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Ambrosia Beetle Occurrence and Phenology of *Xylosandrus* spp. (Coleoptera: Curculionidae: Scolytinae) in Ornamental Nurseries, Tree Fruit, and Pecan Orchards in Georgia

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Abstract

Ambrosia beetles (Coleoptera: Curculionidae: Scolytinae, Platypodinae) in the genus *Xylosandrus* are problematic in ornamental nurseries and are emerging as serious pests in orchard crops. An updated survey of ambrosia beetles focusing on these damaging species, and their corresponding phenology was conducted in Georgia to aid in refining management practices for these beetles. Ambrosia beetles were monitored across nine sites in 2019 and seven sites 2020 at ornamental nurseries, tree fruit, and pecan orchards in Georgia. At each site, six ethanol-baited bottle traps were deployed; with three traps along the edge of a wood-line and three traps placed 30 m from the edge of the nurseries and orchards. Traps were deployed from mid-January through July or August depending on site and year. All captured ambrosia beetles were counted and identified. Captures of *X. crassiusculus, X. germanus*, and *X. compactus*, were analyzed further to investigate spatial distribution and seasonal flight activity. At high population sites, more beetles were captured along adjacent wood lines than in the orchard or nursery interior. At most sites, flight activity began in February and March continued until the termination of the study in July or August. At most sites, sustained flight activities with multiple peaks were observed in March, April, and May, corresponding to average weekly temperatures reaching ≥15.5°C. These results have important implications on temporally and spatially precise management for these beetles across three important agricultural production systems in the southeastern US.

Key words: phenology, spatial distribution, trapping, ethanol

Ambrosia beetles are wood-boring beetles that are destructive and economically damaging to various horticultural production systems (Ranger et al. 2015, 2016; Gugliuzzo et al. 2021). Several species have been introduced into the United States through ports of entry (Rabaglia et al. 2019). Some have been problematic in woody ornamental nurseries (Ranger et al. 2016, Addesso et al. 2019) and recently have become pests of fruit and nut crops (Agnello et al. 2015, 2017, Reed et al. 2015; Walgenbach and Villani 2018; Acebes-Doria 2019). Several species of ambrosia beetles attack pecans (*Carya* spp.), chestnut (*Castanea mollissima* Blume), black walnut (*Juglans nigra* L.), apples (*Malus* spp.), peaches (*Prunus* spp.), and a wide host range of ornamentals (Kovach and Gorsuch 1985, Oliver and Mannion 2001, Agnello et al. 2015, Williams and Ginzel 2020). Infestations can cause severe economic losses of trees in nurseries (Ranger et al. 2016). Not all attacks lead to the death of nursery trees, but they can negatively impact growth and aesthetics as well as the economic value of the trees (Oliver and Mannion 2001, Ranger et al. 2016). In tree fruit crops, ambrosia beetles have been recently associated with rapid apple decline phenomenon in North Carolina and other mid-Atlantic states (Agnello et al. 2015, 2017; Walgenbach and Villani 2018).

In Georgia, woody ornamental commodities and orchard crops are vulnerable to the potential economic impacts of ambrosia beetles. Field nurseries are valued at US$125 million (Wolfe and Stubbs 2019), where ambrosia beetles are considered major pests. Peaches and apples contribute US$46 million yearly to the state's economy (Wolfe and Stubbs 2019). Although ambrosia beetles are currently not considered a major pest in peaches and apples in Georgia, tree fruit orchards have been experiencing increased attacks by ambrosia beetles. Pecan production in GA is valued at US$401 million in 2020 and with new orchard establishment (Wells 2014) and re-establishment due to damage caused by hurricanes in recent years (Wells 2018), ambrosia beetles have re-emerged as economic pests (Acebes-Doria 2019).

Three of the major ambrosia beetle pest species previously recorded in Georgia are the granulate ambrosia beetle, *Xylosandrus crassiusculus* (Motschulsky), the black stem borer, *Xylosandrus germanus* (Blandford), and black twig borer, *Xylosandrus compactus* (Eichhoff), (Coleoptera: Curculionidae) (Ngoan et al. 1976, Mizell et al. 1994, Chong et al. 2009, Ranger et al. 2016, Addesso et al. 2019). Among the three *Xylosandrus* species, *X. compactus* is known to attack healthy trees while the other two are commonly associated with physiologically compromised trees (Gugliuzzo et al. 2021, Ranger et al. 2021). Trees infested with *Xylosandrus X. compactus* normally exhibit 'sawdust' frass outside the entry holes on twigs and branches, and those attacked by *X. crassiusculus* and *X. germanus* have compacted masticated wood extrusion 'noodles' emerging from entry holes on the trunks and branches (Gugliuzzo et al. 2021). In some cases, the infestations of living plant tissues can lead to sap production and staining, wilting foliage, branch dieback, and necrosis (Ranger et al. 2016, Gugliuzzo et al. 2021). Moreover, *Xylosandrus* ambrosia beetles are associated with symbiotic fungi that invade females introduced into the wooden galleries providing food sources for developing offspring and adults (Ranger et al. 2016, Biedermann and Vega 2020, Vega and Biedermann 2020). Although these symbiotic fungi are not known to be pathogenic to host trees, infested trees can also become vulnerable to opportunistic secondary pathogen infections such as *Fusarium* spp (Ranger et al. 2016).

Currently, the management of *Xylosandrus* spp. involves repeated applications of pyrethroid insecticides, such as bifenthrin and permethrin (Ranger et al. 2016, Reding and Ranger 2018, Brown et al. 2020). Use of long-lasting insecticidal netting impregnated with deltamethrin has also been shown to provide some protection for nursery trees from ambrosia beetle attacks (Ranger et al. 2019). Insecticidal interventions have been shown to reduce the attacks on tree trunks especially during peak adult flight periods (Ranger et al. 2016). Thus, a thorough understanding of ambrosia beetle phenology and flight activities through monitoring is critical for precise timing of management decisions (Reding and Ranger 2018).

Knowing the species composition, number of generations, and seasonal phenology of ambrosia beetle species in an area is an important consideration in developing targeted management strategies for ornamental nurseries, as well as nut and tree fruit orchards (Gugliuzzo et al. 2021). In 1994, a survey for *X. crassiusculus* was conducted in Florida and Georgia (Mizell et al. 1994) establishing the occurrence and phenology of *X. crassiusculus* in ornamental nurseries and paving the way for developing management tactics against this species (Hudson and Mizell 1999, Mizell et al. 2004). Given the change in the pest status of ambrosia beetles in recent years in Georgia, our study aimed to provide an updated survey on ambrosia beetles and expanding the scope to other perennial orchard cropping systems impacted by ambrosia beetles, with a focus on *Xylosandrus* species. Thus, our specific objectives included 1) to conduct an updated and expanded survey by examining the relative abundance of the most common ambrosia beetle species in Georgia across three different production systems (ornamental nurseries, tree fruit, and tree nut orchards), 2) analyzing the spatial trends of *Xylosandrus* pest species in the exterior and interior location at each site, and 3) monitoring their seasonal phenology for two consecutive years in relation to mean weekly temperatures.

Materials and Methods

Study Sites

Sites across Georgia were chosen due to previous history of ambrosia beetle infestations or their potential to have infestations. In 2019, three sites were selected for ornamental nursery, tree fruit, and pecan orchards for a two-year-long trapping study. However, in 2020, only one tree fruit orchard site was monitored due to COVID-related complications (Table 1). All sites except for the Univ. of Georgia Horticultural Research Farm in Watkinsville, GA were managed following commercial standard insecticide management guidelines. The ornamental nursery sites were located in central Georgia. The major ornamental tree species grown in the nursery sites were *Magnolia* spp., *Prunus* spp., *Cercis* spp., *Illex* spp., *Ginkgo* spp., *Lagerstroemia* spp., *Stewartia* spp., *Camellia* spp., *Acer* spp., and *Cupressus* spp. The planted nursery trees were spaced ~1.5 m apart between rows and trees at Meansville A and B sites, and variable spacing (~0.3 m to ~0.9 m) was used in the container field nursery at Barnesville. The age of the majority of the growing trees ranged from 0 to 4 yr. The apple orchards and peach

Table 1. Summary of the trapping locations, trapping period and nearest weather stations for each study site

Cropping System	Location	GPS Coordinates	Trapping Period		Weather Station Locations
			2019	2020	
Apple	Mercier (Blue Ridge)	34°53′11.1″N 84°20′34.9″W	7 Feb.–23 July	3 Feb.–30 Aug.	Fannin County
	R&A (Ellijay)	34°39′08.0″N 84°25′24.1″W	8 Feb.–23 July	–	Gilmer County
Peach	UGA Hort Farm (Athens)	33°53′12.9″N 83°25′21.7″W	12 Feb.–23 July	–	n/a
Pecan	Quitman, GA	30°48′10.7″N 83°32′21.6″W	18 Jan.–30 Aug.	8 Jan.–30 Aug.	Dixie, GA
	Nashville, GA	31°10′25.8″N 83°14′10.3″W	18 Jan.–30 Aug.	8 Jan.–30 Aug.	Alapaha, GA
	Irwinville, GA	31°40′05.0″N 83°29′32.3″W	18 Jan - 30 Aug	8 Jan.–30 Aug.	Tifton-Bowen, GA
Ornamental	Mid-Georgia Site 1	33°02′18.1″N 84°20′03.5″W	16 Jan.–28 Aug.	30 Jan.–26 Aug.	Williamson, GA
	Mid-Georgia Site 2	33°04′04.5″N 84°18′03.9″W	16 Jan.–28 Aug.	30 Jan.–26 Aug.	Williamson, GA
	Dorsey Farms	33°03′28.1″N 84°14′49.7″W	16 Jan.–28 Aug.	30 Jan.–26 Aug.	Williamson, GA

orchard were located in North Georgia. The apple orchards only contained *Malus* spp. within the area that the traps were placed. The apple trees at the Blue Ridge site were spaced ~1.8 m apart and were 8 yrs old, while apple trees at the Ellijay site were spaced ~5.5 m apart and were 15 yrs old. The peach orchard in Watkinsville only contained 7-yr-old *Prunus* spp. within the area that the traps were set and were spaced ~5.5 m apart. The pecan orchard sites only contained *Carya* spp. and were spaced ~12 m apart and the ages of the planted trees ranged from 4 to 7 yr.

Traps and Monitoring

Ethanol-baited traps have been used to effectively monitor ambrosia beetle populations (Reding et al. 2011, 2013, 2020; Ranger et al. 2021). At each site, six traps were deployed, three along the edge of the woodline (~3 m from woodline) and three about 30 m from the woodline in the interior of the ornamental nursery or orchard. Each trap was at least 20 m from any other. At the ornamental sites, bottle traps consisted of a clear rectangular-shaped 1774 ml plastic bottle (VTM LLC, Lexington, KY; Supp Fig. 1A [online only]). At the tree fruit and pecan sites, clear square-shaped 1774 ml plastic bottles (Berlin Packaging, Chicago, IL; Supp Fig. 1B and C [online only]) were used. The plastic bottle traps were baited with one commercially available ethanol dispenser (AgBio Inc., Westminster, CO) across all study sites. The ethanol dispenser had 7–8 ml 95% ethanol and a 65 mg/day release rate at 30°C. The plastic bottles (Supp Fig. 1 [online only]) were modified by cutting the sides (~5 cm × ~9 cm) to create two (ornamental and pecan) or four (tree fruit) access windows across from each other. Two small holes (6 mm) were drilled on the bottom of bottle where one zip tie (152.4 mm × 4.76 mm) was inserted into the bottle to suspend the ethanol lure. The bottle trap was suspended to a wooden or metal stake (1–1.2 m in length) using another second zip tie (152.4 mm × 4.76 mm). The bottle trap was hung upside down and placed ~0.5 m above the ground. The incoming ambrosia beetles attracted to ethanol lure were trapped and retained in the soapy water added to the bottle. The soap solution was prepared by adding 0.5 ml of dish wash soap (Dawn, P&G, Kansas City, KS) in 300 ml tap water. The soap solution and ethanol dispensers were changed at weekly and monthly intervals, respectively.

One temperature logger (HOBO, Bourne, MA) was placed at each site to record the seasonal temperature fluctuations. However, device malfunctions occurred at certain periods across several sites, thus logger-obtained data were supplemented with data from the closest Georgia weather station to each study site (http://www.georgiaweather.net/, Table 1). Temperature data were computed as mean daily temperatures and presented as weekly averages for each trapping week on Figs. 1–3.

The trapping was conducted from late winter to late summer in both years (Table 1) coinciding with the anecdotal grower reports of ambrosia beetle attacks during which management decisions would have to be made. Some sample dates in 2020 were missed due to severe weather and COVID-related issues (i.e., 3/5, 3/25, 4/8). The traps were emptied at weekly intervals by removing the bottle caps over a coffee filter and sieve and filtering the soapy water through. The collected beetles were sorted and preserved in 70% ethanol vials for subsequent identification. During the colder months, propylene glycol was added to prevent water from freezing. The beetles were identified to the genus or species using a lucid key for Southeast Asian *Xyleborini* species (Smith et al. 2019) and Bateman and Hulcr's ambrosia beetle guide (Bateman and Hulcr 2017).

Data Analyses

The total relative abundance of each species captured at each site was calculated for 2019 and 2020. Although there were higher numbers of non-*Xylosandrus* beetles (*Hypothenemus* spp.) present in some sites, we excluded them from the statistical analyses and focused on the main damaging *Xylosandrus* pests. When captures of *Xylosandrus* species at each site were high enough to warrant statistical analyses, data were further examined for spatial distribution and seasonal trends. Average weekly captures of *Xylosandrus* species at each site for each year were examined and approximated following assumptions of parametric test, and data that did not satisfy normality assumptions were transformed using log and exponential transformations, accordingly. Data were analyzed using a two-way analysis of variance using standard least squares with trap location and sampling date as model effects or factors. Subsequently, a Tukey-Kramer HSD test was used for post-hoc multiple mean comparisons. Data from each site within cropping systems were analyzed separately as conditions (i.e., plant variety, age, management programs) across all sites were not homogenous (Table 1). Data collected each year were analyzed and reported separately given the inherent differences between each year. All analyses were conducted using JMP ver. 15 (SAS Institute Inc., Cary, NC, 2019) at $\alpha = 0.05$.

Results

Relative Beetle Abundance of *Xylosandrus* spp and Other Ambrosia Beetles Across All Sites

Xylosandrus crassiusculus and *X. germanus* were present across all nine sites; while *X. compactus* was detected at seven sites (Table 2). *X. crassiusculus* was most prevalent among the three *Xylosandrus* species with overall captures across all sites comprising 68% in 2019 and 23% in 2020. *X. germanus* had fewer overall captures than *X. crassiusculus* across all sites at 12 and 17% of the total captures in 2019 and 2020, respectively. *X. compactus* was prevalent in the southern region of the state where it was the most abundant among the *Xylosandrus* species in the pecan orchards, covering 8% of the overall captures in 2019 and 36% in 2020. Other ambrosia beetles found across the sampled locations include *Hypothenemus* spp., *Xyleborus* spp., *Xyleborinus* spp., and *Ambrosiodmus rubricollis*.

Relative Beetle Abundance Per Site

Ornamental Nursery

Across all sites within ornamental nurseries, the most abundant species in 2019 were *X. crassiusculus* and *X. germanus* constituting 82–94 and 3–11% of the overall captures, respectively (Table 2). Less than 1% of the captured beetles were *X. compactus*. The other beetle species constituted 0.5–9% which included *Hypothenemus* spp., *Xyleborus* spp., and *Xyleborinus* spp. Although the total captures in 2020 were less than 2019 at all sites, the relative species abundance was similar with *X. crassiusculus* and *X. germanus* being the most abundant at 40–46 and 9–21%, respectively (Table 2). *X. compactus* numbers were only 1-5%. The other beetles contributed to 39–46% and consisted of *Hypothenemus* spp., *Ambrosiodmus rubricollis*, *Xyleborus* spp., *Xyleborinus* spp., *Cyclorhipidion* sp., *Euwallacea* sp., and *Anisandrus* spp.

Tree Fruit

The most abundant species in 2019 across all tree fruit orchard sites were *X. crassiusculus* and *X. germanus* constituting 27–96 and 2–67% of the captures, respectively (Table 2). The other beetles constituted 1–5% of the total captures and were *Hypothenemus*

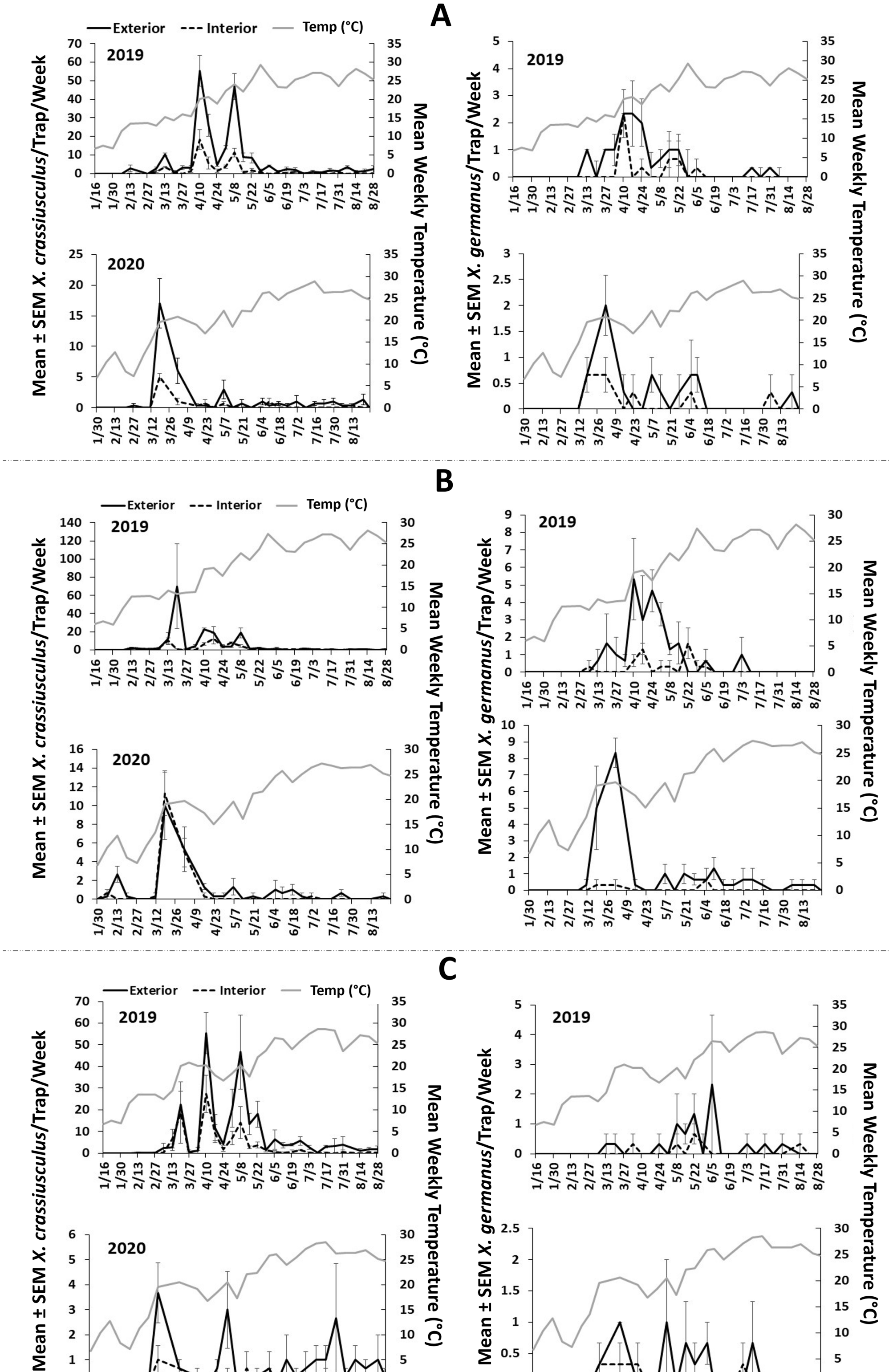

Fig. 1. Mean ± SEM numbers of *X. crassiusculus* and *X. germanus* captured per trap per week and mean weekly temperature (°C) in 2019 and 2020 at ornamental nurseries in Meansville, GA site (A), Meansville, GA site (B), and Barnesville, GA (C). Some 2020 sampling dates were missed due to severe weather and COVID-related issues (3/5, 3/25, 4/8).

spp., *Ambrosiodmus rubricollis*. *Xylosandrus compactus*, *Xyleborus* spp., *Xyleborinus* spp., *Cyclorhipidion* sp., *Euwallacea* sp., and *Anisandrus* spp. In 2020, at the Blue Ridge site, the most abundant species were *X. germanus* and *X. crassiusculus* contributing 47 and 42% of overall captures, respectively. The other beetles contributed 1–4% of the overall beetle captures including *Hypothenemus* spp.,

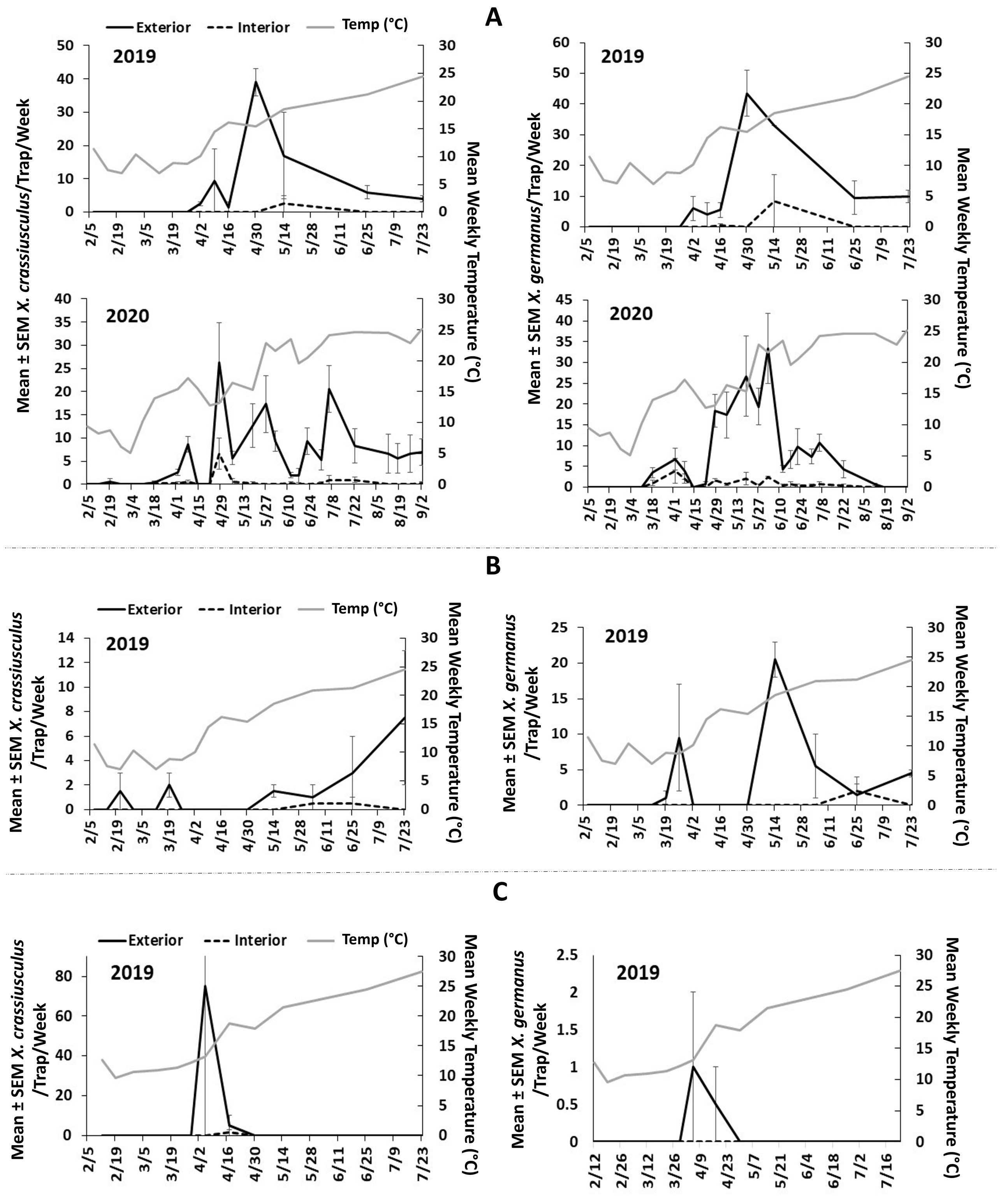

Fig. 2. Mean ± SEM numbers of *X. crassiusculus* and *X. germanus* captured per trap per week and mean weekly temperature (°C) in 2019 and 2020 at the apple orchard site in Blue Ridge, GA (A). Mean ± SEM of *X. crassiusculus* and *X. germanus* captures per trap per week at the apple orchard in Ellijay, GA (B), and peach orchard in Watkinsville, GA (C) in 2019.

Xyleborus spp., *Xyleborinus* spp., *Euwallacea* sp., *Anisandrus* spp., and *Cnestus mutilatus*.

Pecans

In 2019, *X. compactus* and *X. crassiusculus* were the most abundant species at Quitman making up 45 and 28%, respectively. In Nashville, *X. crassiusculus* and *X. compactus* were the most abundant with 21 and 7% of the total captures, respectively. In Irwin, *X. crassisuculus* and *X. germanus,* were the most abundant species present with 47 and 14% of captures, respectively. Across all sites, other beetles contributed to 1–41% of the captures which included *X. germanus*, *Xyleborus* spp, *Xyleborinus* spp., and *A. rubricollis*.

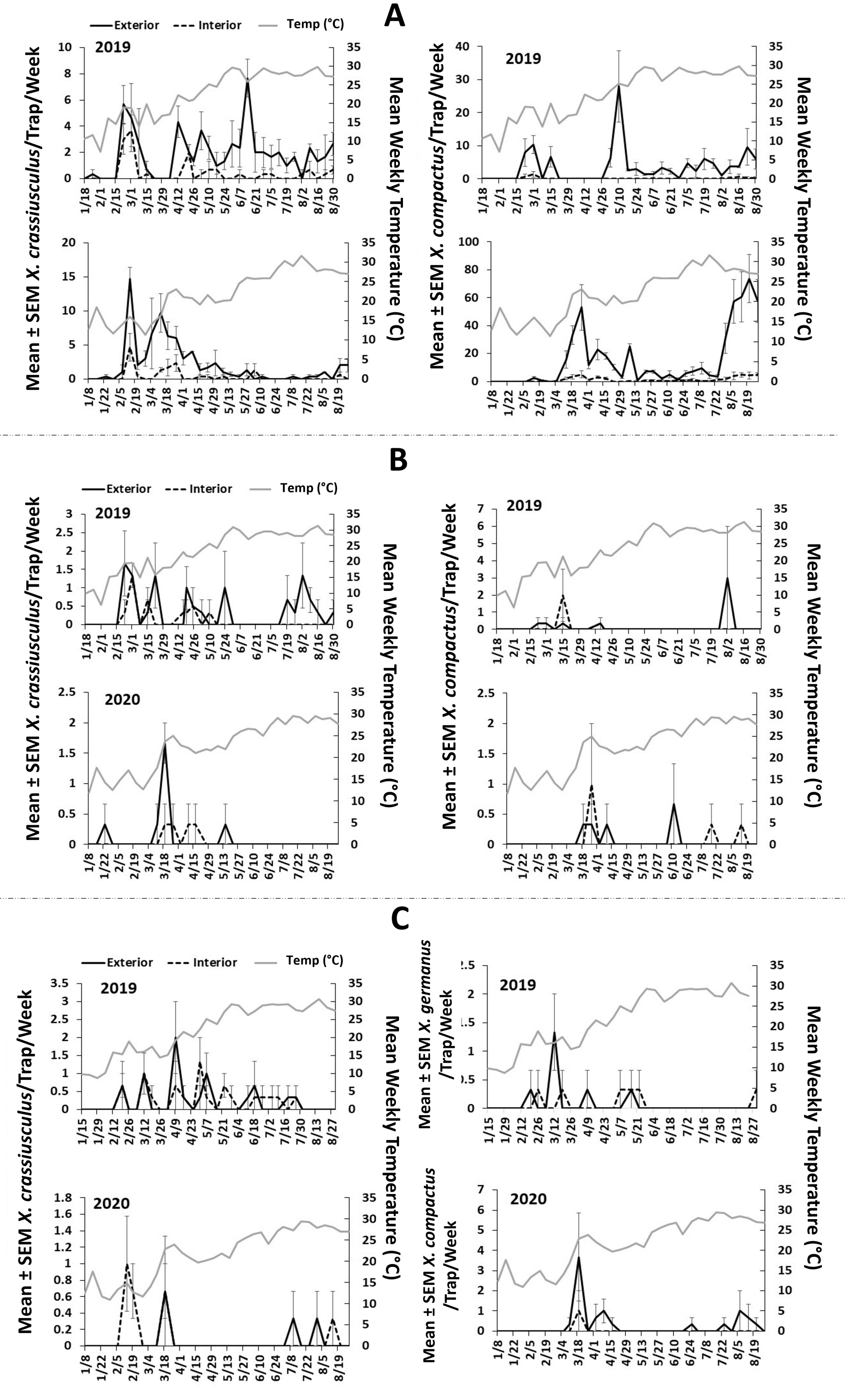

Fig. 3. Mean ± SEM number of *X. crassiusculus* and *X. compactus* captured per trap per week and mean weekly temperature data (°C) in 2019 and 2020 at pecan orchard sites: Quitman, GA (A) and Nashville, GA (B). Irwin, GA site (C) shows mean ± SEM weekly trap captures of *X. crassiusculus* and *X. germanus* in 2019 and of *X. crassiusculus* and *X. compactus* in 2020.

At some sites, high numbers of *Hypothenemus* spp., were recorded. In 2020, at Quitman, *X. compactus* and *X. crassiusculus* made up 65 and 10%, respectively; while in Nashville. *X. crassiusculus* and *X. compactus* constituted 7 and 6% of captures, respectively (Table 2). At Irwin, the most common *Xylosandrus* species were *X. crassisuculus* and *X. germanus* making up 15 and 6% of

Table 2. Relative species abundance of ambrosia beetles captured in ethanol-baited bottle traps deployed at ornamental nurseries, tree fruit, and pecan orchards in Georgia in 2019 and 2020

Ornamental Nursery Sites						
	2019			2020		
Beetle Species	**Meansville, GA (A)**	**Meansville, GA (B)**	**Barnesville, GA**	**Meansville, GA (A)**	**Meansville, GA (B)**	**Barnesville, GA**
X. crassiusculus	790 (84.2%)	684 (81.6%)	1012 (94.0%)	133 (45.9%)	133 (40%)	69 (42.9%)
X. germanus	53 (5.7%)	91 (10.9%)	28 (2.6%)	25 (8.6%)	70 (21%)	18 (11.2%)
X. compactus	1 (0.1%)	4 (0.5%)	0	12 (4.1%)	15 (4.5%)	2 (1.2%)
Hypothenemus spp.	54 (5.8%)	13 (1.6%)	11 (1.0%)	75 (25.9%)	63 (18.9%)	32 (19.9%)
*Xyleborinus*spp.	14 (1.5%)	6 (0.7%)	7 (0.7%)	15 (5.2%)	36 (10.8%)	28 (17.4%)
*Xyleborus*spp.	15 (1.6%)	25 (3.0%)	19 (1.8%)	12 (4.1%)	11 (3.3%)	5 (3.1%)
A. rubricollis	9 (1.0%)	15 (1.8%)	1 (0.1%)	8 (2.8%)	3 (0.9%)	5 (3.1%)
Other	2	0	0	10 (3.4%)	3 (0.9%)	2 (1.2%)
Total	938	838	1078	290	334	161

Tree Fruit Orchard Sites						
	2019			2020		
Beetle Species	Blue Ridge, GA	Ellijay, GA	Watkinsville, GA	Blue Ridge, GA	Ellijay, GA	Watkinsville, GA
X. crassiusculus	164 (36.0%)	36 (27.3%)	163 (95.9%)	509 (42.5%)	-	-
X. germanus	241 (53%)	89 (69.4%)	3 (1.8%)	574 (47.9%)	-	-
X. compactus	0 (0.2%)	0	2 (1.2%)	0	-	-
Hypothenemus spp.	16 (3.5%)	0	1 (0.6%)	28 (2.34%)	-	-
*Xyleborinus*spp.	1 (1.5%)	1 (0.8%)	1 (0.6%)	3 (0.25%)	-	-
*Xyleborus*spp.	0	2 (1.5%)	0	48 (4.0%)	-	-
A. rubricollis	26 (5.7%)	0	0	18 (1.5%)	-	-
Other	7 (1.5%)	4 (3%)	0	14 (1.17%)	-	-
Total	455	132	170	1198		

Pecan Orchard Sites						
	2019			2020		
Beetle Species	Quitman, GA	Nashville, GA	Irwin, GA	Quitman, GA	Nashville, GA	Irwin, GA
X. crassiusculus	224 (28.3%)	33 (20.6%)	40 (46.5%)	255 (9.8%)	12 (7.2%)	12 (6.1%)
X. germanus	52 (6.6%)	3 (1.9%)	12 (14.0%)	116 (4.4%)	4 (2.4%)	11 (5.6%)
X. compactus	357 (45.2%)	11 (6.9%)	10 (11.6%)	1721 (65.9%)	10 (6.0%)	29 (14.8%)
Hypothenemus spp.	135 (17.0%)	66 (41.3%)	12 (14.0%)	422 (16.2%)	94 (56.6%)	43 (21.9%)
*Xyleborinus*spp.	6 (0.8%)	0	0	69 (2.6%)	22 (13.3%)	77 (39.3%)
*Xyleborus*spp.	16 (2.0%)	11 (6.9%)	5 (5.8%)	12 (0.5%)	15 (9.0%)	3 (1.5%)
Other	0	36 (22.5%)	7 (8.1%)	18 (0.7%)	9 (5.4%)	21 (10.2)
Total	790	160	86	2613	166	196

captures, respectively. Across all sites, the other beetles present contributed to 2–39% of overall captures. Some sites had a high number of other beetle species such as *Hypothenemus* spp. and *Xyleborinus* spp. The other beetles with lower numbers consisted of *X. germanus*, *Xyleborus* spp, *Xylosandrus amputatus*, and *A. rubricollis*, depending on the site.

Spatial and Seasonal Trends of *X. crassiusculus, X. germanus,* and *X. compactus* Trap Captures in Three Cropping Systems

Ornamental Nursery

Trap Location Effect in Ornamental Nurseries

In 2019, captures of *X. crassiusculus* at Meansville A and Barnesville sites were higher along the exterior of the nurseries than in the interior (Meansville (A): $F_{1,\ 190}$ = 11.83, P = 0.0007; Barnesville: $F_{1,\ 184}$ = 6.83, P = 0.0097). As well, numbers of *X. germanus* at the Meansville sites A and B were more along the exterior than in the interior of the nurseries (Meansville A: $F_{1,\ 190}$ = 6.77, P = 0.0100; Meansville B: $F_{1,\ 189}$ = 10.51, P = 0.0014). While captures of *X. crassiusculus* and *X. germanus* did not differ between trap locations at Meansville (B) and Barnesville, respectively (Meansville B: $F_{1,\ 189}$ = 3.69, P = 0.0561; Barnesville: $F_{1,\ 184}$ = 3.40, P = 0.0667). In 2020, higher numbers of *X. crassiusculus* were also captured along the exterior of the nurseries compared to the interior areas at Meansville A and Barnesville (Meansville: A: $F_{1.\ 165}$ = 5.52, P = 0.0199; Barnesville: $F_{1,\ 166}$ = 13.19, P = 0.0004). Similarly, *X. germanus* numbers were also higher in the exterior areas than in the interior at the two Meansvilles sites (Meansville A: $F_{1,\ 165}$ = 4.03, P = 0.0464; Meansville B: $F_{1,\ 166}$ = 11.87, P = 0.0007). No difference between trap locations was found on the numbers of *X. crassiusculus* at Meansville B ($F_{1,\ 166}$ = 0.64, P = 0.4265), and of *X. germanus* at Barnesville ($F_{1,\ 166}$ = 3.88, P = 0.0506).

Phenology of *X crassiusculus* in Ornamental Nurseries

In 2019, captures of *X. crassiusculus* varied across the sampling period at all sites (Meansville A: $F_{63, 128}$ = 25.16, P < 0.0001; Meansville B: $F_{63, 127}$ = 9.92, P < 0.0001; Barnesville: $F_{61, 124}$= 7.45, P < 0.0001; Fig. 1). The first flight activity was observed on the week of 13 February at all sites, where the mean weekly temperature was 15.5°C. At Meansville site A, the peak flight activities were observed in mid-April and early May (Fig. 2A). At Meansville B site, peak flight activity occurred mid to late March (Fig. 1B). Peak flight activities at Barnesville happened in late March, mid-April, and mid-May (Fig. 1C). The peak flight activities at all sites were observed when the temperature was ~15 to ~24°C (Fig. 2). In 2020, the number of *X. crassiusculus* captured were significantly different throughout the sampling period at all sites (Meansville A: $F_{55, 111}$ = 11.58, P < 0.0001; Meansville B: $F_{55, 112}$ = 10.18, P < 0.0001; Barnesville: $F_{55, 112}$ = 2.10, P = 0.0005). The first flight activities of the season occurred on the weeks of 27 February, 6 February, and 18 March for Meansville A, B, and Barnesville, respectively. During these differing weeks of activity, the first flight occurred when the mean weekly temperature reached 15.5°C. The peak flight in all sites was detected in mid-March (Fig. 1). Some locations showed low numbers of captures, but the presence of ambrosia beetles was observed. The peak activities coincided with average weekly temperatures reaching ~15 to ~24°C.

Phenology of *X. germanus* in Ornamental Nurseries

In 2019, the numbers of *X. germanus* captured significantly differed throughout the sampling period at Meansville A and B sites (Meansville A: $F_{63, 128}$ = 3.57, P < 0.0001; Meansville B: $F_{63, 127}$ = 3.97, P < 0.0001). Similar to that of *X. crassiusculus*, the first flight activity of *X. germanus* occurred when mean weekly temperatures reached ~15.5°C. The first captures occurred on the weeks of 13 March at Meansville A and Barnesville sites, and on week of 6 March at Meansville B. Flight activities of *X. germanus* occurred at mean weekly temperatures of 15°C to 23°C. In 2020, the number of *X. germanus* captured were generally low but differed significantly throughout the sampling period at all sites (Meansville A: $F_{55, 111}$ = 2.96, P < 0.0001; Meansville B: $F_{55, 112}$ = 8.33, P < 0.0001; Barnesville: $F_{55, 112}$= 1.48, P = 0.0401). The first flight activities occurred on the weeks of 18 March for Meansville A and Barnesville, and on week of 11 March for Meansville B. The first flight activity occurred when the temperature reached ~15.5°C and was observed in early March at all sites (Fig. 1).

Tree Fruit

Trap Location Effect in Tree Fruit Orchards

In 2019, the captures of *X. crassiusculus* and *X. germanus* were significantly greater at the exterior than in the interior of the apple orchards in Blue Ridge (*X. crassiusculus*: $F_{1, 54}$ = 6.34, P = 0.0148; *X. germanus*: $F_{1, 54}$ = 7.69, P = 0.0076) and Ellijay (*X. crassiusculus*: $F_{1, 57}$ =4.41, P = 0.0401; *X. germanus* ($F_{1, 57}$ = 5.68, P = 0.0205). While no difference between trap locations was observed at the peach orchard in Watkinsville (*X. crassiusculus*: $F_{1, 45}$ =1.04, P = 0.3114; *X. germanus*: $F_{1, 45}$ = 1.84, P = 0.1882) due to low number of captures. Similarly, in 2020, the numbers of *X. crassiusculus* (Blue Ridge: $F_{1, 153}$ = 36.46, P < 0.0001) and *X. germanus* (Blue Ridge: $F_{1, 153}$ = 28.06, P < 0.0001) were higher in the orchard exterior than in the interior.

Phenology of *X crassiusculus* in Tree Fruit Orchards

In 2019, the numbers of *X. crassiusculus* captured were different throughout the sampling period at the two apple orchards (Blue Ridge: $F_{27, 28}$ = 6.20, P < 0.0001; Ellijay: $F_{29, 29}$ = 2.14, P = 0.0226; Fig. 2A and B). While captures of *X. crassiusculus* at the peach orchard in Watkinsville did not vary throughout the season ($F_{23, 23}$= 0.96, P = 0.5411). First flight activity of *X. crassiusculus* was observed on the week of 21 February in Ellijay, on the week of 2 April in Blue Ridge, and on the week of 5 April in Watkinsville. The first flight activities at each site coincided with mean weekly temperatures between 10 and 22°C. Peak flight activity at Blue Ridge occurred in early April, with another peak in mid-April (Fig. 2A). In Ellijay, the number of beetle captures was low throughout the trapping season. Flight activities were observed and were sporadic from mid-February through August (Fig. 2B). At Watkinsville, peak flights were observed in early April and mid-May (Fig. 2C). The highest peak in activity occurred when temperatures reached ≥15.5°C. In 2020, the first flight activity at Blue Ridge occurred earlier than in 2019, on the week of 19 February, when the mean weekly temperature was <15.5°C. The peak flight activities at Blue Ridge occurred in early April, late April into early May, and mid-August (Fig. 2A), when mean weekly temperatures were between 15.5 and 25°C.

Phenology of *X germanus* in Tree Fruit Orchards

Number of *X. germanus* trapped in 2019 differed throughout the sampling period at the two apple orchards (Blue Ridge: $F_{27, 28}$ = 14.47, P = <0.0001; Ellijay: $F_{29, 29}$ = 5.55, P < 0.0001; Fig. 2A and B). While at the peach orchard in Watkinsville, the number of *X. germanus* were very low throughout the season ($F_{23, 23}$ = 0.94, P = 0.5583; Fig. 2C). The first flight activities of *X. germanus* occurred on the weeks of 19 March, 2 April, and 5 April at Ellijay, Blue Ridge, and Watkinsville, respectively, when mean weekly temperatures were between 7.2 and 15.5°C. Peak flight activity in Blue Ridge was observed in early April, and another peak in early May (Fig. 2A). In Ellijay, peak activities were seen in late March, mid-May, and late August (Fig. 2B). The highest peak of *X. germanus* activity at the apple orchards in Blue Ridge and Ellijay occurred when temperatures were ≥15.5°C. Similar to the 2019 results, the 2020 captures of *X. germanus* in Blue Ridge varied significantly throughout the sampling period ($F_{25, 26}$ = 6.17, P < 0.000). The first flight activity was observed on the week of 18 March with peak captures in early April, early to late May, and later in mid-August (Fig. 2A). The first flight activity coincided with mean weekly temperatures between 7.2 and 15.5°C and with the highest peak activity coinciding with mean weekly temperatures of ≥15.5°C.

Pecans

Trap Location Effect in Pecan Orchards

In 2019, significantly more *X. crassiusculus* were captured in the orchard exterior than in the interior at Quitman and Nashville (Quitman: $F_{1, 195}$ = 31.43, P < 0.0001; Nashville: $F_{1, 196}$ = 7.28, P = 0.0076). Captures of *X. compactus* in exterior traps were significantly greater than in interior traps at Quitman ($F_{1, 195}$ = 27.16, P = <0.0001) while no difference between trap locations was observed at Nashville for *X. compactus* ($F_{1, 196}$ = 0.32, P = 0.57) and Irwin for *X. crassiusculus* ($F_{1, 190}$ = 0.02, P = 0.90) or *X. germanus* ($F_{1, 190}$ = 0.06, P = 0.8045). In 2020, *X. crassiusculus* ($F_{1, 202}$ = 20.19, P < 0.0001) and *X. compactus* ($F_{1, 202}$ = 38.80, P < 0.0001) were captured more at the orchard exterior than in the interior at Quitman. Significantly more *X. compactus* were captured along the edge of the orchard than inside the orchard at Irwin ($F_{1, 208}$ = 5.32, P = 0.0221). Trap location did not affect the captures of *X. crassiusculus* at Nashville ($F_{1, 202}$ = 1.04, P = 0.3088) or Irwin ($F_{1, 190}$ = 0.0161, P = 0.8991), and captures of *X. compactus* at Nashville ($F_{1, 202}$ = 0.00, P = 1.0000).

Phenology of *X. crassiusculus* in Pecan Orchards

In 2019, numbers of *X. crassiusculus* were generally low but varied significantly across the sampling period at all sites (Quitman: $F_{32, 32} = 4.18$, $P = 0.00006$; Nashville: $F_{32, 32} = 2.90$, $P = 0.0017$; Irwin: $F_{31, 31} = 3.50$, $P = 0.0004$). The first flight activities as observed through trap captures occurred on the weeks of 25 January, 20 February, and 22 February at Quitman, Irwin, and Nashville, respectively, with some of the flights occurring at weekly temperatures below 15.5°C while others at ≥15.5°C. At Quitman, flight activities were observed in late February, in mid-April, and again by mid-June (Fig. 3A). In Nashville, flight activity also occurred in late February, late May, and early August (Fig. 3B). In Irwin, beetle flight activities occurred in early April and May (Fig. 3C). The peaks in activity across the sites coincided with average weekly temperatures of 15.5–26°C. In 2020, numbers of *X. crassiusculus* trapped across the sampling period varied significantly (Quitman: $F_{33, 33} = 9.94$, $P < 0.0001$; Nashville: $F_{33, 33} = 6.30$, $P < 0.0001$; Irwin: $F_{34, 34} = 2.50$, $P < 0.0001$). The onset of flight activities was observed during the weeks of 23 January at Nashville, 24 January at Quitman, and 14 February at Irwin with first activity occurring when mean weekly temperatures were between above 7.2 and 15.5°C. At Quitman, increased flight activities were first seen in mid-February and mid-March, with another slight peak in late May and mid-August (Fig. 3A). At Nashville, flight activity of *X. crassiusculus* was observed through mid-May (Fig. 3B). Flight activity of *X. crassiusculus* at Irwin was recorded through August (Fig. 3C). Peak flight activity occurred when mean weekly temperatures were at 12–18°C.

Phenology of *X. compactus* and *X. germanus* in Pecan Orchards

In 2019, the number of *X. compactus* captured across the sampling period were significantly different at Quitman and Nashville ($F_{31, 31} = 5.73$, $P < 0.0001$; Nashville: $F_{33, 33} = 1.57$, $P = 0.0388$). While captures of *X. germanus* differ significantly throughout the trapping period at Irwin ($F_{31, 31} = 2.62$, $P = 0.0045$). The first flight activities of *X. compactus* were observed on the week of 22 February in Quitman and Nashville; while that of *X. germanus* on the week of 20 February in Irwin. For both *X. compactus* and *X. germanus*, the first flight activities occurred at mean weekly temperatures of 15.5°C. At Quitman, high flight activity of *X. compactus* occurred in early to mid-May (Fig. 3A). At Nashville, *X. compactus* flight activity occurred in mid-March and once again in early August (Fig. 3B). At Irwin, highest captures of *X. germanus* was recorded in mid-March (Fig. 3C). The flight activities at all sites occurred at mean weekly temperatures ≥15.5°C. In 2020, the numbers of *X. compactus* captured across the sampling period varied significantly at Quitman and Irwin (Quitman: $F_{33, 33} = 20.44$, $P < 0.0001$; Irwin: $F_{34, 34} = 2.99$, $P = 0.00098$), but not in Nashville ($F_{33, 33} = 1.11$, $P = 0.3831$). In Quitman, *X. compactus* first became active in early February with flights observed in late March into early April and again late July into mid-August (Fig. 3A). At Irwin, *X. compactus* were first detected on the week of 11 March with high numbers in mid-March (Fig. 3C). At Nashville, the first flight activity was recorded on the week of 19 March with flight activity occurring in mid-March (Fig. 3B). Similar to the 2019 results, the first flight activities and increased flight activities—occurred at 15.5– 27°C mean weekly temperatures.

Discussion

This is an expanded survey of ambrosia beetles, with emphasis on *Xylosandrus* spp. impacting three different agricultural systems: woody ornamentals, tree fruits, and tree nuts in the southeastern United States. Moreover, this study provided an updated information on relative beetle abundance as well as *Xylosandrus* ambrosia beetle spatial distribution and phenological trends across multiple locations in Georgia. Findings from this study are crucial to developing monitoring and management strategies for these invasive beetles in the affected production systems.

Ambrosia Beetle Abundance

All of the beetle species found had previously been recorded in Georgia. The beetle species composition remained mostly the same in both years across the sites regardless of the cropping system; however, the relative beetle abundance varied among sites (within and across cropping systems). The main *Xylosandrus* species found in all the ornamental and tree fruit orchard sites were *X. crassiusculus* and *X. germanus*, which are both invasive species from Asia and are known pests of ornamental nurseries and fruit tree orchards (Ree and Knutson 1997, Ranger et al. 2016, CABI 2019, Gugliuzzo et al. 2021). In the two pecan orchards (Quitman and Nashville) located in the southern part of the state, the most common *Xylosandrus* species captured in traps were *X. crassiusculus* and *X. compactus*, both of which have been reported to attack pecan trees (Dixon et al. 2003, CABI 2019). *X. compactus* is also a pest of ornamental crops (Ranger et al. 2016) and coffee (Greco and Wright 2015). At the pecan orchard in Irwin, GA, *X. crassiusculus* and *X. compactus* were the most abundant in 2019, while *X. crassiusculus* and *X. germanus* were most common in 2020. The difference in the *Xylosandrus* beetle abundance at the various study locations could be attributed to the subtle differences in the climatic conditions (Urvois et al. 2021, Urvois et al. 2022) at the different regions in the state. For example, in the northern Blue Ridge, GA the yearly average temperate is 13.39°C with a yearly rainfall of 153.67 cm. In the middle of the state at Meansville, GA, the average temperature is 16.7°C with a yearly rainfall of 127.76 cm, while the southern location of Quitman, GA has a yearly temperature average of ~19°C and average 131.57 cm rainfall (USAFacts.Org; NCEI-NOAA.Org). Moreover, given the broad host range of these beetle species (Weber and McPherson 1983b; Ranger et al. 2016, 2021; Gugliuzzo et al. 2021), the tree compositions of the wooded areas adjacent to the nurseries and orchards, and the diversity of trees in the nurseries may affect the abundance of the beetle present in an area. The tree fruit and pecan orchards are mainly monoculture of the same crop in contrast to the higher diversity of plants found in tree nurseries. Also, the pecan orchards in the southern regions of the state are mainly surrounded by pine trees while more diverse vegetation can be found around the vicinity of cultivated areas in the northern regions of the state.

The other non-*Xylosandrus* Scolytine species found in this study have been present in North America for years (Rabaglia et al. 2006, Gandhi et al. 2009, Kambestad et al. 2017), such as *Hypothenemus* spp. and *Xyleborus* spp., however, these particular genera are not considered economically important to the three agricultural systems in this study. In addition, *Cnestus mutilatus*, a polyphagous species, were found at low numbers in tree fruit and pecan orchard sites in either of the two years. Continued monitoring of *C. mutilatus* in the future would be beneficial as it can potentially impact nurseries and orchards if its numbers would continue to increase (Olatinwo et al. 2014).

Trap Location Effect

Our findings demonstrated that in areas where *Xylosandrus* ambrosia beetle populations are high, beetle numbers are greater at the exterior areas of the nursery or orchard, along the wooded areas than 30 m inside the nursery or orchard interior. Similar findings were found with *X. germanus* being higher in numbers at the orchard-woods interface than within the apple orchard interior in New York (Agnello et al. 2017). The higher number of beetles in the exterior areas could be attributed to the presence of alternate hosts in these wooded areas. Werle et al. (2015) found that numbers of Scolytine beetles captured were greatest inside forest habitats adjacent to tree nurseries, and numbers decreased closer to the nursery edge and in the nursery interior. These findings highlight the importance of trap placement in monitoring and management of these beetles. Deploying traps along the edge of nurseries or orchard adjacent to wooded areas could provide a more sensitive and precise timing of activity particularly at the onset of spring flight activity when tree attacks are more common and damaging (Hudson and Mizell 1999, Oliver and Mannion 2001, Mizell et al. 2004). Werle et al. (2015) noted that a perimeter trapping program may help in protecting nursery trees from dispersing female populations from the forested or wooded areas.

Beetle Flight Activity and Temperature

Xylosandrus ambrosia beetle flight activity has previously been established to occur when the maximum temperature reaches 20°C (68°F; Reding et al. 2013). This current study showed that initial flight activity can occur when the average weekly temperature was 7.2°C, but sustained peak flight activities occurred at weekly temperatures 15.5°C or higher. Our findings concur with results from other studies indicating that trap captures, nor attacks have been observed before a maximum temperature of 20°C was reached, but that trap captures and/or attacks increase with consecutive days the temperature remained ≥20°C (Reding et al. 2013, Addesso et al. 2019, Gugliuzzo 2019). Used of accumulated degree days over absolute temperature to ascertain temperature effects on ambrosia beetle flight activity may also be used as shown by Reding et al. (2013) and Agnello et al. (2015) with *X. germ*anus using the base temperature of 10°C from 1 January. Degree day models using minimum temperature thresholds relating to initial flight activity of *X. crassiusculus* and *X. compactus* have not yet been established. Thus, we used absolute temperature values to examine the relationship with ambrosia beetle flight activities in this study.

Number of Generations

There were multiple peak flight activities observed for the three *Xylosandrus* ambrosia beetle species at high population sites, indicating bi- or multivoltine generations per year for these beetle species in Georgia. Additional studies on the number of broods produced per year by dissecting infested trees may be done to verify these trapping results. In other regions of the world, *X. crassiusculus* has been reported to have several overlapping generations in tropical areas (CABI 2019), Taiwan (Wu et al. 1978), Italy and Spain (Hoppe et al. 2020), and northern Brazil (de Souza et al. 2021). In the US, the number of generations for *X. crassiusculus* per year vary depending on the location indicating two generations per year in Tennessee (Oliver and Mannion 2001), and one generation per year in South Carolina (Kovach 1987). Similarly, *X. germanus* has shown to have one or two generations in a year in Europe (Galko et al. 2018) and two generations per year in Tennessee, Ohio, Illinois, North Carolina, and Virginia, and three generations in New Jersey, if conditions are favorable (Hoffman 1941, Weber and McPherson 1983a, Mannion and Oliver 2001, Gandhi et al. 2010, Reding et al. 2010, Ranger et al. 2016). As well, *X. compactus* has been reported to have overlapping generations per year in Uganda (Egonyu et al. 2016), five generations in Italy (Gugliuzzo et al. 2020) and although generations per year were difficult to establish in Florida, their active flight activity occurred from March to September (Ngoan et al. 1976). Having multiple generations in a year can be challenging in the management standpoint especially if vulnerable trees are present, thus, consistent monitoring of adult flight activities is crucial to time management interventions.

Phenology and Management

The initiation of sustained spring flight activities of *Xylosandurs* beetles across the different regions in Georgia overlapped but with distinct progression of activity. First flights occurred in early February through early March at the pecan orchards in south Georgia, while at the ornamental nurseries in middle Georgia, initial flights were recorded in late February to mid-March. Lastly, at the orchard sites in north GA, initial flights were observed in mid-March to late-March. This could be attributed to the onset of warmer temperatures (weekly average of 15.5°C or consecutive days with maximum temperature of 20°C) first occurring in the south and progressing into northern areas as the season continued. In Florida, Ngoan et al. (1976) noted that *X. germanus* emerges from overwintering diapause in late February. In Tennessee, Ohio, and Virginia, first emergence of *X. crassiusculus* and *X. germanus* occurs in late March to mid-April (Reding et al. 2010). While in New York, first sustained captures of *X. germanus* ranged from early – mid May (Agnello et al. 2017). Ambrosia beetle attacks are normally correlated with this period of initial sustained flights in the spring (Reding et al. 2013, Addesso et al. 2019). Thus, an ambrosia beetle trapping network involving Federal scientists, university researchers, and Extension specialists was recently initiated to monitor spring flight activities along the eastern coast of the United States to provide a real-time alert system for Extension agents and growers (AgPestMonitor: StopAB 2022).

In early spring, trees naturally produce ethanol during bud break, along with dealing with other potential stressors such as flooded conditions, which can cause ethanol levels to spike (Ranger et al. 2013, 2016). At around the same time that the bud break occurs, the increased spring temperatures cause the ambrosia beetles to emerge after overwintering and begin their search for increased ethanol within the stressed trees (Ranger et al. 2016). Since beetle activity is observed throughout the season and is influenced by the increased temperatures in spring, monitoring for beetle activity can provide precise timing for management interventions in ornamental nurseries and tree crop orchards. This is particularly important since most of the current management options available to growers are contact-based insecticides (Ranger et al. 2016, Reding and Ranger 2018, Brown et al. 2020). It should be noted, however, that given the propensity of these beetles to attack stressed and physiologically compromised trees, reducing tree stress should be the primary choice of infestation management.

In summary, this study provided an updated and expanded evidence of the relative abundance and phenology of ambrosia beetles, with emphasis on *Xylosandrus* spp, in three different production systems relevant to the Southeastern US agriculture. Results conferred with previous studies indicate that flight activity is temperature dependent and protracted throughout the growing season with distinct peaks implying multiple generations. Findings also highlighted the importance of trap placement, that *Xylosandrus* beetles can be reliably monitored by placing traps along wooded areas adjacent to nurseries and orchards. This is particularly crucial earlier in the season when susceptible trees are more vulnerable to infestations and thus, management interventions, if necessary, can be prioritized at the orchard or nursery borders. Continued monitoring of these problematic invasive beetle species on affected agricultural production systems is helpful in developing proactive measures for their sustainable management.

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Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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