (115). Although a populous state, New Jersey has significant agricultural land and BMSB associations with the agro-urban interface and wetlands were identified (149). In outbreak populations observed in 2010–2011, the strength of the relationship between agriculture and BMSB densities increased by 70%. Initially, BMSB was hypothesized to disperse by hitchhiking on vehicles, but

a relationship to highways was not observed nor was an association with buildings (149), which differs from expectations due to the overwintering habitat of BMSB in human-made structures.

There is a gap between the time period in which BMSB disperses from overwintering sites and when it appears in agricultural crops, specifically tree fruits. It is suspected that during this early spring period, BMSB utilizes host trees within the forest edge habitats for early-season feeding and perhaps oviposition. Then BMSB disperses from wild hosts into suitable crops following availability of fruiting structures (91). Higher densities of BMSB in agricultural crops also occur when arboreal hosts *Paulownia tomentosa*, *Ailanthus altissima*, and *Prunus serotina* are present along the crop edge (8, 111, 145). A strong edge effect occurs in multiple crops (17, 21, 61, 79, 84), and the association of BMSB with adjacent forested areas may drive this border effect. Specifically, the size of the forest edge has a positive relationship with stink bug injury in processing tomatoes (127), and higher densities of stink bugs, predominantly BMSB, were observed in row crops adjacent to wooded habitats (145). The strong edge effect and relationship with significant landscape features are likely due to the polyphagous nature of BMSB as it moves across the landscape tracking crop phenology (111, 146) to meet its nutritional requirements (5). Distinctly lower populations have been recorded in coastal plains regions of North Carolina and Virginia than in mountain and piedmont areas in the same states (12). The reason for this difference is unknown, but it may be due to environmental factors or ecological niche partitioning among Pentatomidae. Studies of landscapes where BMSB has been present for a period of time but has not increased in density are critical for understanding factors that may limit its establishment and impact.

4. MANAGEMENT

4.1. Short-Term Control

When the 2010 outbreak occurred in the mid-Atlantic United States, there were no recommendations for managing BMSB in any cropping system, with only data from a single laboratory study evaluating select available technical grade insecticides (116). Many tree fruit growers that applied materials labeled for native stink bug species reported extremely poor results (84). Several reasons for this failure are now known. First, knockdown and recovery of BMSB from a range of pyrethroids (77, 83, 116) and neonicotinoids (77, 83) have been observed. Second, many of the available materials effective against BMSB are broad-spectrum insecticides that have use restrictions for some vulnerable crops such as tree fruit (83) but not in others such as soybean. Third, most foliar insecticides have extremely short residual activity against BMSB. Last, overwintered adults are easier to kill than F_1 and F_2 adults (85), thereby reducing the ability of even the best materials to adequately manage BMSB in the late season when populations are greatest (78).

Some tree fruit growers use an alternate-row-middle insecticide application, in which half the orchard is sprayed, followed by the other half usually seven days later (57). This method allows fresh residue to be present over a greater timeframe and reduces sublethal exposure that results in knockdown and recovery of BMSB (77, 107). Soil-drench application of systemic neonicotinoid insecticides significantly reduced stink bug feeding injury in peppers and tomatoes (9), although such an approach is not available for tree fruit.

For home gardeners and organic growers, controlling BMSB has been particularly challenging because few effective chemical options exist. Ready-to-use products, including insecticidal soap, neem oil, essential oils, and capsaicin, were ineffective against adults (<30% mortality) but yielded higher mortality (>60%) against nymphs (19). Among organic insecticides, insecticidal soaps, spinosad, or pyrethrins alone or in combination with kaolin increased adult mortality in laboratory trials (76); although none were effective against adults in field trials on pepper (35).

In general, some synthetic insecticides are effective against BMSB in most affected conventional cropping systems as long as they are applied frequently when damaging BMSB populations are present (130), whereas organic systems are primarily limited to cultural or behavioral strategies. However, broad-spectrum materials and the frequency of their application in conventional systems have not been without consequences. In mid-Atlantic tree fruit orchards where applications increased as much as fourfold (84) in outbreak years, the use of broad-spectrum pyrethroids has led to secondary pest outbreaks of woolly apple aphid (*Eriosoma lanigerum*), San Jose scale (*Comstockaspis perniciosus*), and European red mite (*Panonychus ulmi*), which are normally controlled by natural enemies (84).

4.2. Integrated Pest Management Strategies

4.2.1. Semiochemicals and trap-based monitoring.
On the basis of reports from Asia that BMSB was cross-attracted to methyl (2E,4E,6Z)-decatrienoate (MDT) in its native range (75), the pheromone of the brown-winged green bug, *Plautia stali* Scott (133), Aldrich et al. (10) and Khrimian et al. (63) confirmed that BMSB was attracted to traps baited with this semiochemical in the United States as well. Why BMSB is cross-attracted to MDT is unknown, but this stimulus may serve as a kairomone when BMSB forages for host plants (10, 41). MDT has some serious shortcomings (78, 106); BMSB adults are not attracted to traps baited with MDT until later in the growing season in the invaded (United States) and native (South Korea) ranges. Nymphal BMSB is attracted to MDT season long (78, 106), although the reason for differences in life-stage-dependent attraction remains unknown.

The need for a season-long attractive semiochemical was considered critical for monitoring programs (84). Khrimian et al. (64) identified the BMSB male-produced aggregation pheromone following isolation of male-specific volatiles. Single males produce much more pheromone than groups do, with male pheromone production beginning approximately 13 days posteclosion (47). Subsequently, a stereoisomeric library of single isomers of natural sesquiterpenes containing a bisabolane skeleton with known configurations was assembled. On the basis of captures in traps baited with these isomers, the two-component pheromone was identified as a 3.5:1 ratio of (3S,6S,7R,10S)-10,11-epoxy-1-bisabolen-3-ol to (3R,6S,7R,10S)-10,11-epoxy-1-bisabolen-3-ol (64). Captures in traps baited with either component alone were lower than captures in traps baited with both components (64). The presence or absence of nonpheromonal isomers with pheromonal components yielded similar BMSB captures in traps, indicating that nonpheromonal isomers are not antagonistic and that some are moderately attractive to BMSB (81). BMSB adults and nymphs are attracted to the pheromone season long (78, 106). Moreover, when traps are baited with the pheromone and MDT in combination, a synergistic response from adults and nymphs occurs (151). This synergistic response has been documented in the native (South Korea) (106) and invaded (United States) (78) ranges, with the largest populations trapped in the late season. BMSB exhibits a dose-dependent response to increasing amounts of pheromone alone (81), MDT alone (86), and pheromone and MDT in combination (81). BMSB is not strongly attracted to traps baited with pheromone and MDT while in diapause (100). Select host plant volatiles evaluated as potential attractants in traps have not resulted in increased trap captures thus far (101), though it is still considered an important topic for future chemical ecology research efforts (152).

A number of trap designs for BMSB have been evaluated. Tree canopy–deployed traps include funnel traps (10), baffle traps (11), bucket-style water traps (86), and smaller pyramid traps (86, 103); ground-deployed traps include various colors (86) and sizes (103) of pyramid traps similar to those used to monitor native stink bug species (80). Ground-deployed black pyramid traps became the standard owing to overall captures (86, 103). Smaller pyramid traps deployed in the canopies of trees yielded lower captures than did ground-deployed black pyramid traps of various sizes (103).

Notably, nymph captures were significantly lower when pyramid traps were hung from limbs of trees likely because nymphs are positively gravitactic (4).

Because the BMSB pheromone and MDT are aggregatory stimuli, both adults and nymphs are attracted to and then arrested by these stimuli within approximately 2.5 m of the stimulus source regardless of dose or release rate (104). Deploying pyramid traps on the ground rather than in tree canopies reduces the number of structures on which foraging BMSB become arrested to a single upright pathway, compared with tree canopies containing many branching structures (103). Thus, ground-deployed trap designs are likely the most sensitive for all mobile life stages. Captures in ground-deployed pyramid traps baited with the pheromone and MDT in combination were used to guide management of BMSB in apple orchards, with insecticides applied only when predetermined cumulative adult captures in traps were reached. With this method, insecticide applications were reduced by more than 40%, and the crop was still adequately protected against BMSB injury (130). However, the optimal trap density and deployment pattern remain unknown but could be resolved by quantifying the maximum dispersive distance of BMSB and plume reach of the pheromonal stimuli (95).

Ground-deployed pyramid traps equipped with compact fluorescent white-, black-, and blue-wavelength-restricted light bulbs led to season-long captures of adults but not nymphs, with captures peaking about mid-summer and declining thereafter (82) with or without pheromone lures present (125). Because BMSB will not fly when temperatures are below 15°C (73), there are limitations to using light traps as a monitoring tool.

4.2.2. Exploiting behavioral ecology. Several studies have measured adult dispersal between and among hosts throughout the growing season. The highest densities of BMSB along crop edges occur in orchards (21), ornamentals (147), row crops (145), and vineyards (16). The highly polyphagous and mobile behavior of BMSB has been exploited by investigating the use of trap crops as a management tactic, with grain sorghum and sunflower identified as the most attractive among five plant species (109). Sunflower alone used as a trap crop for peppers did not reduce injury (132); the use of sorghum plus sunflower as trap crop species attracted BMSB, although injury to organic peppers was only minimally reduced (92). The use of harmonic radar and protein markers to quantify retention within the sunflower and sorghum trap crop showed that the trap crop itself was more attractive than the pepper cash crop but did not act as a population sink (22).

The behavior of BMSB along borders as it invades a crop has been exploited for management purposes. In soybean, high densities of BMSB within the crop perimeter can delay plant senescence and cause crop losses (79), but they can be combated with a single well-timed border spray application (53). On the basis of spatial injury distribution in cultivated orchard crops (61, 84), BMSB adults are thought to invade from wild hosts to the perimeter of cultivated crops. Through immunomarking, Blaauw et al. (21) confirmed that BMSB exhibits a strong edge effect in peach orchards and is strongly arrested on this highly suitable host plant (5). Within a one-week period, 79.7% of adults within a peach orchard were recovered along the orchard border (21). Restricting insecticide application for BMSB to the orchard border on a weekly basis during critical risk periods was combined with existing IPM tactics for a systems-level management approach in commercial peach farms. Stink bug injury at harvest was equal in the blocks that received border-only applications compared with grower standard management, while applying an average of 2.5-fold less insecticide (23).

Attract-and-kill requires that the target organism is attracted to and retained at a spatially limited location where it can be killed and removed from the population (36). Deploying the BMSB pheromone and MDT in combination with a host plant increased retention of BMSB. For example, baited and unbaited apple trees retained BMSB adults for nearly 24 h and only

approximately 3 h, respectively. In a season-long trial in which baited, border-row apple trees served as attract-and-kill sites, the number of BMSB adults killed and the amount of injury to fruit in baited attract-and-kill trees were significantly greater than those in adjacent unbaited trees, indicating border-based attract-and-kill sites could be used to protect orchard fruit (104). However, such an approach has not been evaluated for other vulnerable crops.

Mass trapping relies on olfactory stimuli to attract targeted organisms to a trapping device where they can be captured and killed. Citizen scientist volunteers deployed small, pyramid-style traps baited with MDT at the row ends of small garden plots and compared BMSB numbers and tomato fruit injury in plots with and without traps. In gardens with baited traps, 19 times more BMSB were present on row-end plants and fruit injury was significantly greater (129). Several hurdles surrounding mass trapping for BMSB management are apparent based on the results of this study (129). First, plots were likely too small because of trap spillover. Indeed, traps, particularly those baited with aggregation pheromones, often result in increased plant injury near the trap (123), as pests are attracted to and arrive near the baited trap but remain outside the trap itself (134). BMSB aggregates within 2.5 m of traps baited with pheromonal stimuli, with "trap spillover" estimated to be less than 10% (104). Second, at close range, BMSB may utilize substrate-borne vibrational signals that are involved in courtship (121), as has been found with other stink bug species (30). Using these signals in combination with baited traps could improve overall trap captures by bringing adults together at close range and reducing spillover into crops.

4.2.3. Degree-day models.

Developmental parameters for BMSB in the laboratory and in the field show a long-lived species with high reproductive output (48, 113) that results in overlapping generations, which make traditional degree-day (DD) models unreliable for timing damaging life stages (55, 108). An individual-based model predicted seasonality, including timing of different generations and life stages, at eight geographic locations within the United States. It predicts the potential for bivoltinism across much of the United States, but the apparency of each generation is dependent on accumulated heat units as is the proportion of each generation that enters overwintering (108).

Because BMSB overwinters in the adult stage, photoperiod is presumed to be the primary cue for diapause induction and termination (137) and termination is the point at which DD accumulations should begin. Data suggest that when a photoperiod of 13.5 h is used as a biofix, reproductively immature females disperse into peaches beginning at 100 DD_{14} (110). This model, in combination with border sprays, has been used to initiate management in New Jersey (23). However, the degree-day model needs to be further validated and future work will need to determine the relationship between crop injury and numbers in pheromone-baited traps and how DD models can be incorporated into management programs.

4.3. Biological Control

BMSB is assumed to have undergone enemy escape (release) following invasion into multiple habitats, and initial surveys support this assumption by detecting low, but variable, rates of natural enemy impacts ranging from <1.0% to 55.3% in the United States (31, 32, 59, 105, 118). In Europe, 31% and 62% of sentinel BMSB and native stink bug egg masses were preyed upon, respectively (49). Laboratory and field studies have documented generalist predators consuming BMSB. A survey of organic farms across multiple US states identified predation rates on BMSB egg masses to be between 4.1% and 5.0% for chewing predators and between 0.6% and 4.9% for sucking predators, with up to 12.8% of eggs missing after 48 h (118). Orthopterans have been identified as opportunistic predators feeding on sentinel eggs that would have otherwise been marked

as missing by researchers (105, 122). Ground beetles (Carabidae), earwigs (Forficulidae), jumping spiders (Salticidae), and crickets (Gryllidae) were reasonably efficient predators of BMSB eggs (105, 124). In ornamental crops, egg predation averaged 4.4% and was highest in summer (31). Most natural enemy surveys have focused on the egg stage, as it is easy to work with and sessile. However, eggs may not provide the visual cue some generalist predators utilize during searching behavior. Laboratory experiments showed that Tettigoniidae preferred the egg stage; Reduviidae and Nabidae consumed the first and second instars, respectively; and predation by Coccinellidae was minimal (105, 122). Surveys of spider predation associated with human-made structures revealed that BMSB introduced into webs of Theridiidae, Pholcidae, and Agelenidae had a greater than 50% chance of being ensnared and consumed (102). Vertebrate predators also appear to utilize BMSB adults as a food resource, and there are anecdotal reports of birds and mice consuming BMSB adults though the level of consumption has not been quantified. Guano samples from the big brown bat, *Eptesicus fuscus*, in New Jersey have also tested positive for BMSB DNA (142).

Hymenopteran egg parasitoids are the primary natural enemy of endemic stink bug species in the United States (67, 139), but parasitism of BMSB has been low. Based on an analysis of field studies conducted in North America and Europe, genera belonging to three families are most commonly recovered from BMSB eggs—Scelionidae, Eupelmidae, and Encyrtidae (3). In the United States, where most of the studies have been conducted, *Anastatus reduvii* (Howard), *A. mirabilis* (Walsh & Riley), *A. pearsalli* Ashmead, *Anastatus* spp. (Hymenoptera: Eupelmidae), *Trissolcus brochymenae* (Ashmead), *T. euschisti* (Ashmead), *T. hullensis* (Harrington), and *Telenomus podisi* (Ashmead) (Hymenoptera: Scelionidae) have emerged from wild and sentinel egg masses in the United States, but parasitism rates are highly variable among sampling protocols and habitats (31, 32, 54, 59, 118). *Te. podisi* is a common egg parasitoid of North American Pentatomidae (2, 67), including BMSB in vegetable crops (32, 118), and parasitism of naturally laid BMSB eggs reached 55% in ornamental plantings, with *Anastatus* spp. responsible for most of the parasitism (59). In Europe, frozen BMSB egg masses had a parasitism rate of 0.5–4.4% by *T. cultratus* Mayr (syn. *T. flavipes*) (Hymenoptera: Scelionidae) and *A. bifasciatus* Geoffroy (49).

Parasitism has been surveyed largely through the use of sentinel eggs; this approach underestimates the rates of parasitism and parasitoid species richness owing to egg mass age or handling methods that may eliminate host-finding kairomones (2, 31, 32, 59, 118). Additionally, the lack of coevolved relationships between specialist egg parasitoids and an invasive species may result in a disjunction between behavior and physiology. In fact, partially developed parasitoids were found inside 10% of sentinel BMSB eggs (32). Although the developing BMSB eggs were killed, parasitoids did not emerge, resulting in a potential evolutionary trap or population sink for native parasitoid species (1, 2).

4.4. Classical Biological Control

Because BMSB has not been adequately regulated by endemic natural enemies, a classical biological control program has been initiated in the United States (124). Classical biological control offers the opportunity to control BMSB at a landscape scale, as effective biological control agents identified from the endemic range are introduced into the invaded range (144). Hymenopteran egg parasitoids of the genus *Trissolcus* have been targeted; at least five species attack BMSB in Asia (75). *T. japonicus* Ashmead (Hymenoptera: Scelionidae) has produced parasitism rates as high as 70% in China (159). Although *T. japonicus* was described as a new species (159), *T. halyomorphae* and *T. japonicus* are conspecifics (135); thus, the usage of *T. halyomorphae* should be eliminated.

Since 2007, *T. japonicus* and other *Trissolcus* spp. have been held in quarantine facilities in the United States to evaluate their potential as classical biological control agents (124, 136). In 2014,

sentinel egg mass surveys in Beltsville, Maryland, revealed that adventive populations of *T. japonicus* were present in the wild in wooded habitats (54, 136). In 2015, *T. japonicus* was also recovered from egg mass surveys conducted in Vancouver, Washington, with specimens recovered from a sparsely wooded site. For both of these findings, molecular analysis revealed that populations were distinct from those held in quarantine and from each other (96). To date, adventive *T. japonicus* populations, presumed to be accidently introduced, have been detected in Maryland, Virginia, West Virginia, Delaware, New Jersey, New York, Pennsylvania, Oregon, Washington, and the District of Columbia. In the United States, endemic *Trissolcus* species as well as *T. japonicus* attacked BMSB eggs in wooded habitats, although *T. japonicus* was more successful (54). Indeed, endemic parasitoids could end up in an evolutionary trap as they unsuccessfully attempt to parasitize BMSB eggs, leading to increases in endemic Pentatomidae (2), although the European species *T. cultratus* actually acted as a facultative hyperparasitoid of *T. japonicus* at certain points in its development (66). Monitoring the effects of classical biological control agents on both target and nontarget taxa after field introduction is important (99). Ultimately, endemic natural enemies together with *T. japonicus* may better regulate BMSB populations and reduce pest problems in the United States.

5. CONCLUSIONS

BMSB shares many biological characteristics that make it a successful invader, including a primarily *r*-selected life history, high dispersal capacity and reproductive output, association with human-modified ecosystems, and ability to compete with native species (reviewed in 128). BMSB also has limited top-down pressure from natural enemies in its invaded range, although the accidental introduction of *T. japonicus* in the United States may change this scenario. While we have learned much about the biology, ecology, and management of BMSB, additional questions remain, including (*a*) abiotic and biotic factors limiting or enhancing populations in invaded areas; (*b*) optimal nutrient requirements for development and survivorship; (*c*) early-season biology and ecology of BMSB; and (*d*) differences in haplotype fitness and invasiveness. A key finding was the identification of the aggregation pheromone utilized by BMSB, and researchers have begun to incorporate this and behavioral aspects of BMSB ecology for management purposes to reduce ecosystem disruption. Additional unanswered questions remain, such as (*a*) what the seasonal and life stage differences in attraction to MDT mean biologically and physiologically and (*b*) what the optimal pheromone trap spacing and densities required for monitoring vulnerable crops are. Ultimately, continued long-term collaborative studies, as has been the case for BMSB for nearly a decade, will likely continue to result in enhanced understanding of BMSB biology and ecology and development and refinement of sustainable management strategies and enhanced biological control across the broader landscape.

SUMMARY POINTS

1. On the basis of life-history characteristics and dispersal behaviors, the brown marmorated stink bug (BMSB) is a successful global invader that can have significant economic impact on a range of agricultural crops and can cause serious nuisance pest problems.

2. BMSB is univoltine or bivoltine throughout its invaded range and likely utilizes multiple host plants for development, invading crop perimeters from adjacent wooded habitats.

3. The BMSB aggregation pheromone is being incorporated into monitoring and surveillance programs.

4. Although short-term mitigation strategies have reduced the threat to vulnerable crops, the development of border-based management tactics provides an IPM foundation to reduce ecosystem disruption.

5. Endemic natural enemies feed on multiple life stages of BMSB, yielding low mortality rates of less than 20% in most studies. The accidental introduction of the Asian parasitoid species *Trissolcus japonicus* may enhance parasitism within the United States.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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