Spatiotemporal distribution of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae), in a southeastern agroecosystem

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Abstract

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), is a generalist xylem feeder insect species and an agricultural pest. In agroecosystems, adults disperse between habitats, foraging on crop and non-crop hosts, oftentimes vectoring a harmful plant pathogen, *Xylella fastidiosa* Wells et al. (Xanthomonadales: Xanthomonadaceae). Understanding the spatiotemporal dynamics of this species in crops and the surrounding non-crop habitat may lead to improved pest management programs that reduce pathogen transmission. Here, we used 3 yr of trapping data across a southeastern US agroecosystem to characterize spatiotemporal distribution patterns of the glassy-winged sharpshooter in a variety of habitats. Adult glassy-winged sharpshooters were captured weekly on yellow sticky cylinder traps. Spatial Analysis by Distance Indices (SADIE) was used to identify significant aggregations and interpolated maps generated to characterize distribution patterns of adults within season and between yrs. Overall, the distribution of glassy-winged sharpshooters varied seasonally with individuals captured primarily in woodlands and fallow fields during early season mo. Later in the growing season and as population levels increased, sharpshooters were captured more commonly in crop habitat, including wheat and corn fields. By evaluating spatiotemporal distribution patterns, we identified likely sources of spring migration into cropping systems. Thus, pest management strategies for the glassy-winged sharpshooter should seek to limit early spring migration from non-crop habitat into crop fields.

Keywords: glassy-winged sharpshooter; leafhopper; insect vector; SADIE; red-blue plot; southeastern agroecosystem

Resumen

La chicharrita de alas cristalinas, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), es una especie de insecto generalista que se alimenta del xilema y es una plaga agrícola. En los agroecosistemas, los adultos se dispersan entre hábitats, alimentándose de hospederos cultivados y no cultivados, a menudo es un vector de un patógeno dañino para las plantas, *Xylella fastidiosa* Wells et al. (Xanthomonadales: Xanthomonadaceae). Al entender la dinámica espaciotemporal de esta especie en los cultivos y su hábitat no agrícola alrededor del campo puede conducir a mejores programas de manejo de plagas que reduzcan la transmisión de patógenos. Aquí, usamos 3 años de datos de captura en un agroecosistema del sureste de los EE. UU. para caracterizar los patrones de distribución espaciotemporal de la chicharrita de alas cristalinas en una variedad de hábitats. Se capturaron los adultos de la chicharrita de alas cristalinas en trampas cilíndricas adhesivas amarillas. Se utilizó el análisis espacial por índices de distancia (SADIE) para identificar agregaciones significativas y se generaron mapas interpolados para caracterizar los patrones de distribución de adultos dentro de la temporada y entre años. En general, la distribución de las chicharritas de alas cristalinas varió según la estación, y los individuos fueron capturados principalmente en bosques y campos en barbecho durante el mes de comienzo de la temporada. Más adelante en la temporada de crecimiento y a medida que aumentaban los niveles de población, las chicharritas se capturaban más comúnmente en el hábitat de cultivos, incluidos los campos de trigo y maíz. Mediante la evaluación de los patrones de distribución espaciotemporal, identificamos fuentes probables de migración primaveral hacia los sistemas de cultivo. Por lo tanto, las estrategias de manejo de plagas para la chicharrita de alas cristalinas deben tratar de limitar la migración temprana de la primavera desde el hábitat sin cultivos a los campos de cultivo.

Palabras Clave: la chicharrita de alas cristalinas; chicharrita; insecto vector; SADIE; parcela rojo-azul; agroecosistema del sureste

Agricultural systems typically consist of managed habitats surrounded by non-crop vegetation. The interface between managed crop fields and the surrounding non-crop habitat is often important for insects that use both types of habitat (Holland et al. 2005; Blackshaw &

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Vernon 2006). For integrated pest management programs, identifying sources of pests in unmanaged or non-crop habitat that later migrate into cropping systems is essential to reduce the overall pest numbers in crop fields (Park et al. 2006). For many insect pests, dispersal between non-crop and crop habitats is often driven by availability of plants that provide food resources (Cooper et al. 2019). Therefore, management of pests requires not only knowledge of plant diversity across habitat types that serve as population sources, but also the timing of distribution and dispersal changes, such as adult overwintering behavior, which may allow for more targeted control measures.

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), is a mobile, generalist, and xylem feeder insect native to the southeastern US and northern Mexico (Turner & Pollard 1959), with greater than 100 known host plant species (Hoddle et al. 2003). This insect vectors a xylem-clogging bacteria, *Xylella fastidiosa* Wells et al. (Xanthomonadales: Xanthomonadaceae), that causes diseases such as Pierce's disease in grapes (Alderz & Hopkins 1979; Wells et al. 1987), citrus variegated chlorosis (Lopes et al. 2003), phony peach disease (Turner & Pollard 1959), and leaf scorch in almond, plum, elm, and oak (Purcell & Saunders 1999). In the southeastern US, *H. vitripennis* spend colder mo in diapause as overwintering adults in forested areas using hardwood and herbaceous hosts (Mizell & French 1987; Lauzière et al. 2008). Adults tend to experience higher mortality during overwintering mo (Son et al. 2010). Glassy-winged sharpshooters travel large distances, frequently between habitat patches (Blackmer et al. 2004, 2006; Tipping et al. 2004; Park et al. 2006; Northfield et al. 2009). Experiments in host patches have shown that glassy-winged sharpshooters adjust dispersal behavior in response to patch quality (Park et al. 2006; Northfield et al. 2009). However, little is known about the seasonal distribution patterns of glassy-winged sharpshooters in both crop and non-crop habitats in the southeastern US. Characterizing the spatiotemporal distribution patterns of glassy-winged sharpshooters in this region will enable growers to predict seasonal changes in insect distribution and optimize control measures designed to reduce crop damage due to pathogen spread.

The purpose of this study was to characterize the spatiotemporal distribution of the glassy-winged sharpshooter, *H. vitripennis*, in crop fields and the surrounding non-crop habitat at a southeastern agricultural experimental station. For 3 yr, glassy-winged sharpshooters were captured on yellow-sticky cylinder traps placed in a grid that spanned a diversified agricultural landscape. We used Spatial Analysis by Distance Indices (SADIE) to identify the location of significant aggregations and generated interpolated maps to visualize distribution patterns.

Materials and Methods

FIELD EXPERIMENT

To detect glassy-winged sharpshooter movement and to correlate trap capture with different types of vegetation, 52 traps were placed in a grid, separated by approximately 229 m, at the North Florida Research and Education Center in Gadsden County, Florida, USA (30.546000°N, 84.594000°W). Each trap consisted of a yellow cylindrical sticky trap that was 8 cm in radius and 30 cm long. This trap design captures *H. vitripennis* better than the typical 2-sided yellow sticky card (Seabright Ltd., Emeryville, California, USA), likely due to the 360° attraction surface (R. F. Mizell, unpublished data). Traps were placed on 1 cm steel rods approximately 1 m above the ground. Trap capture was recorded from 25 Jan to 6 Sep 2001, from 28 Feb to 10 Oct 2002, and from 13 Mar to 7 Aug 2003. Of the 52 traps, 20 were placed in managed crop habitat, which included corn (n = 5), cotton (n = 2), crape myrtle (n = 2), peach (n = 1), vegetable (n = 5), and wheat (n = 5). An additional 32 traps were placed in unmanaged non-crop habitats, which included fallow fields (n = 12), grass (n = 2), wetland (n = 1), and woodlands (n = 17). At each weekly sampling date, the number of adult glassy-winged sharpshooters captured per trap were counted in the field.

DATA ANALYSIS

To analyze the relative effects of crop and non-crop habitat on the mean number of glassy-winged sharpshooters captured on sticky traps, we used R Program Software (R Core Team 2021) to fit general linear mixed effect models (package: lme4; function: lmer; Bates et al. 2015). First, we calculated the mean number of sharpshooters captured in crop and non-crop habitat during each wk of collection over the 3-yr sampling period. Habitat (2 levels; crop or non-crop) was included as our fixed effect and date nested within yr included as a random effect. In the model, we included a weight based on the reciprocal value of the number of crop (n = 20 traps) and non-crop (n = 32 traps) habitats sampled. Model adequacy was assessed with residual plots, and the mean number of sharpshooters captured per wk was log transformed to improve residual fit. We plotted the average number of sharpshooters collected on sticky traps each wk of the study and plotted averages over time. In addition, we plotted the proportion of leafhoppers captured in traps that were along the forest edge compared to all other habitats with R program software.

To analyze weekly spatial distribution patterns of glassy-winged sharpshooters over the 3-yr collection period we used Spatial Analysis by Distance Indices (SADIE; Perry et al. 1999). For each wk, we used R program software (package: epiphy; function: sadie; Gigot 2018) to calculate an aggregation index (I_a), the probability (P_a) that groups of glassy-winged sharpshooters aggregated greater than would be expected by chance, and extracted cluster indices for each collection site. If P_a was less than 0.05, then I_a was considered a significant aggregation (Perry et al. 1999; Winder et al. 2019). For cluster indices by collection site, weekly values greater than 1.5 suggested significant aggregations at that location, and weekly values less than −1.5 suggested gaps in their distribution (Perry et al. 1999; Winder et al. 2019). To visualize significant clusters, we interpolated red-blue maps in ArcGIS version 10.5 (ESRI, Redlands, California, USA; IDW; power = 2, variable = 20 points), with significant aggregations displayed in red (cluster index greater than 1.5) and gaps in blue (cluster index less than −1.5). Based on count data, we generated interpolated maps that showed the distribution of glassy-winged sharpshooters at each collection site and by yr. For each yr of collection, we displayed interpolated count data for 2 wk during the early season months (before Jun), 2 wk during peak sharpshooter population growth (Jun–Aug), and 1 late-season mo (Sep).

Results

From 2001 to 2003, a total of 17,280 adult glassy-winged sharpshooters were collected on yellow sticky traps. Across yr, the average number of sharpshooters captured remained low prior to Apr (Figs. 1 & 2). Beginning in May each yr, the average number of individuals captured increased and reached the highest levels between Jun and Jul (Fig. 1), during which time a high proportion of adults were captured in traps located along the forest edge (Fig. 2). Interpolated density maps showed that the highest rate of capture occurred exclusively in woodlands and fallow fields during spring mo (Fig. 3). During this mid-season peak, glassy-winged sharpshooters were distributed across the landscape, in both non-crop and crop habitats (Fig. 3). Compared with peak numbers in Jun and Jul, fewer individuals were captured in Aug

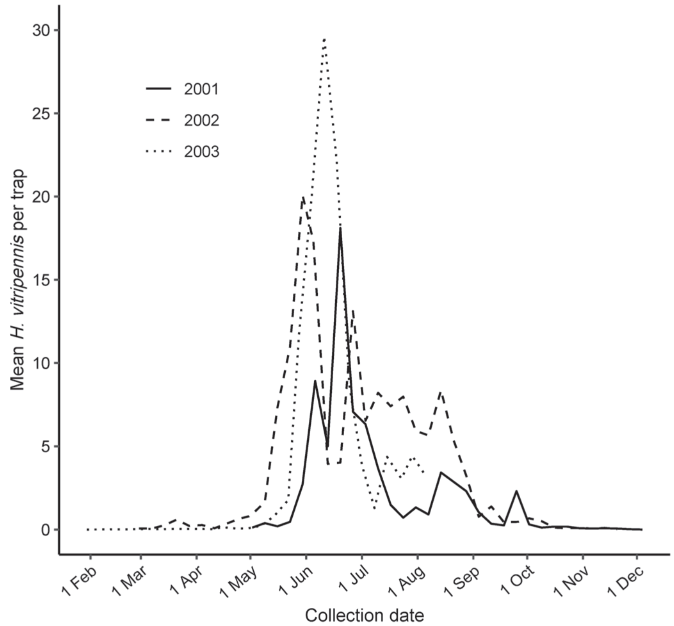

Fig. 1. Temporal distribution of glassy-winged sharpshooters captured on yellow sticky card traps in Gadsden County, Florida, USA, during 2001 to 2003.

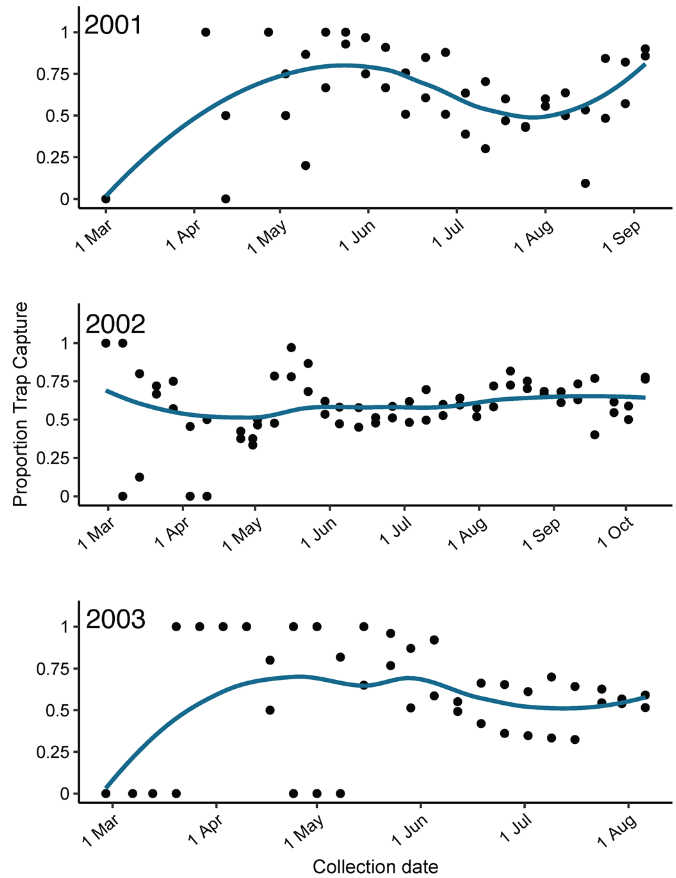

Fig. 2. The proportion of glassy-winged sharpshooters captured on yellow sticky card traps along forest edge in Gadsden County, Florida, USA, during 2001 to 2003. The blue line represents a Loess fit.

and Sep, but most were found primarily in non-crop habitat (Fig. 3). Overall, few individuals were captured during the mo of Nov and Dec (Fig. 1). The average number of glassy-winged sharpshooters captured in unmanaged, non-crop habitat differed significantly from crop habitat (F = 7.4; df = 1, 121; P = 0.007). Over all 3 yr of the study, 3.89 ± 0.22 individuals were captured in unmanaged habitats per trap, and 2.77 ± 0.19 were captured in crop habitats per trap on each collection date.

In 2001, significant clusters were detected during 3 wk of the study (Table 1). The first aggregation occurred during late Jul in corn, vegetable, fallow fields, and woodlands. At the beginning of Aug 2001, individuals aggregated primarily in woodlands but also were detected in corn, vegetable, and wheat. Adults aggregated again during mid-Sep at 3 trap sites located in woodlands (Fig. 3). During 2002, adults significantly clustered during 2 wk of the yr. The first aggregation occurred during mid-Mar in woodlands and wheat fields. The second significant aggregation occurred during mid-Jun in woodlands, fallow fields, and at 1 wheat field trap and 1 vegetable field trap. There were no significant aggregations detected during 2003.

Discussion

Both non-crop (Blackshaw & Vernon 2006) and crop habitats (Holland et al. 2005) play an important role in the distributions of generalist, mobile pest insects. In this study, combined Spatial Analysis by Distance Indices (SADIE) analysis and interpolated maps showed that during the early spring season, high densities of glassy-winged sharpshooters were distributed in non-crop habitat, including woodlands and fallow fields. In general, there were 2 distinct periods of peak trap capture activity at the North Florida Research and Education Center. The first occurred between May and Jun, which corresponded with movement from unmanaged non-crop habitat into crop hosts. A second peak in trap capture occurred typically 2 mo after the early summer peak. The known generation time of glassy-winged sharpshooters is approximately 2 mo (Turner & Pollard 1959; Setamou & Jones 2005), which suggests that each of the 2 annual peaks represent separate generations of sharpshooters. Moreover, during fall mo, glassy-winged sharpshooters have been observed to migrate into wooded areas (Pollard & Kaloostian 1961; Mizell & French 1987; Lauzière et al. 2008; Son et al. 2010). Indeed, during this time period (i.e., Aug until the end of the yr), glassy-winged sharpshooters were found in non-crop habitat, particularly woodlands. Despite a distinct seasonal change in their distribution, from woodlands to crop areas, a proportion of the population remained in woodlands throughout the summer. This may be due to the presence of high-quality summer hosts in woodland habitat.

In addition to habitat composition, host patch quality and connectivity between habitat patches may contribute to additional variation in glassy-winged sharpshooter dispersal behavior and distribution patterns. Glassy-winged sharpshooters show a strong response to preferred host plants, but may change host plants frequently over several spatial scales (Mizell & French 1987). This behavior may be due to underlying plant xylem nutrient chemical profiles that drive variation in movement patterns (Andersen et al. 1992, 1995a; Brodbeck et al. 1993). Glassy-winged sharpshooters tend to spend more time in host patches that are higher quality and disperse over greater distances to new hosts in order to move away from low quality patches (Northfield et al. 2009). Furthermore, the location of a crop host plant relative to non-crop hosts may influence the distribution of glassy-winged sharpshooters. For example, in a patch that is isolated, without other nearby patches of vegetation, glassy-winged sharpshooters were found centrally within the patch (Northfield et al. 2009). In contrast, glassy-winged sharpshooters were distributed along the edge of host plant patches if that particular patch

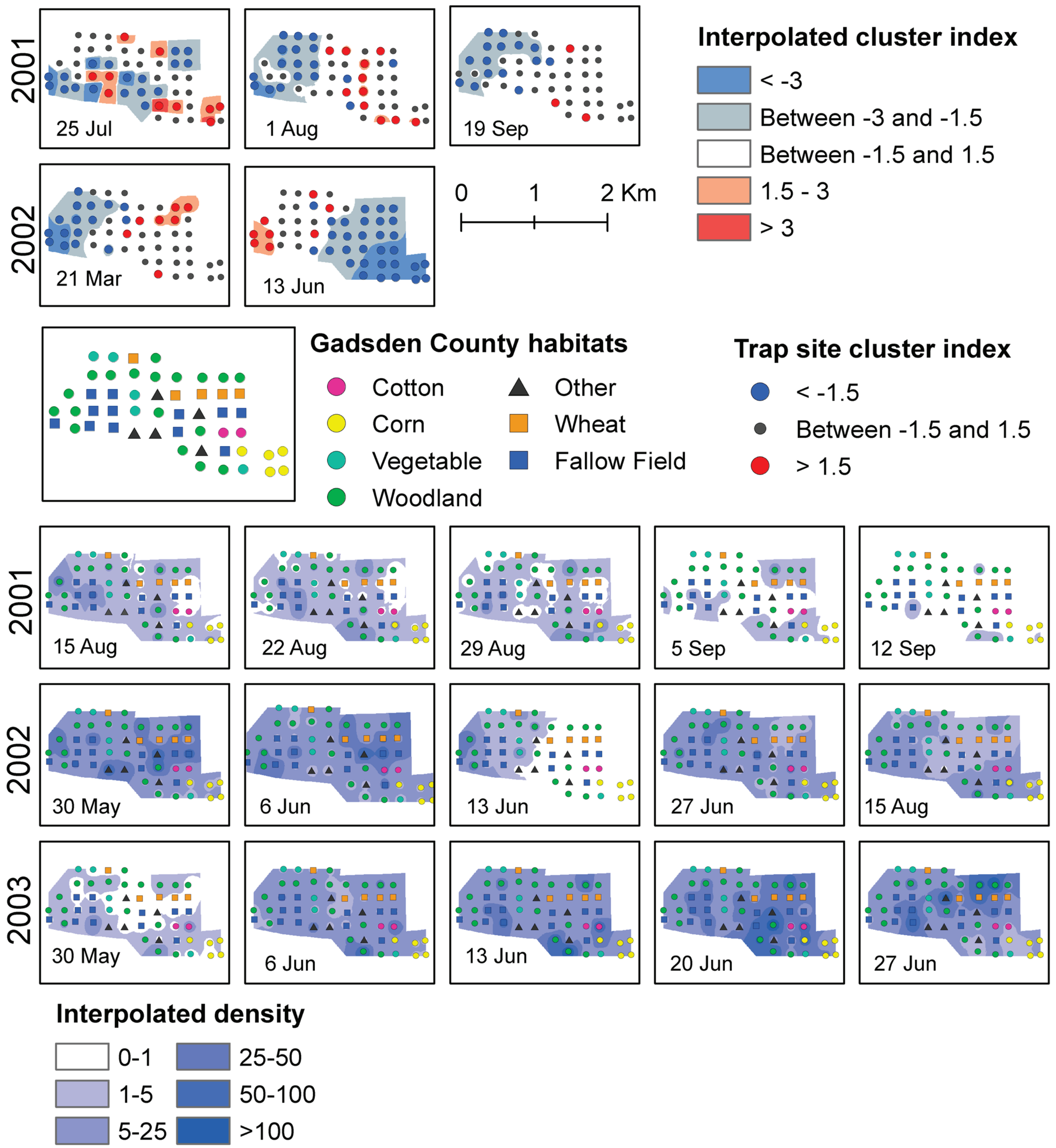

Fig. 3. Spatiotemporal distribution patterns of glassy-winged sharpshooters in Gadsden County, Florida, USA. Top = images display red-blue plots based on interpolation of the cluster index for individuals from 2001 to 2003. Red areas indicate significant aggregations (greater than 1.5), and blue areas indicate significant gaps (less than −1.5). Bottom = interpolated density maps display seasonal distribution patterns of glassy-winged sharpshooters collected in traps during 2001 to 2003, according to habitat.

was adjacent to alternative host plants (Northfield et al. 2009). This suggests that not only composition of host plants, but also configuration (i.e., connectivity) of host plants and habitat patches is an important factor in distribution patterns (Tewksbury et al. 2002; Levey et al. 2005). Accordingly, optimized control measures may include identification of the specific vegetation surrounding crop fields, because the timing and location of an outbreak may vary with both quality and arrangement of host plants in adjacent field margins and unmanaged non-crop habitats.

Table 1. Aggregations (I_a)[a] of glassy-winged sharpshooters, *Homalodisca vitripennis* at Gadsden County, Florida, USA, during 2001 to 2003 based on Spatial Analysis by Distance Indices (SADIE) spatial analysis.

	2001		2002		2003	
Date	*Ia*	*Pa*	*Ia*	*Pa*	*Ia*	*Pa*
28 Feb			0.73	0.9		
7 Mar			1.4	0.08	1	0.4
14 Mar			1.1	0.3	1	0.5
21 Mar			1.7	0.03	1.5	0.01
28 Mar			0.83	0.8	0.8	0.8
4 Apr			1.1	0.3	1.1	0.3
11 Apr			0.68	0.9	0.77	0.8
20 Apr			1.2	0.1	1.1	0.3
27 Apr			1	0.4	0.9	0.6
2 May	0.84	0.7	0.66	1	0.89	0.7
9 May	0.96	0.5	1.3	0.09	1.1	0.3
16 May	1.3	0.2	0.96	0.5	1.3	0.1
23 May	1.3	0.1	0.92	0.5	0.83	0.8
30 May	0.87	0.7	0.79	0.9	0.76	0.9
6 Jun	1.1	0.3	1.1	0.3	1	0.4
13 Jun	1.2	0.1	2.6	< 0.0001	0.96	0.4
20 Jun	0.88	0.7	1.1	0.3	1.3	0.1
27 Jun	0.86	0.6	0.81	0.8	1.2	0.2
4 Jul	1.3	0.08	0.89	0.7	1	0.4
11 Jul	1.3	0.1	0.75	0.9	0.77	0.9
18 Jul	1.1	0.3	0.83	0.8	1.1	0.3
25 Jul	1.8	< 0.0001	1.2	0.2	1.4	0.1
1 Aug	1.8	0.02	1.1	0.2	0.87	0.7
8 Aug	1.1	0.3	0.76	0.9	1	0.4
15 Aug	0.93	0.6	1.1	0.2	1.3	0.1
22 Aug	0.84	0.7	1.3	0.2		
29 Aug	1	0.3	0.98	0.4		
5 Sep	0.91	0.6	1.3	0.1		
12 Sep	1.1	0.2	1.4	0.1		
19 Sep	1.5	0.03	1.1	0.3		
26 Sep	1.1	0.3	0.7	0.9		
3 Oct	1.1	0.2	0.9	0.5		
10 Oct	1.3	0.1	1.3	0.1		
17 Oct	0.89	0.6	1	0.4		
24 Oct	0.98	0.4	1.1	0.2		
31 Oct	1.4	0.02	0.82	0.8		
7 Nov	0.95	0.4	0.73	0.9		
14 Nov	1.2	0.1	1.3	0.08		
21 Nov	1.3	0.1	1.2	0.1		
28 Nov	0.74	0.9				

[a] I_a values in bold indicate that $P_a < 0.05$.

Abiotic factors also may influence the distribution of glassy-winged sharpshooters in agroecosystems. For example, glassy-winged sharpshooters disperse over shorter distances if temperatures are low (< 17 °C; Blackmer et al. 2006) or wind-speeds are high (> 3 m per sec; Blackmer et al. 2004). In addition, many insects feed on irrigated plants more than non-irrigated plants; therefore, the spatial distribution of insects may be affected by water availability (Andersen et al. 1992; Hanks & Denno 1993; Daane & Williams 2003; Kruger et al. 2009, 2012). Water availability is especially important to xylem feeding insects, such as the glassy-winged sharpshooter, because organic nitrogen and amino acid concentrations in xylem fluid may increase and xylem tension may decrease with irrigation (Andersen et al. 1992, 1995a, 1995b). Nutrient concentration within plants also affect insect xylem feeding behavior, which may influence distribution patterns (Redak et al. 2004; Northfield et al. 2009). However, glassy-winged sharpshooters also are sensitive to, and manifested, a plot preference related to the rate of irrigation as it affected plant evapotranspiration (Kruger et al. 2009; Kruger et al. 2012). Because patch quality declines with decreasing xylem nutrition due to low water availability, xylem-feeding insects may exhibit high patch leaving rates during times of low rainfall when water availability also is low in host patches (Charnov 1976). An increase in patch leaving may be especially significant in non-irrigated, natural areas. A high level of patch leaving and increased foraging during times of low water availability or excessive irrigation in crops potentially could lead to greater changes in population distribution compared to times of normal or high rainfall. Therefore, to understand the seasonal timing of glassy-winged sharpshooter distributions, considering abiotic factors such as wind speed, temperature (Son et al. 2010), and water availability (Kruger et al. 2009, 2012) that influence dispersal and distribution patterns may be used to fine-tune management strategies for this pest.

By using a combination of Spatial Analysis by Distance Indices (SADIE) spatial analysis and interpolated maps for 3 yr of trapping data we were able to characterize the seasonal distribution of glassy-winged sharpshooters among a variety of crop and non-crop host plants. Non-crop habitats, particularly woodlands and fallow fields, likely serve as an early season source of glassy-winged sharpshooters that later disperse into crop fields. Trapping data from Florida and California that spans a range of spatial scales, including smaller individual plots within 5.4 ha (Kruger et al. 2009, 2012), intermediate size plots within 253 ha for the current study, and a large 45,000 ha area (Park et al. 2006) all provide similar outcomes and characterizations of annual distribution and movement patterns of adult glassy-winged sharpshooters as well as identify factors that influence dispersal behaviors. Kruger et al. (2012) have suggested that movement from crop to crop is in part a random component of dispersal behavior rather than direct orientation to host characteristics. However, Mizell et al. (2012) reported a unique behavior of this and other sharpshooters whereby individuals respond to feeding congeners, which facilitates food finding, and at the same time decreases predation risk. Thus, such behaviors may be associated with the risk of starvation incurred from feeding on nutrient-poor plant xylem fluid. Moreover, glassy-winged sharpers defensively move to hide behind a host plant in response to approaching humans from 5 to 8 m away (R. F. Mizell, unpublished data).

For implementation of leafhopper pest management that may ultimately reduce the incidence of diseases caused by *X. fastidiosa*, Mizell et al. (2008) provided a conceptual model that integrates leafhopper behavior, life history strategies, and their associated risks with the nutritional requirements of adult and nymphal stages. Pest management also may advance with precision farming technologies, such as remote sensors to improve monitoring change in soil moisture across crop fields and bordering non-crop habitats (Finger et al. 2019; Roy & George 2020). In addition, here we show that pest management strategies for the glassy-winged sharpshooter and other related vector species should seek to limit early spring migration from non-crop habitat into crop fields. For example, barriers may be erected between population sources and cropping systems, preferred hosts could be added as traps, and corridors can be organized to direct insects away from cash crops towards trap crops (Haddad 1999; Tewksbury et al. 2002; Levey et al. 2005; Potting et al. 2005; Mizell et al 2008). In any such strategies, target plant species preferred by leafhopper vectors need to be identified in local areas where they will be used. However, host plants change physiologically (e.g., xylem chemistry; Andersen et al. 1992; Brodbeck et al. 1993), over a short period of time (e.g., hourly, daily, etc.), and xylophages are sensitive to such changes and move accordingly. In this study, we do not provide data on the underlying mechanisms that caused the observed behaviors such as preference of host plants in time (phenology) and space or possible fine grain physical characteristics of the landscape affecting the movements (corridors, barriers, and matrix; Tewksbury et al. 2002). Such characteristics will play a large part in any strategies to develop management tactics such as trap crops, removal of preferred host plants outside crops or targeted use of insecticides in combination with other tactics. However, by focusing on early season distributions within non-crop and crop habitats, along with the vegetation patterns and relationships, growers may limit later season population peaks within crop fields, potentially reducing the likelihood of *X. fastidiosa* transmission. Likely, such strategies would be easier to develop with greater impact in arid areas, such as California, USA, with less species diversity in the non-crop host flora spread among crops of citrus and grape.

Acknowledgments

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