

EVALUATING THE INFLUENCE OF ABIOTIC FACTORS ON PEST ABUNDANCE AND
BIOLOGICAL CONTROL OF THE BROWN MARMORATED STINK BUG
(*HALYOMORPHA HALYS*) IN MICHIGAN

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ABSTRACT

This thesis focuses on pest dynamics and pest control services of the invasive brown marmorated stink bug (*Halyomorpha halys*). The first chapter investigates the role of landscape complexity in the strength of pest suppression services by native parasitoids, and the establishment success of an exotic parasitoid, *Trissolcus japonicus*, for biological control of *H. halys*. To do this, ten sites were selected across the southwestern region of Michigan for their varying degrees of landscape complexity and suitable parasitoid habitat. In 2021, 2,000 *T. japonicus* adults were released at each site. Parasitoid releases were followed up with monitoring in 2021 and 2022 to assess *Tr. japonicus* establishment. The factors that contribute to the establishment of an introduced biological control agent were different from those affecting native parasitoid populations. Metrics associated with increased landscape complexity had no effect or a negative effect on parasitoid establishment, suggesting that the effect of landscape complexity on natural enemy populations cannot be generalized.

The second chapter explores environmental, temporal, and landscape factors that have contributed to population fluctuations of *H. halys* between years and growing regions. A span of four years (2018-2021) of *H. halys* monitoring data at 20 sites was used to compare annual population estimates to various weather variables to understand how seasonal weather changes may disrupt or promote population booms or busts. Our study confirms that weather is one of the factors driving differences in annual abundance of *H. halys*. We found that the susceptibility to weather conditions is dependent on life stage, but more research is needed to understand real-time population responses to weather events.

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CHAPTER 1: MULTI-SCALE LANDSCAPE EFFECTS ON PEST CONTROL SERVICES OF NATIVE AND EXOTIC (*TRISSOLCUS JAPONICUS*) PARASITOIDS OF *HALYOMORPHA HALYS* IN MICHIGAN

Introduction

The conservation of pest control services is vital to maintain long-term, environmentally, and financially sustainable agricultural operations. It has been estimated that natural enemies provide pest control services valued at \$13.6 billion annually in the United States (Losey & Vaughan, 2006). However, modern agricultural demands have pushed producers towards simplified landscapes in which single crops are grown on large swaths of land with a concurrent marginalization of habitats required to support beneficial insect populations like natural enemies (Chaplin-Kramer et al., 2011; Tscharntke et al., 2005).

Complex landscapes are proposed to support diverse and abundant natural enemy populations (Bianchi et al., 2006; Blitzer et al., 2012; Chaplin-Kramer et al., 2011; Rusch et al., 2016; Schmidt et al., 2005). Diversifying and increasing the availability of resources can expand the number of species supported in that landscape. In an agricultural ecosystem, landscape complexity can be evaluated by the prevalence of semi-natural habitats (e.g., woodlots, prairies, or wetlands) that provide undisturbed foraging and refuge for wildlife outside cropland (Bartual et al., 2019; Landis et al., 2000). Within cropland, crop diversity can provide structural and temporal resource variation for beneficial arthropods (Aguilera et al., 2020; Redlich et al., 2018a; Sirami et al., 2019). In theory, these landscape changes may facilitate improved pest suppression by promoting complementary pest control services from a diverse community of natural enemies, or by reducing antagonistic interactions between natural enemies competing in the same guild (Dainese et al., 2017; Perez-Alvarez et al., 2019; Schoch et al., 2022). However, the

observed relationship between landscape complexity and actual pest suppression services is inconsistent between studies and can vary in different systems.

One challenge is that complex landscapes may present hurdles that offset any potential benefit for natural enemies (Costamagna et al., 2004). For example, some microclimates created by crop diversity can inhibit natural enemy development, while structural variation may act as a dispersal barrier (Costamagna et al., 2004). Additionally, many ecological processes can override landscape-mediated effects. The association between higher trophic levels and landscape is difficult to separate from indirect interactions mediated by predator-prey or parasitoid-host dynamics (Chaplin-Kramer et al., 2011; Karp et al., 2018; Tscharrntke et al., 2016). Pest populations are subject to the same landscape contexts as their enemies; landscape complexity may benefit pest populations as much as their enemies, offsetting any benefit gained in natural enemy abundance and diversity (Blitzer et al., 2012; Midega et al., 2014). In addition, it is possible that changes in pest density due to improved habitat conditions may drive natural enemy abundance rather than the effect of landscape (Thies et al., 2005). In consequence, direct measurements of pest control services offer greater insight into the already mixed effects of landscape on ecosystem service enhancement (Chaplin-Kramer et al., 2011).

Perez-Alvarez et al. (2019) found that ecosystem service strength is dependent on landscape context. In their study, augmentative predator introductions decreased overall pest control services in simplified landscapes, but not in complex landscapes. They attribute this to simplified landscapes increasing interference competition and degrading the condition of preexisting pest control services (Perez-Alvarez et al., 2019). This study offers valuable insight into native predator-prey dynamics in cropland, however, further insight into whether these trends can be observed under invasive dynamics is needed. Gardiner et al. (2009) found that

biological control of an introduced crop pest, the soybean aphid (*Aphis glycines*), improved in more diverse landscapes. Furthermore, the presence of generalist predators was found to be greater in landscapes with more grassland and forest habitat (Gardiner et al., 2009). The natural enemies observed in this study were a mix of native and exotic predator species. In the introduced region of *A. glycines*, parasitoids were not a dominant component of the natural enemy community (Gardiner et al., 2009). Further insight into how these trends compare in pest suppression by parasitoid communities is of interest.

The introduction of exotic species can change the dynamics of native ecosystems and further complicate the relationships between landscape complexity and pest suppression. As invasive species become dominant on the landscape, they can displace native species that occupy similar niches and can interfere with existing host-parasitoid dynamics (Cornell & Hawkins, 1993). Native natural enemies, especially generalist species, will start to attack the novel exotic host (Cornell and Hawkins 1993). However, since they lack a co-evolutionary history with the invasive host, they will be less efficient and will exhibit lower attack rates than on their co-evolved native hosts (Cornell & Hawkins, 1993). Additionally, invasive pests may act as a sink for native parasitoids if they use these hosts to lay eggs, but their offspring fail to develop successfully due to the novelty of the host's immune response (Herlihy et al., 2016; Schlaepfer et al., 2005). As a result, preexisting pest control services may be hindered as natural enemy communities shift.

The arrival of a co-adapted natural enemy from the native range of the invasive species into the introduced range can help to restore some of the pest control services. Natural enemies may be introduced as part of classical biological control programs, or they may be co-introduced accidentally with the invasive host. Classical biological control programs most often introduce

highly host-specific parasitoids to control invasive insect herbivores (Heimpel & Cock, 2018; Van Driesche et al., 2020) but adventive parasitoids that arrive accidentally may be less host-specific and thus able to attack native species. This could further alter host-parasitoid dynamics and multi-trophic interactions in the introduced range. While biological control by co-evolved natural enemies have provided long-term suppression of over 200 invasive insect pests worldwide (Heimpel & Cock, 2018) about half of all species introductions failed to establish in North America and only about 27% result in any level of pest control (Van Driesche et al., 2020). Little is known of the relative importance of various biotic and abiotic factors that may mediate establishment and control success of introduced natural enemies and the roles landscape complexity may play.

Halyomorpha halys (Stål) (Heteroptera: Pentatomidae), the brown marmorated stink bug, is a polyphagous pest from Asia that was first detected in North America in 1996 and in Michigan in 2010 (Northeastern IPM Center, 2020; Hoebeke and Carter, 2003). Adventive populations of the co-evolved egg parasitoid, *Trissolcus japonicus* (Hymenoptera: Scellionidae) were first found in Michigan in 2018 and augmentative releases were conducted as part of this study to increase its distribution across Michigan. Field surveys from across the U.S. revealed that a diversity of native stink bug parasitoids of the genera *Anastatus*, *Telenomus*, *Trissolcus*, and *Ooencyrtus* have started parasitizing *H. halys* eggs at low levels (< 10%) (Abram et al., 2017; Dieckhoff et al., 2017; Herlihy et al., 2016). There is evidence that habitat characteristics influence the distribution of these native natural enemies and thus any pest control services they may be able to provide. For example, native *Trissolcus* species appear to prefer wooded habitats, while *Telenomus podisi* were more likely to be captured in soybean crop fields and *Anastatus* species were rarely found in agricultural settings (Herlihy et al., 2016). The exotic *Tr. japonicus*

has a much higher control potential because of its estimated 50-80% attack rate on *H. halys* eggs in the native range (Abram et al., 2017; Z. Q. Yang et al., 2009; Zhang et al., 2017). However, we do not know what factors may impact *Tr. japonicus* establishment success and population growth. As with most other parasitoids, *Tr. japonicus* requires non-crop habitats like woodlots and prairie strips that can provide nectar for nourishment and places for overwintering (McIntosh et al., 2020). Previous studies found that *Tr. japonicus*, similarly to native *Trissolcus* species, is more commonly found in natural areas like woodlots (Herlihy et al., 2016). Thus, the long-term population growth and persistence of *Tr. japonicus* may be affected similarly by landscape complexity as those of native parasitoids. However, different landscape patterns may be important for initial establishment of this novel species in a new range.

In this study we investigated the influence of landscape complexity at multiple spatial scales on pest control services that native natural enemies may provide against the invasive *H. halys* in Michigan. In addition, we assessed how landscape complexity may affect the establishment success of an adventive biological control agent, *Tr. japonicus* that followed *H. halys* to North America. We used parasitoid attack rates as a proxy for parasitoid abundance and establishment, and ultimately, to estimate the strength of pest suppression services. Our measurement of landscape complexity incorporated five metrics. The increased proportion of cropland and developed land (impervious surfaces and human-made structures) was associated with less complex landscapes, while higher values of forest cover, semi-natural habitat, and Shannon's Diversity Index of landscape diversity, were associated with more complex landscapes.

Materials and Methods

Site Selection

We selected 10 agricultural sites across the southwestern region of Michigan to evaluate how landscape complexity influences pest suppression of the invasive *H. halys* by native and exotic (*Tr. japonicus*) parasitoids (Fig. 1.1). This region had been surveyed in the year prior to confirm abundant host density and the absence of *Tr. japonicus* (unpublished data). The southwest region of Michigan is characterized by crops such as apples, grapes, pears, and peaches, making it particularly vulnerable to *H. halys* infestations. Sites with known populations of the target host, *H. halys*, were selected for their varying degrees of landscape complexity and suitable parasitoid habitat (the presence of woodlots and nectar resources).

Parasitoid Rearing

We reared a colony of *Tr. japonicus*, for release on a mixture of frozen (stored at -80°C) and fresh ($<72\text{ h}$) *H. halys* egg masses. Groups of 15 mixed-sex adults were aspirated into 10-dram clear plastic vials (Thornton Plastic Co., Salt Lake City, UT, USA) with three *H. halys* egg masses and honey on the lid for nutrient provisions. The parasitoids were left to parasitize the egg masses for 5 days in an incubator at $20 \pm 2^{\circ}\text{C}$, 65-70% RH, and a photoperiod of 16:8 (L:D). After 5 days, the adult parasitoids were removed and transferred into empty vials with honey and placed in a separate incubator at $10 \pm 2^{\circ}\text{C}$. This procedure lowers metabolism and prolongs life of adult parasitoids without apparent adverse fitness effects (Linder et al., 2022). Parasitized egg masses were left in the incubator at $20 \pm 2^{\circ}\text{C}$ and checked daily for parasitoid emergences between days 10 and 25. Newly emerging parasitoids were either used to start the next generation as described above or placed at $10 \pm 2^{\circ}\text{C}$ until release. For the field releases a mix of

freshly emerged and incubated adult parasitoids were used, where over 75% of released parasitoids were freshly emerged.

Host Rearing

Halyomorpha halys egg masses used for parasitoid rearing and monitoring were obtained either from our laboratory colony or the New Jersey Department of Agriculture Phillip Alampi Beneficial Insect Rearing Laboratory. Egg masses and, upon hatching, first instars were placed in 60 ml clear plastic cups (Gordon Food Service) and provided with a moistened dental wick and organic green bean. When second instars emerged, individuals were transferred to 250 ml clear plastic containers (Ziplock) and provided with dental wicks in 60 ml cups filled with water and a mixture of organic green beans, carrots, bell peppers, snap peas, apples, peanuts, and sunflower seeds. The food in the containers was changed every other day to prevent mold growth, with a complete container change once per week. Populations were kept at densities of about 30 individuals per container and maintained this way until they fully developed into adults. Adults were transferred out of containers and into small mesh cages (Rest Cloud) (30 x 30 x 60 cm) of approximately 50 mixed-sex individuals. Cages of adults were supplied with two potted green bean plants and crumpled paper towels to encourage oviposition on these surfaces. Adults were fed the same diet as 2nd-5th instars. Food was removed and replaced every other day, with a complete cage change once per week. All life stages were kept in incubators set to 25 ± 2 °C, 65-70% RH, and a photoperiod of 16:8 (L:D). The adult *H. halys* colony was checked daily for egg production. Any eggs <72 hours old were collected and either frozen at -80 °C for later use, turned over to continue rearing, or used for parasitoid monitoring or rearing.

Parasitoid Release

In 2021, we released 2,000 *Tr. japonicus* parasitoids at each of the 10 sites, for a total of 20,000. The release date was determined according to growing degree day models to synchronize *Tr. japonicus* releases with peak *H. halys* oviposition. *Halyomorpha halys* oviposition is estimated to peak between 460 and 734 growing degree days based on models for Geneva, New York, using a 14.17 °C base temperature (Nielsen et al., 2016). In 2021, the southwest region of Michigan fell within this peak range between June 13 to July 6. Sites received the first release of 1,000 parasitoids on June 18 and the second release of an additional 1,000 on July 9.

On the day prior to release, parasitoids were counted and aspirated into 292 ml clear plastic cups at 1,000 adults/cup. Cups were covered with mesh tops for ventilation. On the release day, parasitoids were removed from cold storage and transported to sites. At the site, a suitable woodlot along the edge of cropland was identified. Woodlots varied in size; all were at least 10 acres of continuous wooded habitat with most sites exceeding 50-acres of continuous habitat. All woodlots in our study were dominated by deciduous trees, like Oak (*Quercus* spp.), Maples (*Acer* spp.), Beech (*Fagus* spp.), Sassafras (*Sassafras albidum*) and Aspen (*Populus* spp.). The tree lines where parasitoid monitoring took place at each site were frequently dominated by aggressive native and non-native species like grape (*Vitis* spp.) and tree-of-heaven (*Ailanthus altissima*). Parasitoids were released ten meters into the woodlot by holding the cup into the air and allowing parasitoids to fly off.

Parasitoid Monitoring

Trissolcus japonicus establishment and native stink bug parasitoid communities were monitored using *H. halys* sentinel egg masses the same year (2021) and one year following the parasitoid releases (2022). In 2021, monitoring began one week after release, the week of June

23rd. In 2022, monitoring began the week of June 20th. Twenty sentinel egg masses were deployed at each site four times (20 egg masses x 10 sites x 4 weeks = 800) between June and August in two-week intervals for a total of 800 egg masses each year (Table 1). In 2021, an equal portion of fresh (<72 h old) and frozen (-80 °C) egg masses were used at each date and site for monitoring. In 2022, all sentinel eggs were frozen.

In both years, pairs of egg masses (fresh and frozen (2021), or both frozen (2022)) were glued (Elmer's extra strength non-toxic) to the underside of adjacent leaves, approximately two meters from the ground. Ten sets of egg mass pairs were spaced 10 m apart, across a 90 m stretch of the woodlot in which the *Tr. japonicus* release took place. In total, each site received 20 egg masses for each monitoring week. The location of the egg mass pairs was marked with flagging tape. After 48 hours in the field, egg masses were retrieved and placed in an incubator at 20 ± 2 °C, 65-70% RH, and a photoperiod of 16:8 (L:D). Emerging parasitoids were counted and monitored for 10 weeks. They were kept in 90% ethanol and sent to the Florida Department of Agriculture for identification.

Landscape Analysis

We assessed different landscape metrics using a raster analysis of multiple fixed buffer distances around each release spot. Land cover data for both monitoring years was obtained from the USDA's National Agricultural Statistics Service (NASS) CropScape 2021 data layer. Shapefiles of each site were created, and three fixed buffer distances (100 m, 250 m, 500 m) were generated around the coordinates of each parasitoid release. We selected these buffer distances as numerous studies have suggested the importance of smaller spatial scales on small-bodied organisms like hymenopteran parasitoids (Bosem Baillod et al., 2017; Jaworski et al.,

2022; Roland & Taylort, 1997). These buffer distances were clipped to the CropScape raster and used to calculate different landscape metrics.

Statistical Analysis

The attack rate of *H. halys* egg masses was calculated as the percentage of egg masses that yielded any parasitoids across the entire monitoring period. The attack rate of *Tr. japonicus* a year after release was used to estimate abundance and establishment. The attack rate of native stink bug parasitoids was used to estimate abundance and pest control pressure by native parasitoids. To understand the landscape composition at each site, we used R to calculate the proportion of each land cover type (cropland, developed land, forest cover, and semi-natural habitat) and the Shannon's Diversity Index measurement of landscape diversity. Cropland proportion was calculated as the percentage of land devoted to perennial and annual crops. The proportion of developed land was calculated as the percentage of land devoted to human-built structures and impervious surfaces. Higher values of these metrics were associated with reduced landscape complexity. On the other side of the spectrum, increased presence of forest cover, semi-natural habitat, and Shannon's Diversity Index measurement of landscape diversity were metrics that indicated more complex landscapes. Forest cover was calculated as the percentage of land devoted to forested land, including deciduous and coniferous cover. Semi-natural habitat was calculated as the percentage of land composed of wetland, grassland, and forested habitat. Lastly, landscape diversity (SHDi) measured the likelihood that a pixel will be of the same land cover class of an adjacent pixel.

All analyses were performed in R 4.2.2. To construct generalized linear mixed models, we used the lme4 package (Bates et al., 2015). Differences between parasitization of fresh and frozen egg masses were analyzed using a generalized linear mixed model (GLMM) with a

binomial distribution (parasitoid emergence vs. no emergence) and logit link function. The egg mass type (fresh vs. frozen) was used as a fixed variable, while monitoring week and site were used as random variables. To evaluate whether the number of parasitoids emerged was influenced by egg mass type, we used a generalized linear mixed model with a Poisson distribution. The number of parasitoids emerged was the response variable, egg mass type was a fixed variable, and week and site were random variables.

To understand how landscape composition influenced *Tr. japonicus* establishment, we used a GLM with a binomial distribution (parasitoid emergence vs. no emergence). Each landscape metric was evaluated in a model independent from other landscape metrics to avoid collinearity issues that could interfere with the reliability of regression coefficients (S1). We used the proportion of egg masses that yielded *Tr. japonicus*, referred to as attack rate, as the response variable and landscape metrics as fixed variables. This analysis was done separately for 2021 and 2022. A similar model was used with native parasitoid attack rate as the response variable to assess the influence of landscape composition on native stink bug pest control services.

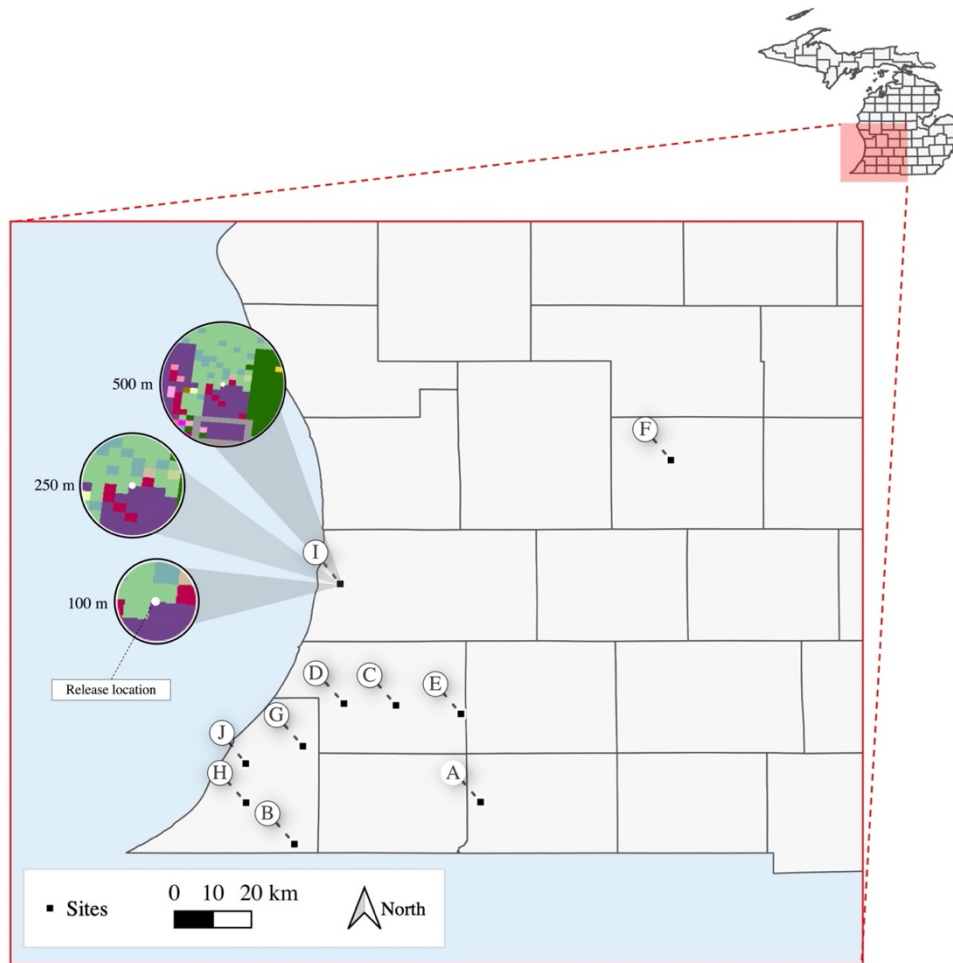


Figure 1.1. Black dots represent 10 study sites that received releases of the exotic parasitoid, *Tr. japonicus*, for biological control of *H. halys*. Sites were selected for their varying degrees of landscape complexity and known populations of *H. halys*. Landscape metrics were obtained for each site at three spatial scales (100 m, 250 m, 500 m) as shown for site “I”. Landscape metrics were calculated through a raster analysis of the USDA’s National Agricultural Statistics Service (NASS) CropScape 2021 data layer.

Results

Monitoring (2021)

Trissolcus japonicus was captured at four out of the 10 sites in the first- and second-weeks following release in 2021 (Fig 1.2 & 1.3). Eleven sentinel egg masses were parasitized by *Tr. japonicus* yielding 136 total parasitoids that constituted 18% of all emerging parasitoids. Five native parasitoid species/genera parasitized the *H. halys* sentinel eggs: *Trissolcus brochymenae*, *Tr. euschisti*, *Te. podisi*, *Anastatus* spp., and *Ooencyrtus* spp.. Parasitoid emergences were highest for the two congeneric native species of *Tr. japonicus*, with 207 *Tr. euschisti* and 189 *Tr. brochymenae* accounting for 29% and 26% of the total emerging parasitoids, respectively. The other three native species (*Te. podisi*, *Anastatus* spp., and *Ooencyrtus* spp.) together accounted for the remaining 26% of parasitoids that emerged. Significantly more *Tr. euschisti* adults emerged from frozen (n=204) than fresh (n=3) egg masses ($p=0.0001$) and were more likely to parasitize frozen egg masses in general ($X^2=14.54$, $Df=1$, $p=0.0001$) (Fig. 1.4B). *Trissolcus brochymenae* exhibited a similar pattern with a strong preference to parasitizing frozen egg masses over fresh ($X^2=14.96$, $Df=1$, $p=0.001$); additionally, *Tr. brochymenae* were much more successful emerging from frozen (n=183) egg masses than fresh (n=6) ($p=0.053$) (Fig 1.3C). Conversely, another native parasitoid, *Anastatus* sp., was more successful at developing in fresh (n=82) than in frozen (n=5) egg masses ($p=0.097$) (Fig. 1.3D). However, attack rates of frozen and fresh eggs masses were similar for *Anastatus* spp.. ($X^2=2.93$, $Df=1$, $p=0.0872$). *Telenomus podisi* ($p=0.29$) and *Ooencyrtus* spp. ($p=0.16$) yielded similar parasitoid emergences on fresh and frozen egg masses in 2021 (Fig. 1.4A & 1.4E).

Native parasitoids attacked 74 out of 702 retrieved sentinel egg masses, yielding an attack rate of 11% in 2021. Attack rates by native parasitoids were as high as 21% of sentinel egg

masses at one site (F – see Table 1.2), and as low as 0% at another site (D). *Trissolcus japonicus*, in the weeks following release, exhibited a 2% attack rate on sentinel egg masses, with only 11 sentinel egg masses yielding any parasitoids. Attack rates by *Tr. japonicus* were relatively low across all sites, with the highest recorded attack rate being 8% at one site (C), while seven other sites (A, B, D, F, G, H, and I) had a 0% attack rate. For all statistics on parasitoid attack rates in 2021 see Tables 1.1-1.2.

Monitoring (2022)

Overwintering success of *Tr. japonicus* was confirmed at five of the 10 release sites (Fig. 1.3). Attack rates by *Tr. japonicus* were relatively low across all sites, with the highest recorded attack rate being 7% at one site (G) and six sites (A, B, C, D, E, and H) exhibiting 0% attack rate. *Trissolcus japonicus* adults (n = 80) emerged from 9 sentinel egg masses representing 1.2 % attack rates between late June and early August. Native parasitoids attacked 166 out of 750 retrieved sentinel egg masses, yielding an attack rate of 22% in 2022. Attack rates by native parasitoids were as high as 43% of sentinel egg masses at one site (C), and as low as 8% at another site (D). For all statistics on parasitoid attack rates in 2022 see Tables 1.1-1.2.

The same species of native parasitoid species were found to parasitize *H. halys* sentinel eggs in 2021 than in 2022 (Fig. 1.2). All native species/genera had higher parasitism and emergence rates in 2022 compared to 2021. *Trissolcus euschisti* captures increased by nearly 300%, and *Tr. brochymenae* exhibited a 110% increase. Together, they accounted for 76% of native parasitoid captures. The remaining native parasitoid species exhibited increases between 120%-500% in emergence.

Landscape Composition

At 100 m, landscape diversity (SHDi) varied between 0.80 (site G) and 1.67 (site C) across sites. At the same spatial scale, all sites had some proportion of forest cover and semi-natural habitat, with the lowest proportions being 17% and 20% of the land, respectively, both at one of the sites (site H). Semi-natural habitat alone dominated the landscape of one site (site A) covering 79% of the 100 m buffer distance. Forest cover was as high as 51% (site E). The proportion of cropland at this scale varied greatly between sites, with some values being as high as 80% (site H) and as low as 12% (site A). Developed land was overall the least dominant landcover type at this scale, with the highest proportion being 22% (site C), and most sites (B, D, E, F, G, H, I) having no developed land within this buffer distance.

At 250 m, landscape diversity (SHDi) values varied between 1.45 (site H) and 2.37 (site A). Forest cover dominance diminished compared to 100 m, with the minimum observed value being 14% forest cover (site A) and most others (site C, D, E, F, G, H, I, J) falling between 20%-30% forest cover. The proportion of semi-natural habitat remained high at 250 m, with the highest proportion being 63% (site B) of landcover and the lowest proportion being 28% (site E). Cropland was once again a dominant landcover type at most sites within this spatial scale, with the highest calculated value being 73% cropland (site E). The lowest proportion of cropland across sites was 33% (site A). Within a 250 m buffer distance, developed land was non-existent at most sites (site B, D, E, G, H, I). The highest recorded proportion of developed land across sites was 15% of the land cover (site C).

At 500 m, landscape diversity (SHDi) values varied between 1.88 (site F) and 2.41 (site A). Forest cover was less than 20% at half of the study sites, with some sites possessing larger values of 45% (site B) and 41% (site F) forest cover. The proportion of semi-natural habitat at

this spatial scale was as low as 24% (site G) and as high as 57% (site J). Cropland remained high at many sites, with most sites (site C, D, E, G, H, I) being composed of more than 50% cropland. The proportion of developed land increased at this spatial scale for many sites. However, it remained low compared to other metrics, with the highest proportion being 12% (site J) and the smallest proportion being 0.2% (site I). For a summary of all landscape metrics, see Table 1.3.

Landscape Effects on Native Parasitoid Attack Rates of an Invasive Host

In 2021, no significant relationships were seen with native parasitoid attack rates and the proportion of semi-natural habitat, cropland, or developed land (all p – values > 0.05) (Fig. 1.5 & 1.6). In the same year, native parasitoid attack rates were negatively correlated with increased landscape diversity (SHDi), but only at the largest spatial scale included in our study, 500 m (Estimate=0.06, SE=0.01, $p=4.2e-07$) ($R^2=0.46$). Also in 2021, native parasitoid attack rates were higher at sites that had greater proportions of forest cover at 100 m (Estimate=0.02, SE=0.0098, $p=0.038$) ($R^2=0.11$).

In 2022, the proportion of developed land was positively correlated with attack rates of native species at 100 m (Estimate=0.06, SE=0.01, $p=4.2e-07$) ($R^2=0.46$), 250 m (Estimate=0.08, SE=0.014, $p=4.7e-08$) ($R^2=0.55$), and 500 m (Estimate=0.06, SE=0.03, $p=0.026$) ($R^2=0.10$) (Fig. 1.6). Native parasitoid attack rates were negatively correlated with cropland percentage at 100 m (Estimate=-0.02, SE=0.05, $p=2.56e-06$) ($R^2=0.45$), 250 m (Estimate=-0.023, SE=0.01, $p=0.0001$) ($R^2=0.28$), and 500 m (Estimate=-0.02, SE=0.007, $p=0.003$) ($R^2=0.16$) (Fig. 1.6). High proportions of semi-natural habitat were positively associated with higher native parasitoid attack rates at 100 m (Estimate=0.02, SE=0.006, $p=0.0008$) ($R^2=0.22$), 250 m (Estimate=0.01, SE=0.007, $p=0.046$) ($R^2=0.08$), and 500 m (Estimate=0.02, SE=0.007, $p=0.015$) ($R^2=0.11$) (Fig.

1.6). In 2022, landscape diversity (SHDi) at 250 m was positively associated with native parasitoid attack rates (Estimate=0.93, SE=0.32, $p=0.003$) ($R^2=0.16$

Trissolcus japonicus Establishment

One-year post-release (2022), *Tr. japonicus* establishment was negatively associated with increased landscape diversity (SHDi) (Estimate=-3.91, SE=1.32, $p=0.003$) (Fig. 1.8). This interaction was only significant at 100 m and explained 49% of the variance in the data (Fig.

1.7). The proportion of forest cover at 100 m was positively associated with *Tr. japonicus* establishment (Estimate=0.06, SE=0.03, $p=0.05$), this interaction explained 21% of the variance in the data. The final metric associated with increased landscape complexity, semi-natural habitat, and one of the metrics associated with decreased landscape complexity, cropland, demonstrated no significant correlation with *Tr. japonicus* establishment (all p – values > 0.05). Lastly, the proportion of developed land was positively associated with *Tr. japonicus* establishment at 500 m only (Estimate=0.37, SE=0.14, $p=0.008$).

Table 1.1. Overview of native and introduced stink bug parasitoid monitoring efforts across ten sites in Michigan in 2021 and 2022.

Year	2021		2022
Sentinel Egg Mass Type	Frozen	Fresh	Frozen
Number Deployed	400	400	800
Number Retrieved	353	349	750
Egg Masses Parasitized	54	31	175
Attack Rate	15.3%	8.9%	23.3%
Number of Emerging Parasitoids	543	240	1717
Number of Parasitoid Species	6	6	6

Table 1.2. Summary statistics demonstrating differences in parasitoid emergences between sites (A-J) in 2021 and 2022. Egg attack rate was calculated by dividing parasitoid abundance (n) by the product of the total number of egg masses collected at a site multiplied by 28 (the mean number of individual eggs in an *H. halys* egg mass). Attack rate was calculated by dividing the number of egg masses that yielded any parasitoids by the total number of egg masses collected at a site.

	Mean # of Parasitoids Emerged		Parasitoid Abundance		Native Parasitoid Attack Rate		<i>Trissolcus japonicus</i> Attack Rate	
Site	2021	2022	2021	2022	2021	2022	2021	2022
A	0.92 ± 3.79	2.73 ± 6.13	67	213	8%	27%	0%	0%
B	0.77 ± 3.19	1.38 ± 4.17	58	109	9%	26%	0%	0%
C	2.81 ± 6.43	4.12 ± 6.65	211	350	19%	43%	8%	0%
D	0.00 ± 0.00	1.32 ± 4.96	0	104	0%	8%	0%	0%
E	2.38 ± 6.16	0.85 ± 2.46	155	63	20%	16%	5%	0%
F	1.56 ± 4.10	3.21 ± 6.64	114	247	21%	36%	0%	1%
G	0.20 ± 1.19	1.00 ± 3.74	15	83	6%	13%	0%	7%
H	0.80 ± 2.97	1.20 ± 4.16	66	95	10%	12%	0%	0%
I	0.75 ± 3.35	1.82 ± 5.55	58	144	6%	14%	0%	1%
J	0.70 ± 2.90	2.04 ± 4.59	39	141	5%	28%	3%	3%

Table 1.3. Landscape metric values for 10 sites (A-J) calculated in R using a raster analysis of the 2021 CropScope data layer at three fixed buffer distances (100 m, 250 m, 500 m).

A. 100 m					
Site	Landscape Diversity (SHDi)	Forest Cover (%)	Semi-Natural Habitat (%)	Cropland (%)	Developed (%)
A	1.58	26.47	79.41	11.76	8.82
B	1.30	50.00	50.00	50.00	0.00
C	1.67	25.00	46.88	31.25	21.88
D	1.59	21.88	28.13	71.88	0.00
E	1.41	51.43	57.14	42.86	0.00
F	0.96	47.06	58.82	41.18	0.00
G	0.80	51.43	54.29	45.71	0.00
H	1.14	17.14	20.00	80.00	0.00
I	1.53	33.33	52.78	47.22	0.00
J	1.35	29.41	64.71	29.41	5.88
B. 250 m					
Site	Landscape Diversity (SHDi)	Forest Cover (%)	Semi-Natural Habitat (%)	Cropland (%)	Developed (%)
A	2.37	13.62	57.28	33.33	9.39
B	1.52	53.02	63.26	36.74	0.00
C	2.09	20.66	36.15	49.30	14.55
D	1.95	24.77	28.50	71.50	0.00
E	1.91	22.48	27.52	72.48	0.00
F	1.77	28.64	36.62	59.15	4.23
G	1.79	30.23	34.42	65.58	0.00
H	1.45	23.72	33.49	66.51	0.00
I	1.71	37.04	54.63	45.37	0.00
J	1.97	30.23	53.02	32.56	14.42
C. 500 m					
Site	Landscape Diversity (SHDi)	Forest Cover (%)	Semi-Natural Habitat (%)	Cropland (%)	Developed (%)
A	2.41	16.20	48.95	45.34	5.71
B	2.03	45.08	57.61	34.19	8.20
C	2.09	15.21	30.78	61.21	8.01
D	2.21	33.29	39.35	56.69	3.96
E	2.21	14.04	20.70	72.05	7.25
F	1.88	40.81	48.14	45.23	6.63
G	2.08	20.35	23.60	65.00	11.40
H	2.00	18.53	31.82	62.12	6.06
I	2.26	23.55	43.27	56.50	0.23
J	2.15	16.28	57.44	30.81	11.74

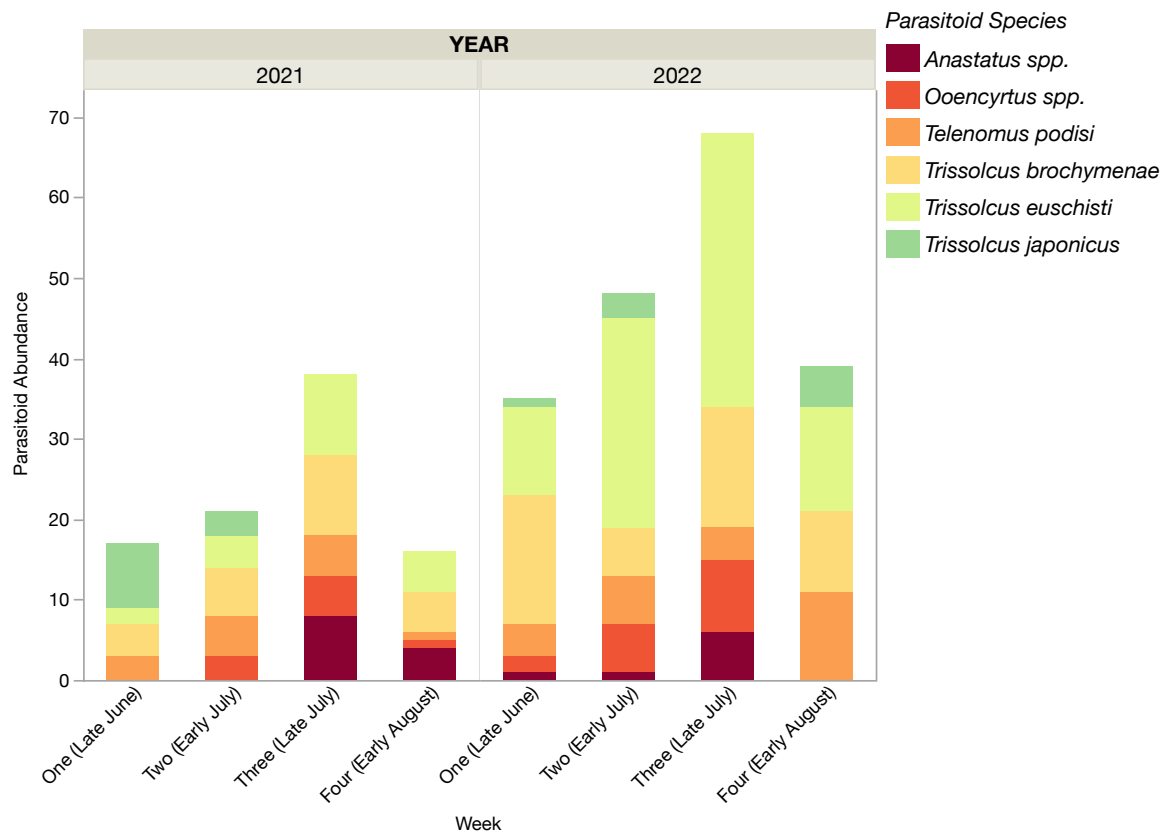


Figure 1.2. Parasitoid abundance of *Tr. japonicus* and native parasitoid species during the four weeks monitoring period in 2021 and 2022.

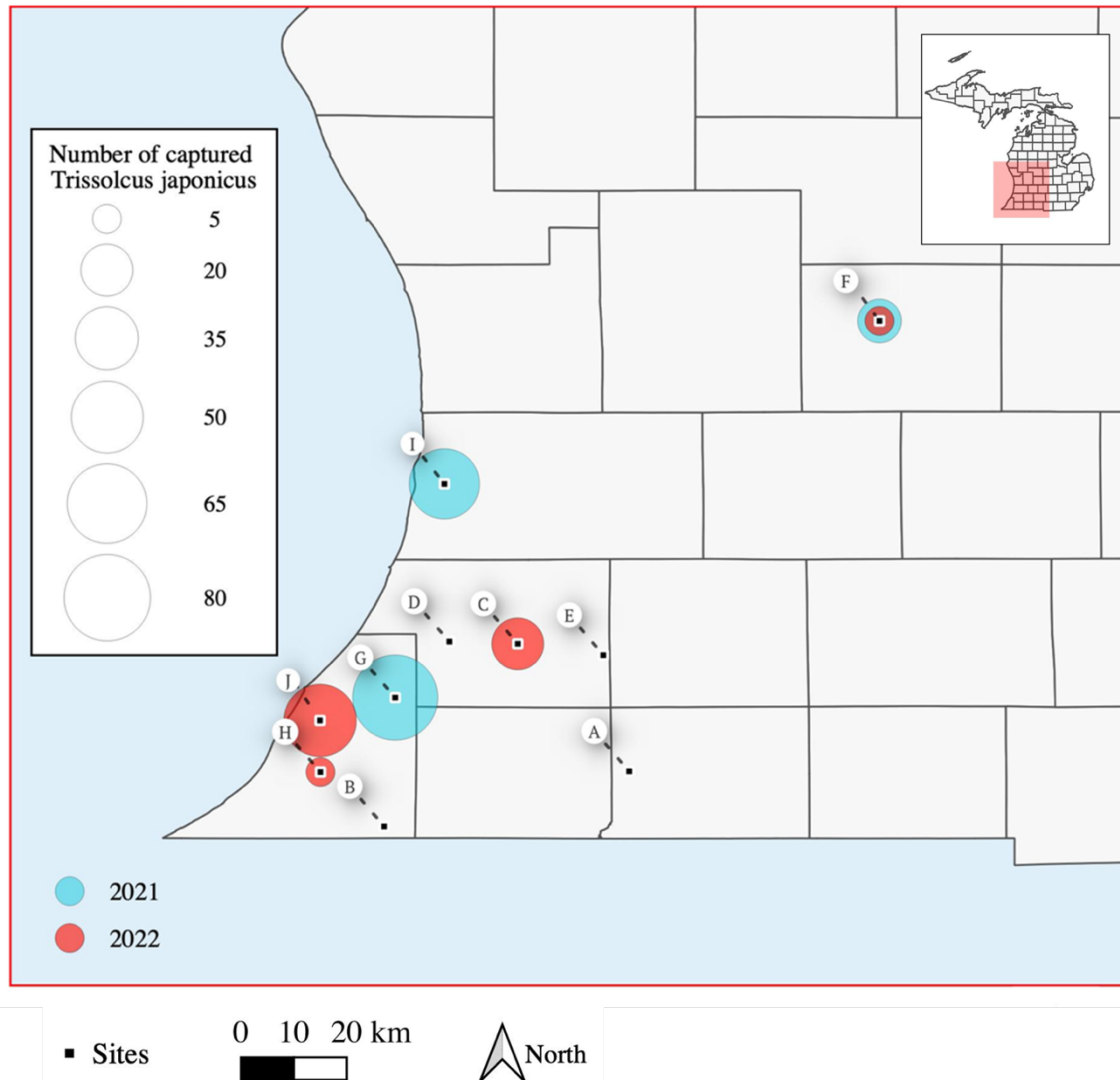


Figure 1.3. The number of *Tr. japonicus* captured in the release year, 2021 (blue), and the year following the release, 2022 (red). Captures in 2021 indicate post-release summer activity, but do not demonstrate establishment. Captures in 2022 suggest overwintering success.

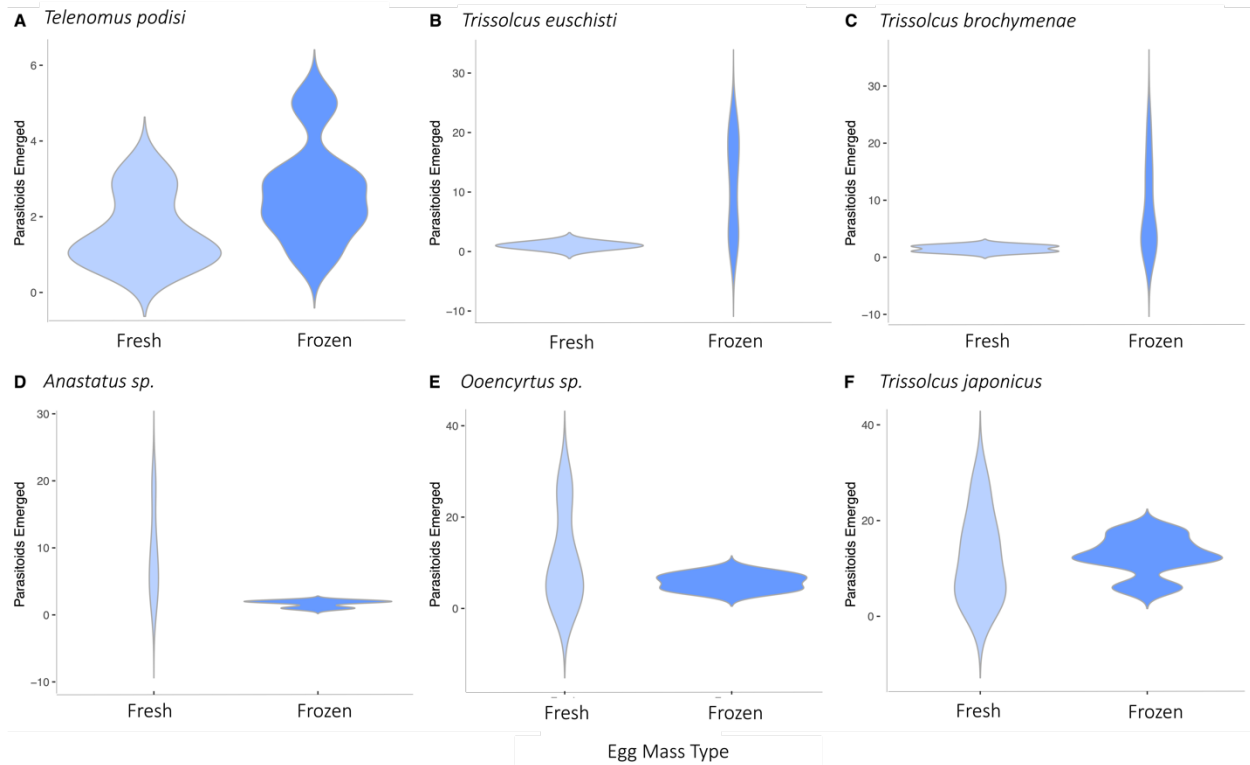


Figure 1.4. Differences in the distribution of values of parasitoid emergences by egg mass type and species. Fresh and frozen egg masses represent sentinel eggs deployed in 2021.

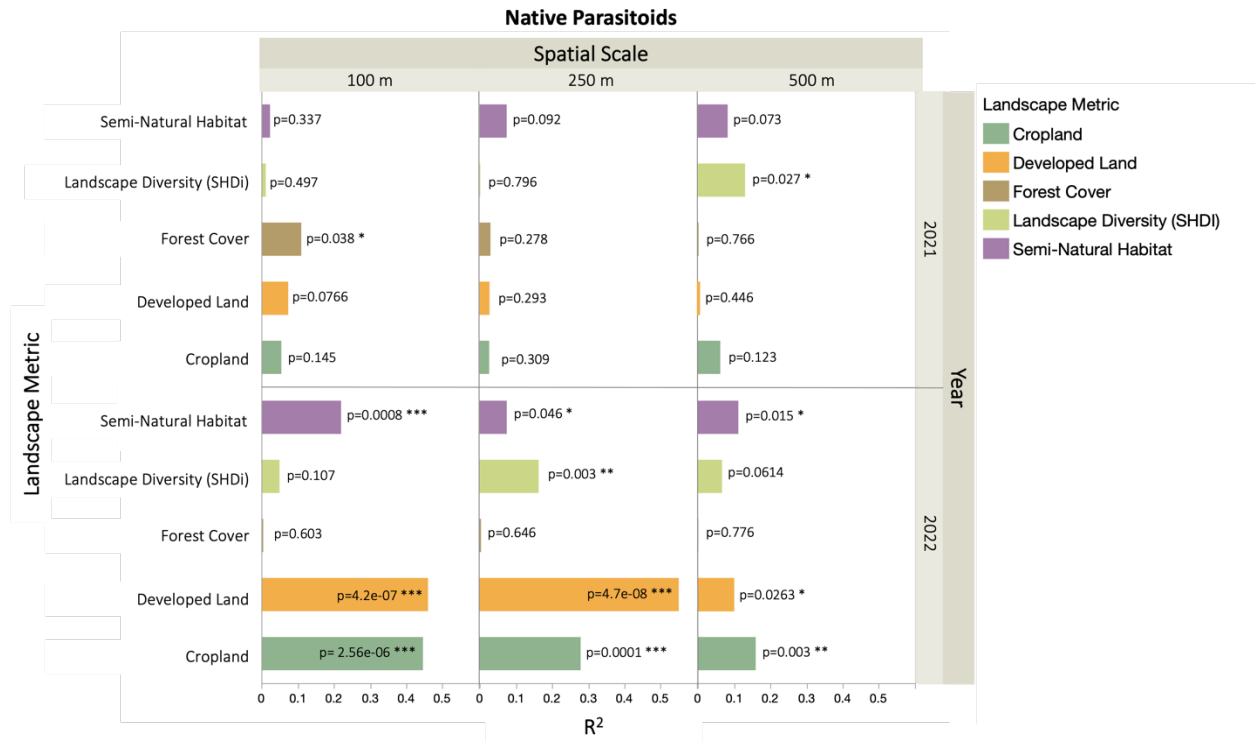


Figure 1.5. The proportion of variance (R^2) that can be explained by each landscape metric's influence on native parasitoid attack rates in 2021 and 2022 at three spatial scales (100 m, 250 m, 500 m).

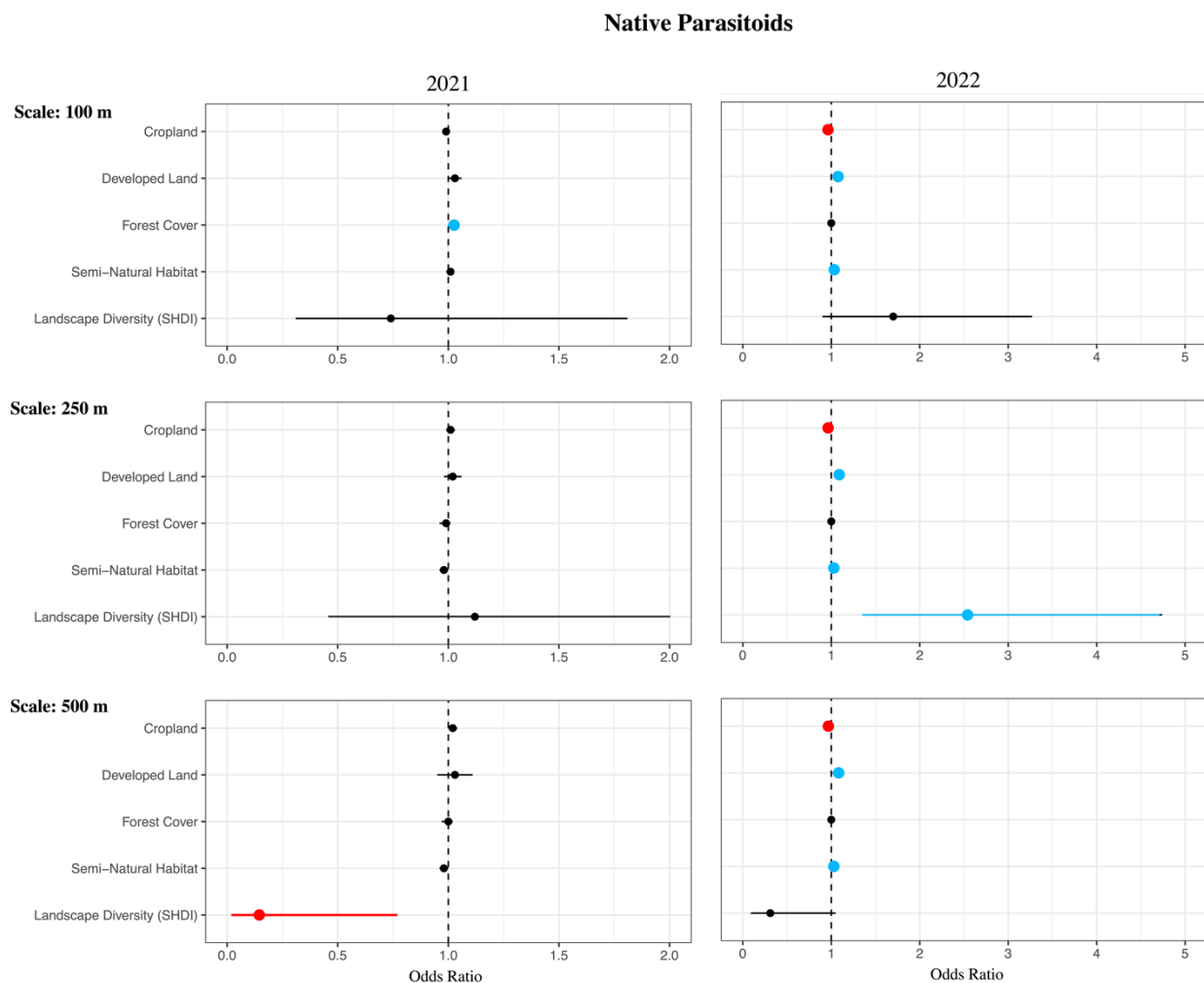


Figure 1.6. Forest plot of the effect of each landscape metric on native parasitoid attack rates in 2021 and 2022 at three spatial scales (100 m, 250 m, 500 m). Attack rates were calculated as the number of egg masses that yielded any parasitoids, divided by the total number of egg masses collected from the field. Odds ratio is a measurement of the strength of association. Values that fall past the dotted line indicate a positive association; values that fall before the dotted line indicate a negative association. Significant interactions are marked in color, where red indicates a negative association, and blue indicates a positive association.

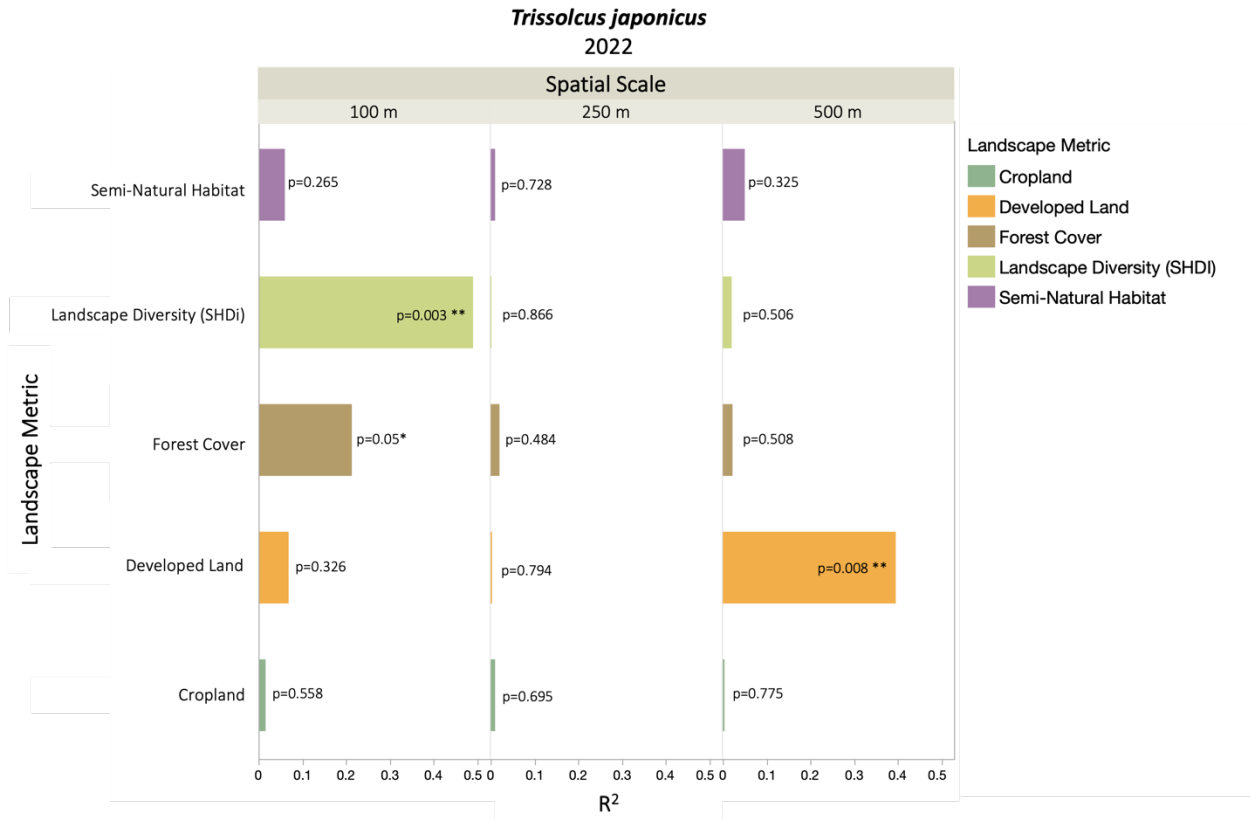


Figure 1.7. The proportion of variance (R^2) that can be explained by each landscape metric's influence on *Trissolcus japonicus* attack rates in 2022 at three spatial scales (100 m, 250 m, 500 m).

Trissolcus japonicus

2022

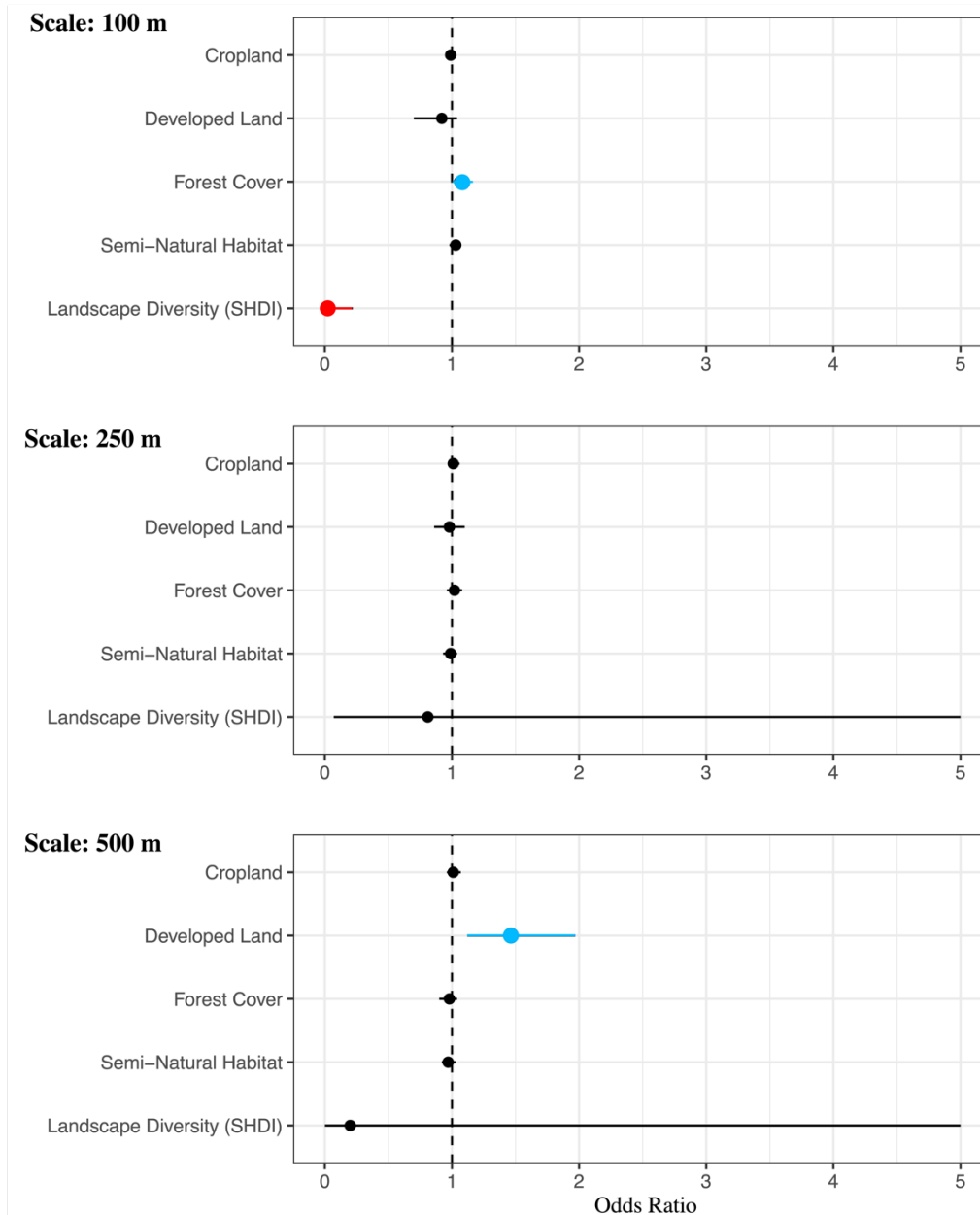


Figure 1.8. Forest plot of the effect of each landscape metric on *Tr. japonicus* attack rates in 2022 at three spatial scales (100 m, 250 m, 500 m). Attack rates were calculated as the number of egg masses that yielded any parasitoids, divided by the total number of egg masses collected from the field. Odds ratios is a measurement of the strength of association. Values that fall past the dotted line indicate a positive association; values that fall before the dotted line indicate a negative association. Significant interactions are marked in color, where red indicates a negative association, and blue indicates a positive association.

Discussion

Our results suggest that pest control of the invasive *H. halys* by native natural enemies and a newly introduced biological control agent, *Tr. japonicus*, is influenced by landscape complexity. We found that the establishment success of a biological control agent was surprisingly lower at sites that had higher values of landscape diversity (SHDi). This relationship was only significant at 100 m, which may be explained by previous research on the reduced dispersal capacity of small-bodied parasitoids. Negative correlation between landscape diversity and natural enemy abundance has been recorded in other studies, suggesting that the effect of landscape complexity on natural enemy populations cannot be generalized (Costamagna et al., 2004; Marino & Landis, 1996). In 2021, low native parasitoid captures limited our findings, however, in 2022, we found consistent trends across spatial scales. Increased proportions of semi-natural habitat at all spatial scales yielded higher native parasitoid attack rates. Contrary to our expectations a metric associated with less complex landscapes, increased proportions of developed land, also yielded higher native parasitoid attack rates at all spatial scales. The inconsistent trends between years and spatial scales are likely due to low capture rates of both native and exotic parasitoids. However, these unexpected findings support the importance of system-specific studies to understand how landscape may differentially influence species or communities (Ali et al., 2022; Redlich et al., 2018a, 2018b). Additional years of monitoring are needed to determine if our landscape metrics hold predictable effects on native and exotic parasitoid populations.

Landscape Effects on Native Parasitoid Pest Suppression of an Invasive Host

Native stink bug parasitoids were captured at much higher quantities than the biological control agent released in this study (Table 1.2). Native parasitoid captures increased by over

100% in 2022 compared to 2021 (Fig. 1.2). This increase can be partially attributed to the change in egg mass type used for monitoring (Fig. 1.4). Because of significant differences in parasitism success on fresh and frozen egg masses of certain native parasitoids, attack rates on frozen egg masses may not accurately represent realized pest suppression capacity of native parasitoids on *H. halys*. However, these data still provide an adequate estimation of native parasitism changes between landscape context, as all sites received the same egg mass treatment. With that, low native parasitoid captures yielded limited interactions with landscape in 2021. In 2022, we were able to see more clear trends and focus on these findings below.

Many studies demonstrate that increased semi-natural habitat harbors more diverse and abundant natural enemy populations, but few tie this relationship to enhanced biological control by parasitoids (Ali et al., 2022; Chaplin-Kramer et al., 2011; Hortal et al., 2009; Karp et al., 2018; Menalled et al., 1999). We found increased native parasitoid attack rates in 2022 at sites that had higher proportions of semi-natural habitat within a 100 m, 250 m, and 500 m radius of where we placed the sentinel eggs (Fig. 6). One possible explanation for this is that semi-natural habitat enables parasitoids to meet nutritional needs and find refuge as they seek out hosts. Semi-natural habitat provides refuge and resources like pollen and nectar for natural enemies as they perform pest control services. Additionally, diversifying the availability of resources, may reduce competition between parasitoids, enabling more diverse, productive populations to generate robust pest suppression services (Schoch et al., 2022; van Veen et al., 2006). This finding explained the greatest amount of variance in the data at the smallest spatial scale, 100 m, which may reflect the dispersal limitations of small-bodied parasitoids, suggesting the importance of local habitat's influence on pest suppression strength (Fig. 6). Roland & Taylor (1997) found attack rates of the forest tent caterpillar, *Malacosoma disstria*, by four species of parasitoids with

variable body sizes to respond to forest structure at spatial scales corresponding to their relative body sizes. Our findings support the importance of small-scale landscape considerations when seeking to enhance biological control by native natural enemies like small-bodied parasitoids. To maximize pest control services, incorporating semi-natural habitat may be most effective in the immediate area of pest concerns.

Our second metric associated with more complex landscapes was forest cover. In 2022, increased forest cover had no influence on native parasitoid attack rates on *H. halys* (Fig. 1.6). However, a positive relationship was seen in 2021 at the 100 m scale. Woodlands not only provide foraging resources but can also protect populations from pesticide exposure and provide overwintering habitat. The two native parasitoid species that were captured in the highest frequency at most sites, *Tr. brochymenae* and *Tr. euschisti* have been recorded to be more prevalent in wooded habitat, and thus, this trend may be skewed towards the habitat preferences of a few but not all parasitoid species (Herlihy et al., 2016). We emphasize the importance of investigation into system-specific management needs, as generalizations about landscape complexity may not hold up across species. This builds on previous research that suggests that landscape composition and its effect on natural enemy populations is system specific (Grab et al., 2018; Le et al., 2018; Perez-Alvarez et al., 2019; Roschewitz et al., 2005; Thies et al., 2005). The overall limited effect of forest cover in both years may be explained by our monitoring methods. All sites in our study held some degree of forest cover due to our choice to monitor populations on the edge of woodlots and thus, we use these wooded monitoring sites as the epicenter for our landscape analysis. In the future, finding sites that occur along a more extreme gradient may reveal more apparent ecological trends. Additionally, our findings that occur only at a 100 m buffer distance may be limited by the fact that the egg masses used for monitoring were spaced

up to 45 m from the release location and thus, the egg masses at the edge of this boundary may have significantly different landscape-contexts at 100 m than those more central to the release epicenter.

Our final metric associated with more complex landscapes was landscape diversity (SHDi). Unexpectedly, in 2021, high landscape diversity values at 500 m were associated with lower attack rates. In 2022, the opposite relationship was seen at a different spatial scale with high landscape diversity values at 250 m being associated with higher attack rates. The difference in results of multiple landscape metrics between years may be a consequence of changes in parasitoid community composition and abundance due to other factors not accounted for in this study. Additionally, it is possible that certain landscape-contexts may be advantageous under only specific conditions. Landscape diversity may indicate greater structural and temporal variation that may be advantageous under ideal conditions but may reflect increased disturbance or dispersal limitations under other conditions (Costamagna et al., 2004; Menalled et al., 2003). Undoubtedly, additional years of monitoring are needed to see which trends hold up over time.

Transitioning to metrics associated with less complex landscapes, in 2022, we found high proportions of cropland were correlated with lower pest control services by native parasitoids at all spatial scales included in this study (Fig. 1.6). This is in line with findings from other studies that suggest increasing the proportion of arable land reduces biological control services (Bosem Baillod et al., 2017; Grab et al., 2018; Letourneau et al., 2015; L. Yang et al., 2019). Increased cropland reduces non-crop habitat cover that provides food resources, refuge, and nesting/overwintering sites. The depletion of these vital resources is one possible explanation for the lower attack rates observed in our study. Another possible explanation is that increased cropland may be associated with increased disturbance through agricultural practices like broad-

spectrum pesticide application that may lead to lethal and sub-lethal impacts on highly susceptible parasitoids (Landis et al., 2000; Schmidt et al., 2005). Management differences, like pesticide-use, between sites was not incorporated into the study, but could explain this finding, as well as obscure any potential benefit natural habitat may provide to natural enemies. Lastly, while the high proportions of cropland had a negative effect on native parasitoid attack rates at all spatial scales, the lower the spatial scale, the more robust the effect cropland had on native parasitoids (Fig 1.6 & 1.7). This is in line with our other findings on semi-natural habitat that demonstrate the most predictive power at smaller spatial scales for some landscape metrics.

For our last metric associated the less complex landscapes, we found that the amount of developed land (impervious surfaces and human-made structures) at all spatial scales had a positive association with native natural enemy attack rates in 2022 (Fig. 1.6). This is a novel finding that may be system specific. Botias et al. (2017) found pesticide contamination risk lower in developed areas than in agricultural land for mobile insects. Thus, proximity to developments may offer native parasitoids refuge from pesticides' lethal and sublethal risks. Alternatively, the correlation may be an indirect product of pest density rather than a direct relationship between parasitoids and developed land. The host in our study, *H. halys*, overwinters in structures like houses, sheds, and warehouses. A higher proportion of developed land may offer more overwintering habitat for *H. halys*. Urban land use has been associated with increased densities of *H. halys* in New Jersey (Wallner et al., 2014). The high proportion of variation that the relationship between attack rates and the amount of developed land explains in our study may suggest pest density is a more significant contributing factor to parasitoid activity than the other landscape metrics evaluated in this study.

Trissolcus japonicus Establishment

In year one (2021), *Tr. japonicus* was only captured within 2 weeks of release indicating some summer activity (Fig. 1.2). In year two (2022), *Tr. japonicus* was captured at half of the release sites indicating overwintering success (Fig. 1.2). Captures occurred from late June to early August suggesting that established populations could provide pest control through the season. It is not surprising that *Tr. japonicus* capture rates were low just one year following release. Clearly, monitoring in subsequent years would improve our understanding of how well *Tr. japonicus* established, their contribution to managing *H. halys* populations and possible connections between landscape factors and its population growth.

High proportions of cropland were not found to affect *Tr. japonicus* establishment in our study. In a recent study by Falagiarda et al. (2023), *Tr. japonicus* and *H. halys* populations were more likely to be found at sites with higher proportions of perennial cropland and less semi-natural habitats. The observation between perennial cropland and *Tr. japonicus* populations may not have been found in our study as all sites were dominated by perennial crops. Our second metric associated with less complex landscapes, developed land, however, was found to positively affect *Tr. japonicus* establishment success. Increased proportions of developed land within a 500 m buffer distance from the release site was associated with *Tr. japonicus* establishment. This trend was seen with native parasitoid attack rates at multiple spatial scales, and once again may be a consequence of reduced pesticide risk, or a product of host density facilitated by increasing *H. halys* overwintering habitat (Botías et al., 2017). While *Tr. japonicus* can parasitize multiple native stink bug species, they demonstrate a strong preference for their co-evolved host, *H. halys* (Talamas et al., 2015; Zhang et al., 2017). Thus, *H. halys* density is

likely to be more influential for *Tr. japonicus* abundance than it is for native parasitoid populations.

Semi-natural habitat, one of the metrics associated with increased landscape complexity, demonstrated no significant effect on *Tr. japonicus* establishment. It is possible that additional years of monitoring could yield clearer results, or that differences between this metrics at sites did not contribute to establishment. Forest cover, however, was associated with *Tr. japonicus* establishment, but only at the smallest spatial scale in our study. Lowenstein et al. (2019) found that *Tr. japonicus* can disperse for up to 50 meters and they likely forage along the edge of woodland habitat. Expanded woodland habitat around the release site may enable *Tr. japonicus* dispersal and expand foraging opportunity to facilitate host-finding.

Lastly, our third metric associated with more complex landscapes, landscape diversity (SHDi), had an unexpected effect on establishment. We anticipated that increased landscape diversity (SHDi) would provide ample resources and reduce competition between native parasitoids and *Tr. japonicus*. However, we found that sites with higher values of landscape diversity (SHDi) at 100 m had significantly lower attack rates than sites with lower landscape diversity (SHDi) values. It is possible that diverse landscapes may benefit native parasitoid populations as they exist at stable population levels, however, minor fluctuations in habitat conditions at the release point could exert extreme bottleneck events that can limit establishment. Establishing exotic parasitoid populations like *Tr. japonicus* may be more sensitive to microclimate fluctuations or dispersal barriers associated with more complex landscapes (Costamagna et al., 2004). This has not been investigated in any known study but may be an area of future research to understand how release area may adversely impact establishing exotic biological control agents. For management considerations, this could emphasize the importance

of large or repetitive releases to limit the chance for poor establishment due to momentary unfavorable conditions during the time of release (Blackburn et al., 2015; Lockwood et al., 2005; Simberloff, 2009). Our results support that the relationship between landscape diversity (SHDi) and natural enemies cannot be assumed when predicting the success of a biological control agent.

Conclusions

We conclude that landscape is one of many factors influencing biological control of invasive pest species by affecting the establishment of newly released exotic biological control agents and attack rates of native natural enemies. Due to the importance of landscape diversity (SHDi) at 100 m on *Tr. japonicus* establishment, we suggest that release site selection is an important consideration in ensuring establishment success early on. Small-scale land composition and management differences may disproportionately affect establishing populations as they have yet to disperse and establish widely. Ensuring a release site provides ideal conditions unique to the habitat requirements of a biological control agent may be an essential consideration for those seeking to implement biocontrol for pest management. Our results and interpretations are constrained by the limited time since release. To understand the observed trends, additional years of monitoring of establishment and changes in population densities would be needed. While we expected to find a negative association with cropland, the positive association with developed land deviated from our expectations of developed land encroaching on natural habitat and thus diminishing parasitoid habitat quality. However, this relationship can be explained by a lowered risk of pesticide contamination. The observed associations between attack rates and land cover may be explained by differences between land management practices

and host densities rather than resource acquisition outside prey items. Future studies should consider factors that indirectly mediate interactions between parasitoids and landscape.

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CHAPTER 2: ABIOTIC FACTORS DRIVE REGIONAL AND ANNUAL VARIATION OF *HALYOMORPHA HALYS* POPULATIONS ACROSS MICHIGAN

Introduction

In ectotherms, including insects, population growth can largely depend on weather conditions. Temperature, precipitation, and relative humidity are known factors to impact insect development, fecundity, and survival (Farias et al., 2020; Skendžić et al., 2021). The range of ideal weather conditions is determined by developmental, physiological, and environmental limitations that can vary greatly between species and life stages. Beyond mean conditions, extreme weather events like drought, heat waves, heavy rainfall, and cold spells can serve as bottleneck events that severely disrupt populations (Smith, 2011). Native species phenological and physiological adaptations to the local environment can improve resilience to these conditions, while invasive species encounter novel climactic pressure that will determine their success in a given range (Liu et al., 2004). The theoretical global range of an invasive species is dependent on climate conditions that closely match the conditions of their native range (Liu et al., 2020; Thuiller et al., 2005). However, discrepancies in expected and realized introduced ranges are recorded (Liu et al., 2020). Adaptive responses by the invader can explain some of these differences (Prentis et al., 2008). Still, it is important to note the role of microclimatic conditions that may offer additional insight into such differences (Rebaudo et al., 2016). This is vital to improving our knowledge of the invasive capacity of a species and predicting the severity of outbreaks.

The invasive polyphagous pest, the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae), is hemimetabolous and goes through numerous critical development periods throughout the year, each exposed to unique vulnerabilities. *Halyomorpha*

halys poses a significant threat to agricultural industries nationwide, feeding on over 120 different crops, including field corn and soybean as well as high value specialty crops like apples, peaches, grapes, sweet corn, tomatoes, and edamame (Leskey et al., 2012; Nielsen & Hamilton, 2009a). Enhancing our understanding of the abiotic and biotic conditions that influence population abundance in their invaded range is critical to developing more effective pest management strategies and to have better predictive power of the timing of pest outbreaks. While many studies have investigated how temperature influences *H. halys* development and reproduction in lab-based settings, we have limited information on how temperature and other environmental variables may influence field populations (Nielsen et al., 2008, 2016). Beyond physiological interactions, weather can mediate interactions between a pest and its natural enemies, food availability, and disease prevalence among others (Brewer et al., 2022; Farias et al., 2020; Skendžić et al., 2021). Field-based studies could account for the complexity of weather-mediated interactions to further our understanding of factors affecting population abundance.

In the upper Mid-West and Northeast U.S., *H. halys* populations are estimated to be univoltine and take the entire growing season to complete their life cycle (Nielsen & Hamilton, 2009b). Adult stink bugs emerge from overwintering habitat in early spring as temperatures rise and day length increases but remain in reproductive diapause until the photoperiod reaches 12.7 hours (Nielsen et al., 2016). This period typically falls between mid-March and April in the Northeastern United States. Adult females coming out of diapause are reproductively immature and can take an estimated 148 growing degree days to finish ovarian development (McDougall et al., 2021; Nielsen et al., 2008, 2017). Reproductive diapause is terminated once the critical photoperiod reaches 13.0-13.5 hours (McDougall et al., 2021). Reproductively mature females

mate and oviposit egg masses on the underside of leaves (Takahashi 1930). Peak oviposition is estimated to occur between 460 and 734 growing degree days based on models for Geneva, New York, using 14.17 °C base temperatures (Nielsen et al., 2016).

Halyomorpha halys nymphs emerge from egg masses after approximately one week. Development can occur at temperatures as low as 14.17 °C and as high as 35.76 °C, but the optimal developmental range estimated for invasive North American populations is between 27-33 °C (Nielsen et al., 2008, 2016). Nymphs pass through five stadia that last, on average, one week (Takahashi 1930). This development period takes an estimated 538 growing degree days from egg to adult (Nielsen et al., 2008). The exposure to diapause-inducing cues in the second to fifth instar development period is critical to overwintering success and later reproductive development (Cira et al., 2018).

Diapause is induced in *H. halys* once the photoperiod reaches 12.7 hr (Nielsen et al., 2017). During this period, *H. halys* release an aggregation pheromone and seek out dry overwintering habitat like houses, sheds, rock outcroppings, or dead-standing trees (Lee et al. 2014, Watanabe et al. 2012). Reports from the mid-Atlantic demonstrate peak dispersal to overwintering sites to occur near the fall equinox (Bergh et al., 2017). *Halyomorpha halys* undergoes facultative diapause in which respiration and metabolic processes are suppressed (Watanabe et al. 1978). This is an advantageous adaptation to survive adverse abiotic conditions (Danks, 1987). In this state, *H. halys* relies on nutrient reserves built up in the growing season to sustain this period of inactivity (Funayama, 2012). These reserves are slowly depleted over the winter with remaining reserves quickly depleted in the spring as stink bugs emerge from diapause to disperse from overwintering habitats (Funayama, 2012, Skillman et al., 2018). In

their diapausing state, *H. halys* are more cold-tolerant than in their non-diapausing state; this is suggested to contribute to their success in temperate regions (Ciancio et al., 2021).

Halyomorpha halys was first recorded in Allentown, PA, in 1996, and has since established widely across 46 states in the United States, becoming a serious crop pest in the mid-Atlantic orchards in the early 2000s (StopBMSB.org, Hoebeke, 2003). In Michigan, populations of the pest were first recorded in 2010, slowly building up to become a nuisance pest in homes by 2015, and then becoming a sporadic or transient pest of orchards in some years and in some areas. While Michigan is considered a suitable ecoclimate for *H. halys*, we have observed interannual and regional variations in *H. halys* populations across the state that point to Michigan as being suboptimal for its development into a major pest (Kriticos et al., 2017).

In this chapter, I will explore environmental, temporal, and landscape factors that may have contributed to population fluctuations of *H. halys* between years and growing regions using a subset of data collected as part of a 9-year statewide monitoring effort in specialty crops. A span of four years (2018-2021) of *H. halys* monitoring data at 20 sites was used to compare annual population estimates to various weather variables to understand how seasonal weather changes may disrupt or promote population booms or busts. Our study hopes to disentangle microclimatic differences between sites, as well as broader patterns at the regional scale, to understand how weather, like temperature and precipitation, can affect pest outbreaks of *H. halys*.

Materials and Methods

Site and Weather Station Selection

Annual changes in *H. halys* abundance were monitored from 2018 to 2021 at 20 sites across Michigan's lower peninsula (Fig. 1). Most sites were orchards, with the primary crop

grown across all sites being apples. The minimum distance between monitoring sites was 1.6 km. Sites were grouped into four regions (Southeast, Southwest, Fruit Ridge, and Northwest) to analyze trends in regional patterns of *H. halys* abundance and to account for region-specific effects in our models. Each region hosted five monitoring sites (Table 1). Region distinctions were based on shared cultural and geographical factors between sites of proximity.

The monitoring sites in our study were categorized into one of four regions (Northwest, Fruit Ridge, Southwest, and Southeast) based on shared cultural and geographical features. Most Michigan specialty crops (i.e. fruits and vegetables) are grown in counties that border Lake Michigan, a large body of water that moderates local climate; the Northwest and Southwest regions benefit from this lake effect on local climate, but differ in the severity of their winters. The Fruit Ridge region of Michigan resides on a glacial esker which provides the soils and microclimates ideal for temperate fruit production and is where most commercial apple production occurs; the area is at a slightly greater elevation than most of southern Michigan at 800 m. The growing region of Southeast Michigan is embedded in the metro-Detroit area and is the most densely populated and developed area of Michigan whereas the other regions tend to be more rural, with more land devoted to agricultural use. Up until recently, the densest populations of *H. halys* associated with orchards has been in Southwest Michigan, likely due to an early influx of *H. halys* inadvertently moved by a homeowner from Pennsylvania when a shed containing overwintering individuals was transported to Stevensville, MI ca. 2009. However, the metro Detroit area is where the Midwest Invasive Species Network (MISIN) has received the most nuisance reports about *H. halys*.

Each site was assigned a weather station to analyze the effect of weather patterns and events on annual *H. halys* abundance trends. The distance between site and weather station did

not exceed 14.5 km. Several sites were clustered around a common weather station and shared weather data (Fig. 2.1).

Halyomorpha halys Collection

To measure *H. halys* abundance, we used traps deployed from mid-August to late October. Each site received one Rescue™ (Sterling International, Inc., Spokane, WA) or pyramid trap (AgBio Inc.) set up at the edge of the crop. Traps were baited with a two-part lure (Pherocon® BMSB Dual Lure for Brown Marmorated Stink Bug, Trécé Inc.). To monitor *H. halys* activity, we used a lure that mimics male aggregation pheromone to attract stink bugs as they seek out overwintering habitat; as a result, it is most effective later in the season, making it difficult to approximate early-season activity. Since the late growing season is when *H. halys* abundance is at its peak (Acebes-Doria et al. 2020) and when the lure is most effective, we use the trap totals in this period to estimate annual population abundance. This number also reflects the population that will overwinter and produce the next generation in the following spring.

Halyomorpha halys are estimated to be univoltine in Michigan; thus, we anticipate the end-of-the-season population totals, as adults enter diapause, to be an adequate proxy to annual population totals. Trap contents were emptied each week, and the number of *H. halys* nymphs and adults were recorded.

Data Analysis

Weekly trap totals were added up for each site to estimate annual *H. halys* abundance. This value was used to analyze the effect of regional and site-specific weather patterns and events on trends in *H. halys* abundance. Each year was separated into five time periods we hypothesized to have important implications for *H. halys* development based on previous studies and development models: early season (April 1st-May 31st), mid-season (June 1st-July 31st),

late season (August 1st-September 31st), entering diapause (September 23rd-Dec 20th) and overwintering (December 21st-March 31st) (Fig. 2.2.). The early season estimates when *H. halys* emerges from diapause and matures reproductively. Mid-season encompasses a period in which *H. halys* are actively reproducing, and instars begin emerging. Late season encompasses a period in which instars develop into adults. Additionally, we evaluated two periods we hypothesize to be critical to populations in the following season: entering diapause (September 23rd-Dec 20th) and overwintering (December 21st-March 31st). These periods were estimates for the change in day length that may induce hormonal changes in *H. halys* to trigger diapause and represent critical periods of seeking overwintering habitat and hibernating for the winter.

For each period, we use weather metrics derived from the MSU Enviroweather Data on Demand database to summarize temperature and precipitation averages and extremes from weather stations assigned to each site. Weather metrics were chosen to represent factors that may impact *H. halys* mortality and population growth during specific seasons and periods of development. In the early season, we evaluate the effect of average temperature (°C) and precipitation (mm), as well as the occurrence of frost events (<0 °C) and extreme precipitation (>25 mm in 24 h). In the mid-season, we evaluate the effect of average temperature and precipitation, as well as the occurrence of extreme heat events (>30 °C) and extreme precipitation (>25 mm in 24 h). In the late season, we evaluate the effect of average temperature and precipitation, as the occurrence of frost events (<0 °C) and extreme precipitation (>25 mm in 24 h). In all periods, we also look at the number of days where the min and max temperatures fall within the development threshold (>14 °C and <30 °C). For the period as they enter diapause, we look at average temperature, as well as the date of the earliest frost event and days that fall below extreme cold temperatures (<-15 °C). For the overwintering period, we look at average

temperature, as well as periods of abnormal warmth, and days that fall below extreme cold temperatures ($<-15^{\circ}\text{C}$).

To analyze these relationships, we used a linear mixed model with a square root transformation of our response variable, the total number of *H. halys* captured between August and October. All analyses were performed in R 4.2.2. To construct linear mixed models, we used the lme4 package (Bates et al., 2015). We ran separate models for each period and weather metric. Weather metrics were scaled and used as fixed variables. Year was incorporated as an interaction with the weather metric, while site nested within region were used as a random variable. To compare the fit models to a reduced model containing only random effects, we used the *anova* function.

Table 2.1. Coordinates of study sites and associated weather stations grouped by region.

Region	Site	Site Latitude	Site Longitude	Weather Station Name	Station Latitude	Station Longitude
Northwest	A	44.88200	-86.67550	Traverse City	44.8831	-85.6777
Northwest	B	43.70710	-86.40210	Hart	43.7366	-86.3594
Northwest	C	43.67990	-86.20240	Elbridge	43.6793	-86.1893
Northwest	D	44.52520	-85.25050	Elk Rapids	44.8448	-85.4062
Northwest	E	44.55380	-85.31210	Old Mission	44.932	-85.4996
Fruit Ridge	F	43.11210	-85.71840	Sparta	43.1166	-85.756
Fruit Ridge	G	43.06228	-85.74383	Sparta	43.0733	-85.7228
Fruit Ridge	H	43.17261	-85.76254	Sparta	43.1771	-85.7378
Fruit Ridge	I	42.95234	-85.75390	Standale	42.9557	-85.7521
Fruit Ridge	J	42.93423	-85.79541	Standale	42.9557	-85.7521
Southeast	K	41.88031	-83.77155	Flint	43.0241	-83.6745
Southeast	L	42.80035	-83.78534	Flint	43.0241	-83.6745
Southeast	M	42.47590	-83.03465	Romeo	42.7768	-83.0211
Southeast	N	42.76090	-83.02640	Romeo	42.7768	-83.0211
Southeast	O	42.50310	-83.66140	Commerce Twp	42.5982	-83.4964
Southwest	P	42.15464	-86.29602	Bainbridge	42.1267	-86.2677
Southwest	Q	42.22793	-86.14246	Hartford	42.2275	-86.1403
Southwest	R	42.08518	-86.35063	Benton Harbor	42.0841	-86.357
Southwest	S	42.59713	-86.15880	Fennville	42.5951	-86.1561
Southwest	T	42.48537	-86.22361	Fennville	42.5951	-86.1561

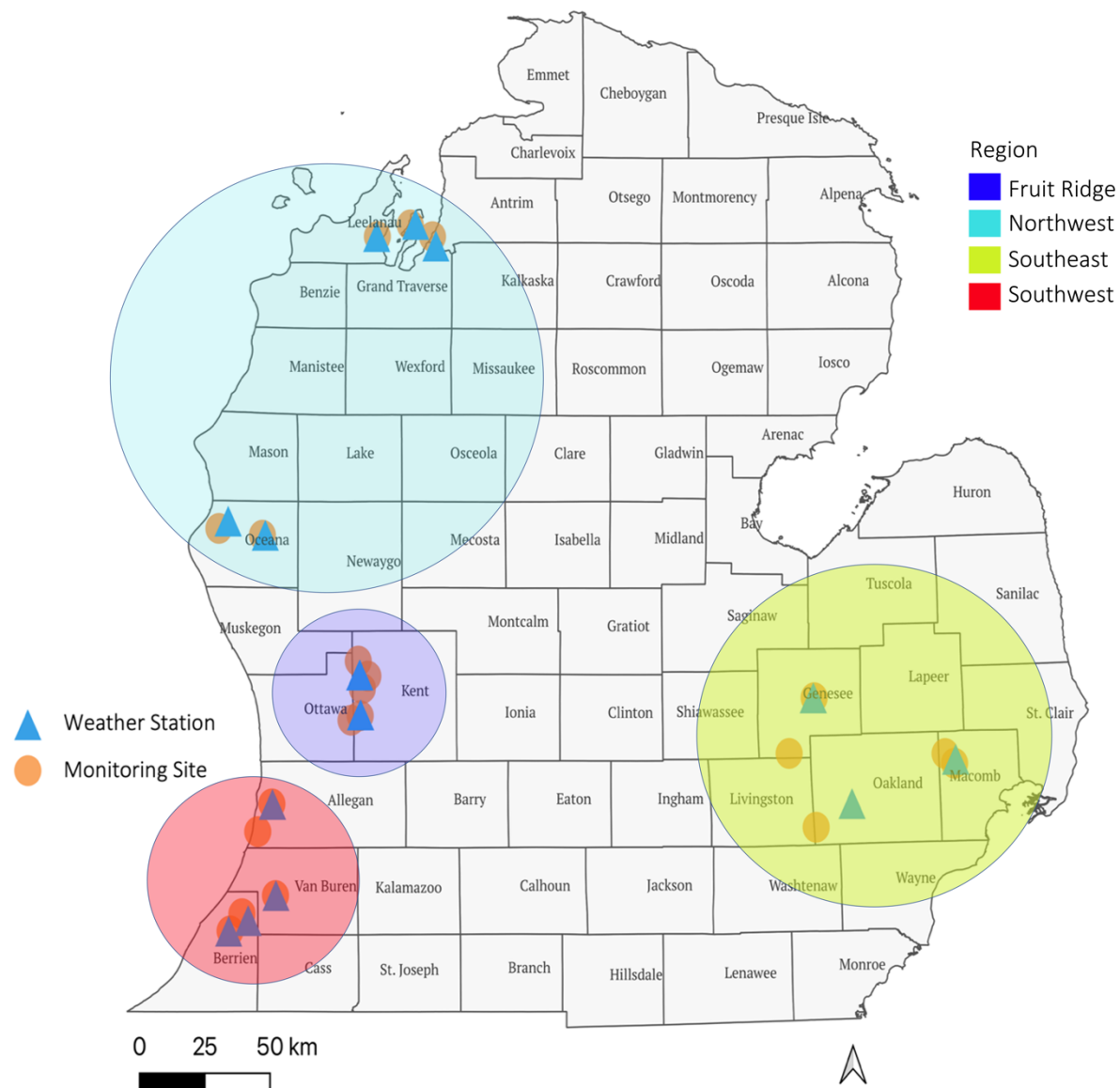


Figure 2.1. Map of study sites and associated weather stations in each of four regions in the Lower Peninsula of Michigan.

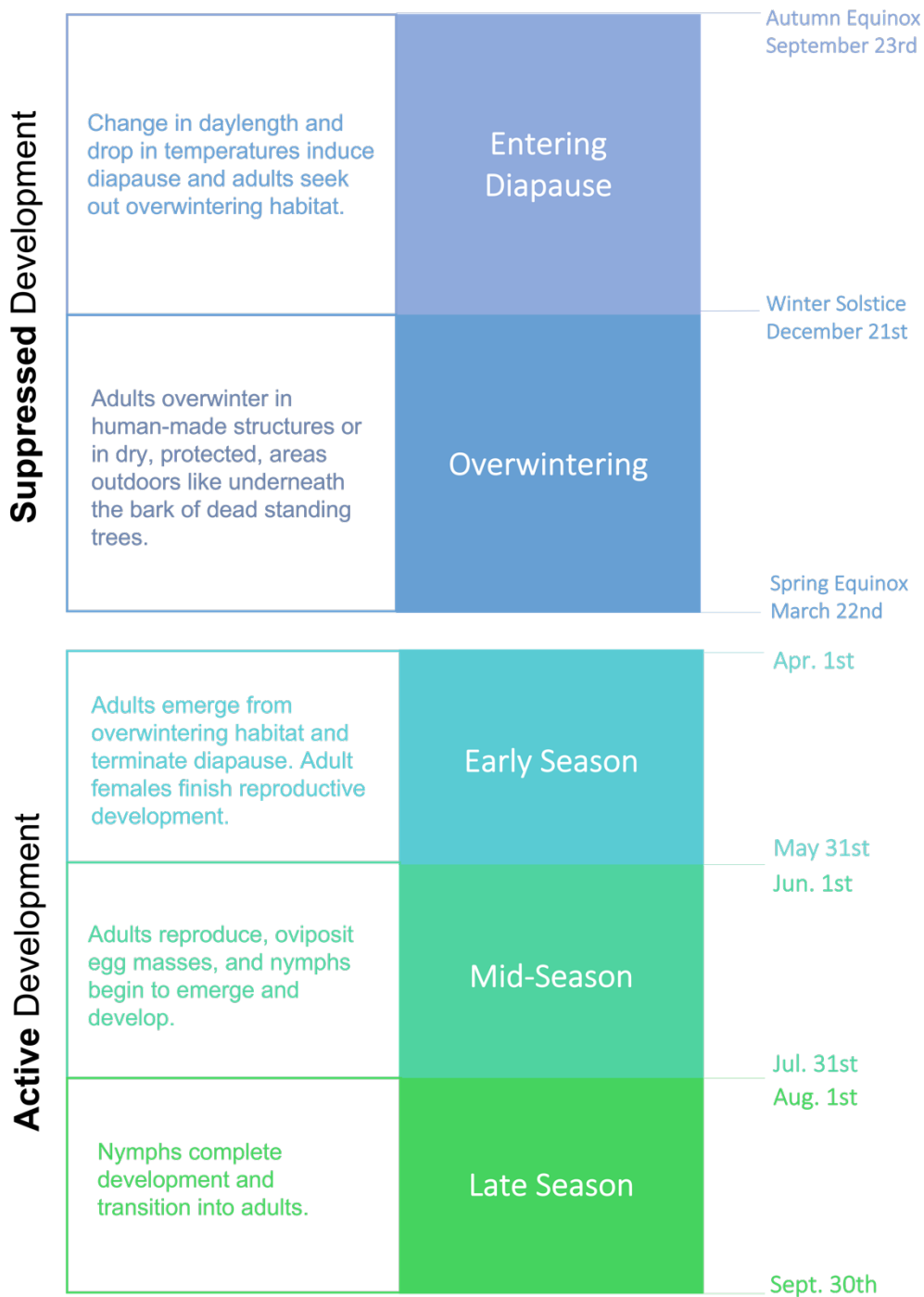


Figure 2.2. A summary of the two developmental periods (suppressed vs. active) divided into five temporal segments (entering diapause, diapause, early season, mid-season, late season) as they relate to *H. halys* phenology.

Results

Regional Trends

Region strongly predicted *H. halys* abundance, explaining 32.5% of the variance between *H. halys* populations ($X^2=32.60$, $Df=3$, $p<0.0001$) ($R^2=0.32$) (Figure 3). Furthermore, as latitude increased, *H. halys* prevalence decreased ($X^2=25.24$, $Df=1$, $p<0.0001$) ($R^2=0.27$) (Fig. 2.4). Sites in the Northwest region of Michigan were associated with lower captures than sites in more southern regions, with only 31 *H. halys* individuals captured across the five sites in this region within four years of monitoring. Conversely, sites at lower latitudes in the Southeast and Southwest were more likely to harbor larger populations of *H. halys*, with total captures of 3,337 and 3,384 across all sites in the four-year monitoring period. The Fruit Ridge region, more centrally located than the other regions, recorded 1,498 total *H. halys* captured.

Halyomorpha halys population counts were the lowest in 2020 across all regions but the Northwest (Fig. 2.5). In the Northwest region, mean captures never reached more than 5.2 individuals in all years surveyed. In the Fruit Ridge region, mean captures decreased from 2018 to 2020, and then increased in 2021. This is the same pattern populations in the Southwest exhibited. In the Southeast, mean captures were somewhat consistent between 2018-2020; however, this region exhibited a 339% increase in population count average in 2021. Site-specific trends were notably similar to the averages of the regions in which they were located (Fig. 2.6). Additionally, sites often exhibited extreme changes in populations from year to year. For example, one site exhibited a 1995% increase in *H. halys* individuals from 2018 to 2019; the following year, the site's population fell to similar levels as in 2018.

Early Season Trends

In the early growing season (April 1st-May 31st), the number of days with an average temperature that falls between the development threshold of *H. halys* was an important predictor for population abundance later in the year ($X^2=14.27$, $Df=2$, $p=0.0008$) and explained 18.5% of the variation in data. Sites with a higher number of days where spring temperatures fell below 14 °C, the lower end of the development threshold, exhibited annual population count declines ($X^2=15.20$, $Df=2$, $p=0.0005$) ($R^2=0.20$). Higher spring temperature averages were strong predictors of annual *H. halys* abundance ($X^2=14.56$, $Df=2$, $p=0.0007$), explaining the greatest amount of variance out of any weather metric at 28% (Fig. 2.6). Unexpectedly, there was no significant relationship between annual population counts and spring frost events (the number of days under 0 °C) ($X^2=3.83$, $Df=2$, $p=0.148$).

Higher occurrences of extreme precipitation events (single-day event >25 mm) in the early season were negatively correlated with *H. halys* abundance ($X^2=5.92$, $Df=2$, $p=0.05$) ($R^2=0.05$). Higher precipitation averages recorded across the entire period were also associated with lower abundance ($X^2=7.61$, $Df=2$, $p=0.02$) ($R^2=0.07$) (Fig. 2.7).

Mid-Season Trends

In the middle of the growing season (June 1st-July 31st), we found no trends between the annual population abundance of *H. halys* and temperature/precipitation averages or extreme weather events (all p -values >0.05) (Fig. 2.7). Extreme high temperatures (>35 °C) were not found in our monitoring periods. Therefore, we lowered this standard to count the number of days with an average of >30 °C. However, we recorded no observed significant effect on annual population abundance ($X^2=1.43$, $Df=2$, $p=0.489$).

Late Season Trends

Toward the end of the growing season (August 1st-September 30th), *Halyomorpha halys* populations were higher when this period had a higher incidence of days with averages above 30 °C ($X^2=5.98$, Df=2, $p=0.05$) ($R^2=0.08$). Years with higher numbers of days with an average temperature within the developmental threshold of *H. halys* during this period had higher population counts ($X^2=14.69$, Df=2, $p=0.0007$) ($R^2=0.11$). Colder events in which the temperature dipped below the lower developmental threshold of 14 °C had no significant effect on annual abundance ($X^2=4.11$, Df=2, $p=0.128$). Additionally, no early frost events occurred within this period for the years included in this study. Unlike in the early growing season, extreme precipitation events ($X^2=8.03$, Df=3, $p=0.018$) ($R^2=0.06$) and higher precipitation averages ($X^2=7.81$, Df=2, $p=0.02$) ($R^2=0.06$) were positively correlated with *H. halys* abundance (Fig. 2.7).

Entering Diapause and Overwintering

Between the fall equinox and winter solstice, the day length shortens, and *Halyomorpha halys* begin to enter diapause as they seek overwintering habitat. During this period, higher average temperatures were associated with increased population abundances in the following year ($X^2=5.82$, Df=1, $p=0.016$) ($R^2=0.05$). Additionally, no significant correlation was found between population abundance and earlier frost events within this period ($X^2=0.19$, Df=1, $p=0.664$). As *H. halys* overwinter, between the winter solstice and spring equinox, uncharacteristically warm days (max >20 °C) were associated with increased *H. halys* abundance for the following growing season ($X^2=5.95$, Df=1, $p=0.015$) ($R^2=0.05$). Cold stretches ($X^2=1.37$, Df=1, $p=0.242$) and singular extreme cold events ($X^2=0.02$, Df=1, $p=0.902$) did not have an observed effect on annual population totals in our analysis.

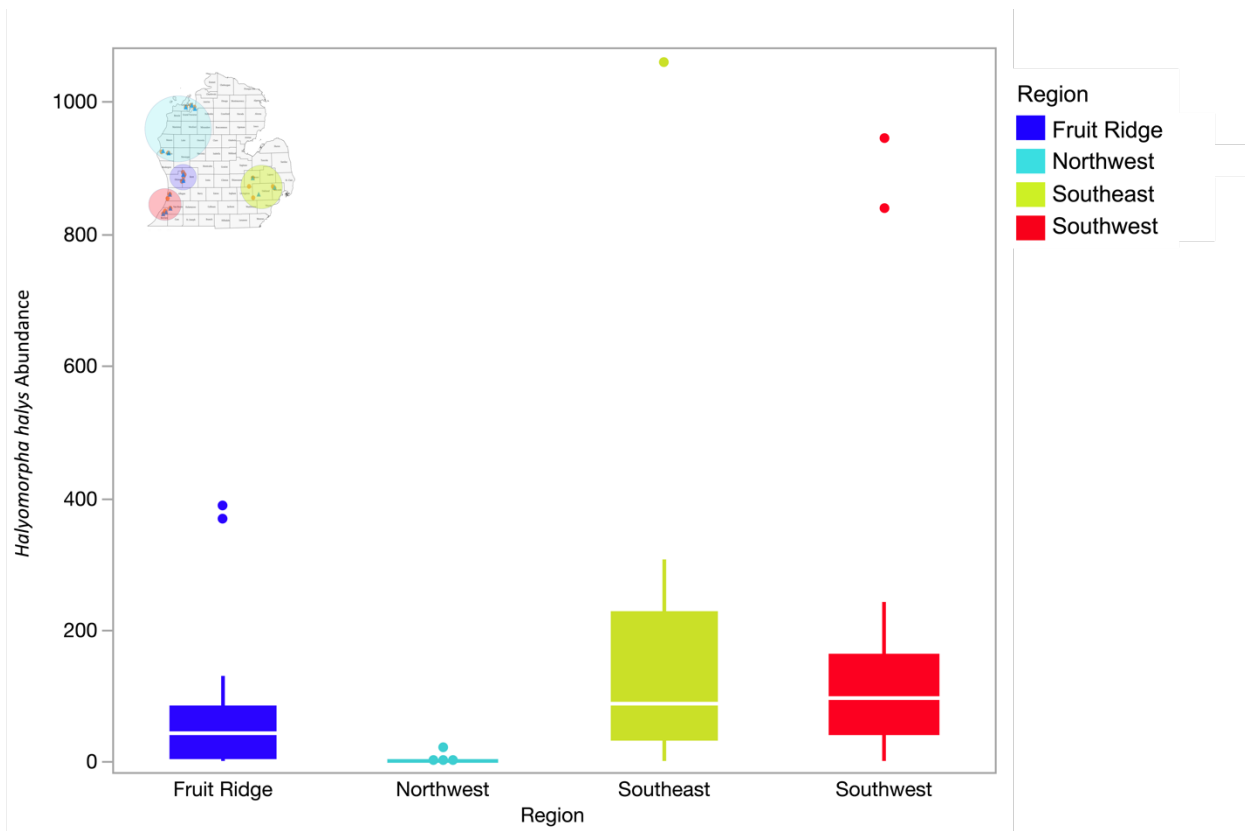
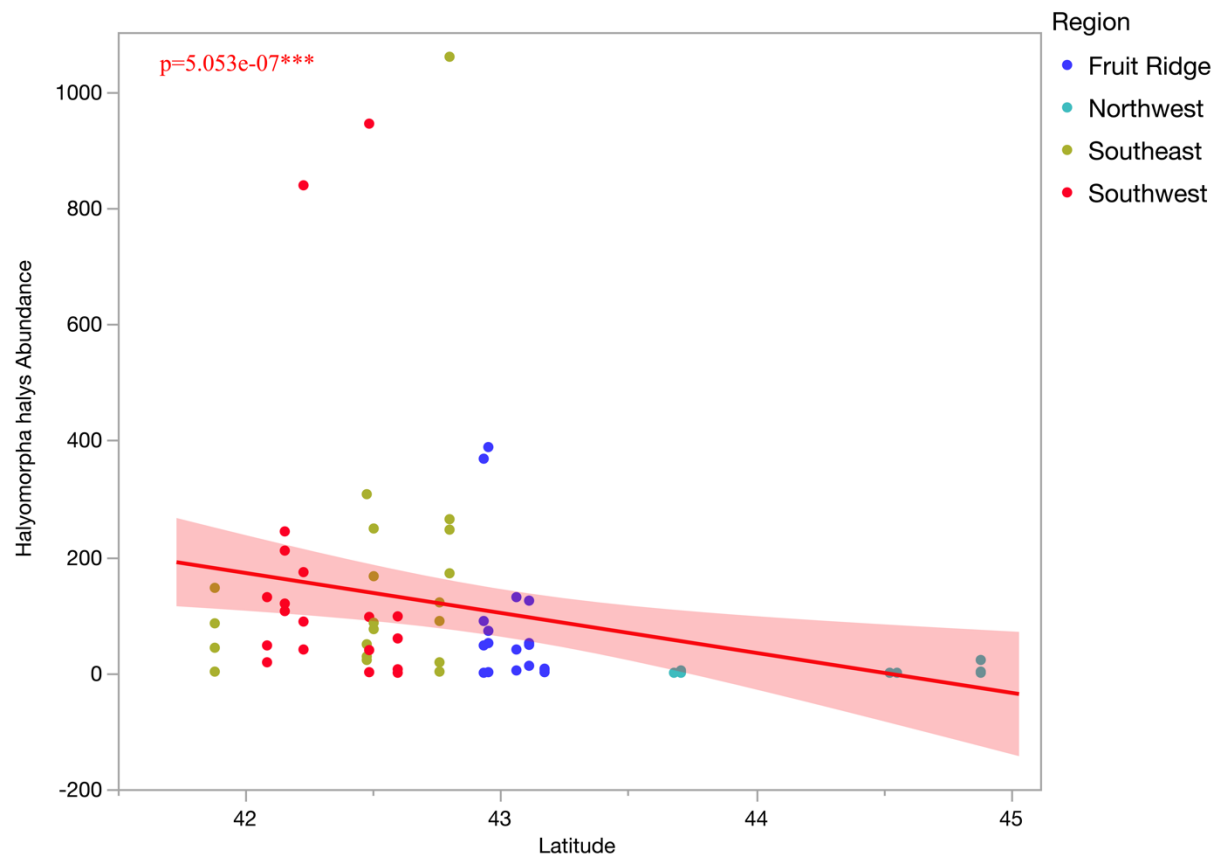


Figure 2.3. Mean *H. halys* abundance over four years (2018-2021) in four key fruit growing regions in Michigan.



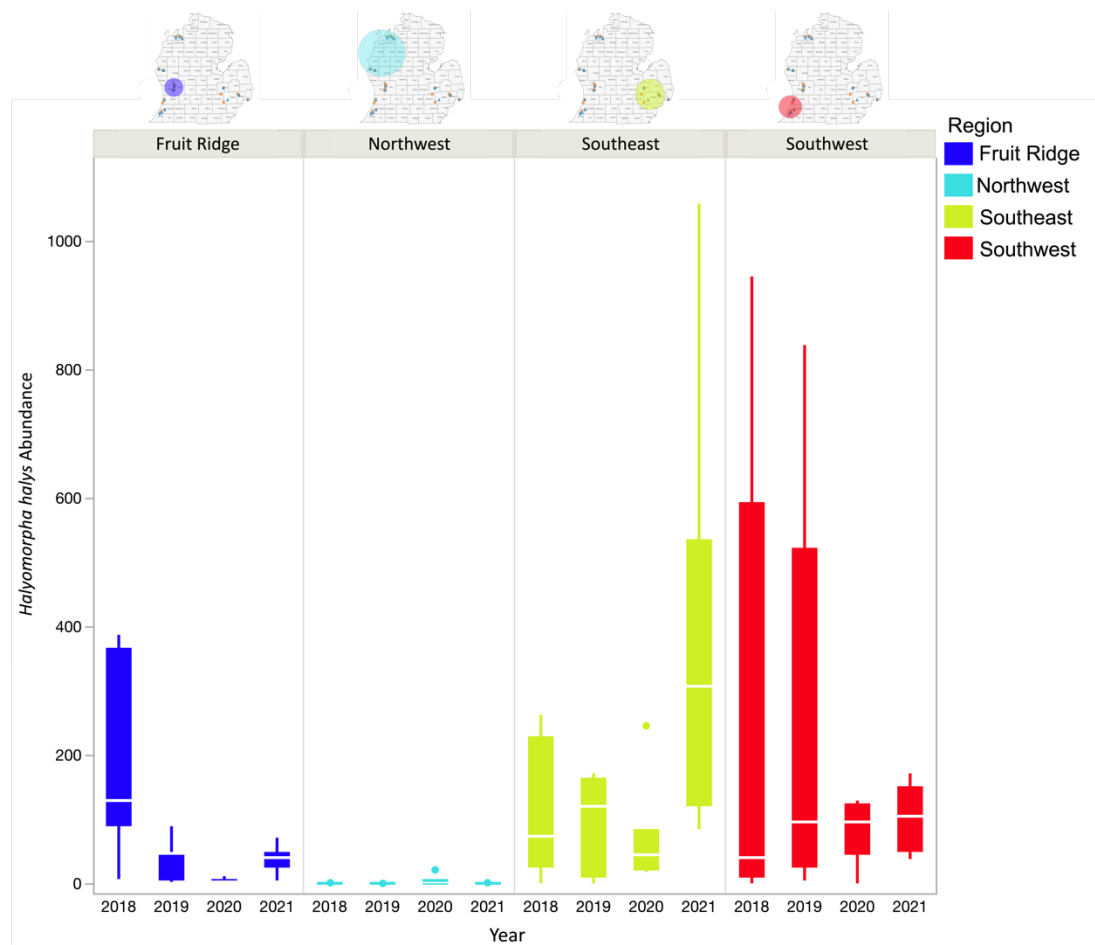


Figure 2.5. Mean *H. halys* abundance of regions between 2018-2021.

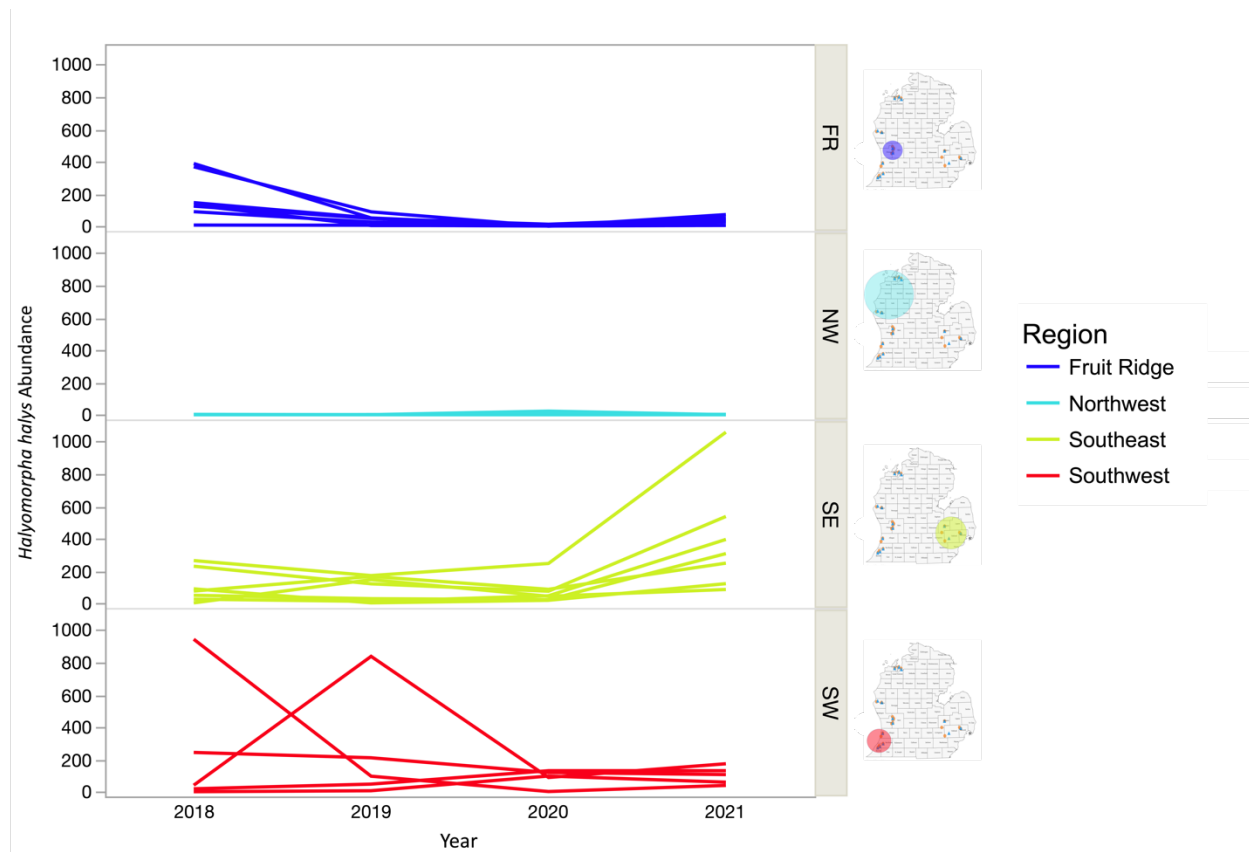


Figure 2.6. Changes in *H. halys* abundance at sites between 2018-2021. Sites are grouped and color-coded by the region that are highlighted on the maps on the right.

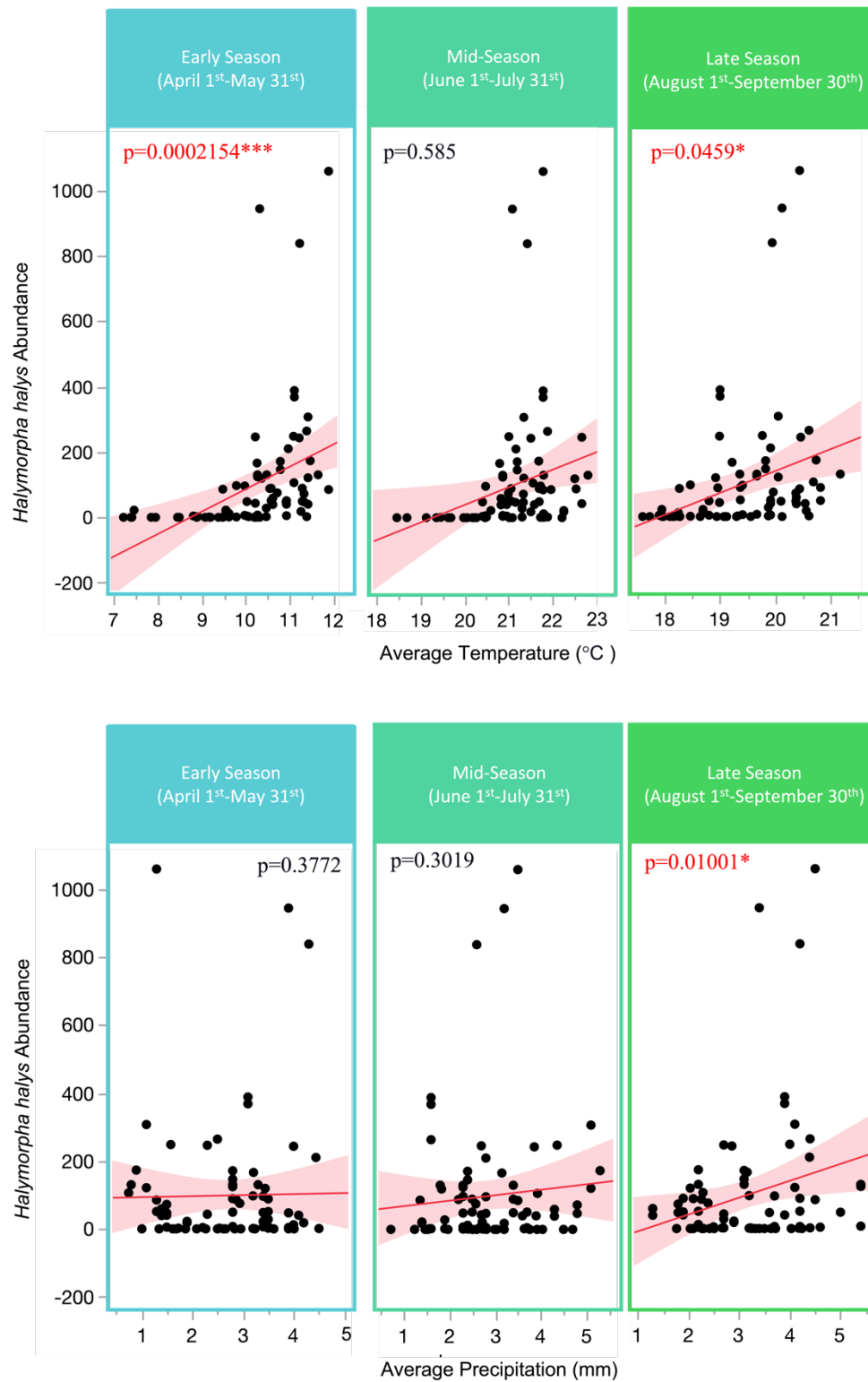


Figure 2.7. Regression plots demonstrating the mixed effects of average temperature (°C) and average precipitation (mm) on *H. halys* abundance across the growing season. Significant trends are represented by p-values marked in red.

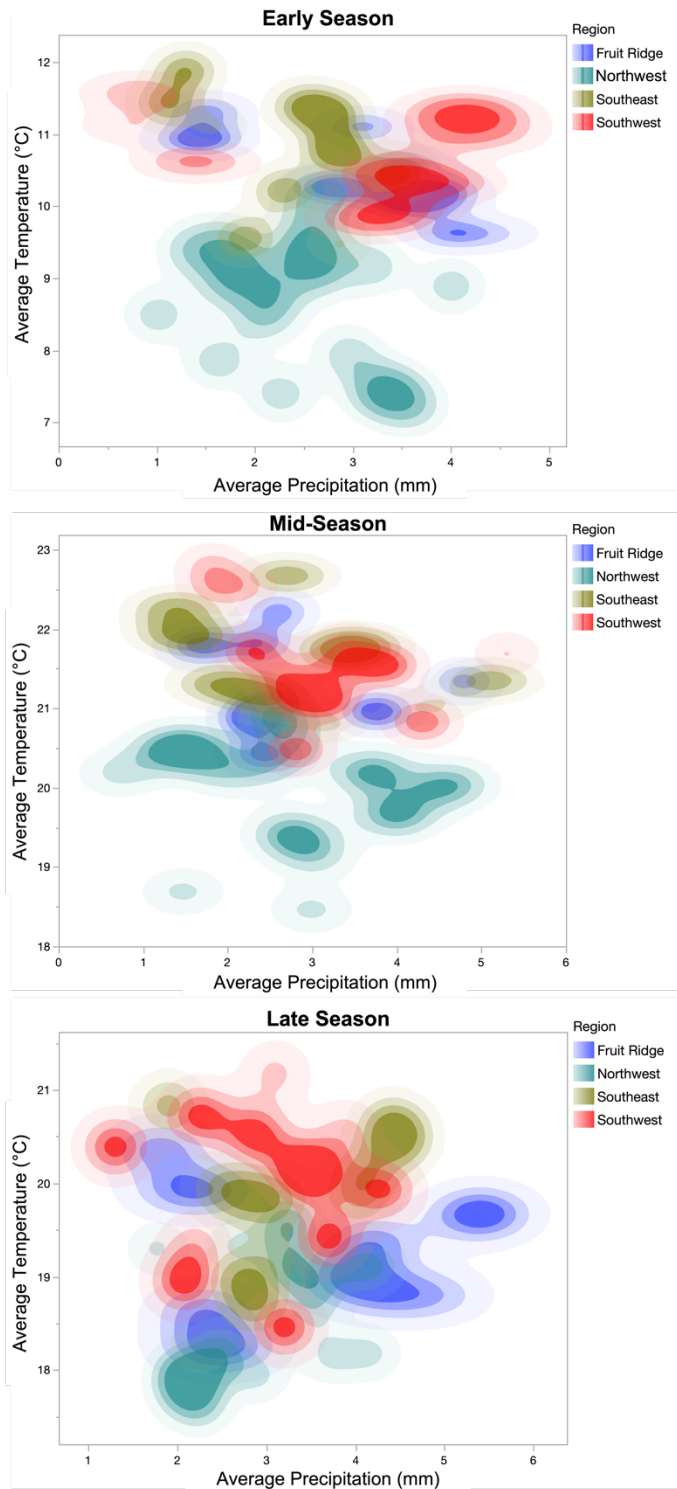


Figure 2.8. Heat map displaying the values of average temperature (°C) and average precipitation (mm) of sites, grouped by region.

Discussion

Latitudinal Trends

As latitude increased, *H. halys* population abundance decreased (Fig. 2.4). This finding is in line with other reports on *H. halys* abundance across Michigan (MISIN). *Halyomorpha halys* populations were first recorded in Northern Michigan just three years after the first occurrences were noted in Southern counties (MISIN). Despite this small difference in establishment time, Southern Michigan exhibits much higher abundances of *H. halys*, suggesting there may be some biological limitation preventing wider establishment and limiting dispersal. Biological explanations for this trend may be attributed to shorter growing periods that limit the time allowed for the development of *H. halys* and host plants. Previous studies demonstrate that nutrient reserves are critical for post-diapause survivorship. Shorter growing seasons and longer overwintering periods may be incompatible with the nutrient reserves required to sustain periods in diapause (Skillman et al., 2018). Another possible explanation is the severity of winter conditions may exert more pressure on overwintering populations. Ciancio et al. (2021) found that *H. halys* is chill-susceptible and require human-made structures to successfully overwinter in Ontario, Canada, as they cannot endure the low temperatures overwintering outdoors. It has also been reported that the presence of human-made structures is particularly important in supporting *H. halys* populations early on in establishment (Wallner et al., 2014). In Northern Michigan, lower human population abundance may decrease the availability of protective overwintering habitat and subject populations to harsh conditions that contribute to higher overwintering mortality. Furthermore, human-populated areas may provide ideal dispersal corridors for *H. halys* to seek refuge from winter conditions. Hence, the combination of human developments at

lower densities and the duration of winter conditions at northern latitudes may be limiting *H. halys* populations as they attempt to disperse North and expand their range.

It is likely that regional differences in *H. halys* abundance were driven by the latitudinal gradient. Among the regions in our study, the Northwest had the lowest population abundance in all four years (Fig. 2.3). The Fruit Ridge, the second-most Northern region, had the second lowest mean population abundance, despite its dominant agricultural landscape and proximity to the metropolitan area of Grand Rapids (Fig. 2.3). *Halyomorpha halys* can feed on over 100 species of ornamental and non-cultivated plants, so while they are often abundant in agricultural landscapes, they are not entirely dependent on them for survival (Bakken et al., 2015; Holthouse et al., 2021). The Southeast and Southwest had the highest mean abundances in our study, with the Southwest hosting slightly higher averages in most years (Fig. 2.4). These regions are at the lowest latitude and contain diverse agricultural and natural lands adjacent to major metropolitan areas that provide adequate climatic and resource conditions for populations to flourish. While human density is lower in Southwest Michigan than the metropolitan area of Detroit in the Southeast region, it is home to a major transportation corridor (I-94) for agricultural producers to transport their products for sale in Chicago. This may serve as an optimal dispersal corridor for a species like *H. halys* which is a known adept hitchhiker. Furthermore, this region hosted the first known introduction of *H. halys* into the state, thus operating as an early epicenter in which populations may have radiated outwards from.

Early Season Trends

Early in the growing season (April 1st-May 31st), *H. halys* adults begin emerging from overwintering habitat and transitioning out of diapause. Females coming out of diapause must finish reproductive development, which is dependent upon photoperiod and temperature

thresholds (Nielsen et al., 2008, 2017). Our study found that annual population abundance was hindered when the early growing season had fewer days that fell within this development threshold. This finding supports developmental model conclusions made by lab experiments in other studies (Nielsen et al., 2008, 2017). Extended periods within this development threshold optimize stink bug reproduction and growth, while deviations may limit reproduction and nymph development (Nielsen et al., 2008, 2017).

Additionally, we found that cold springs yielded lower annual population abundances than warm springs (Fig. 2.7). Colder springs may slow or impede the reproductive development of the emerging population, yielding lower reproduction rates. Scaccini et al. (2020) reported that adults emerging from overwintering habitat were more sensitive to low temperatures than adults entering overwintering habitat in Italy. Spring populations coming out of diapause are operating on lower nutrient reserves than when they entered diapause, making them more susceptible to the lethal or sublethal effects of adverse temperature conditions (Scaccini et al., 2020).

Cold temperatures also may facilitate the spread of an entomopathogenic fungus like *Nosema maddoxi*. Increased prevalence of *Nosema* spp. in honey bees (*Apis mellifera*) was tied to colder ambient temperatures, which authors attributed to reduced dispersal of honey bees from their hives, enabling higher infection levels within hives (Retschnig et al., 2017). As *H. halys* aggregate in overwintering locations, colder spring temperatures may slow or delay dispersal and increase the prevalence of *N. maddoxi* in populations. Infection in stink bugs may adversely affect host fecundity and development, as well as the development of their offspring (Preston et al., 2020). *Nosema maddoxi* is a widely distributed native parasite of native stink bug populations in North America and has been recorded in North American *H. halys* populations since 2012 (Hajek et al., 2018). Preston et al. (2020) surveyed *N. maddoxi* in *H. halys* in 11 states

and detected infections in all states surveyed. The same study found infection prevalence in field populations of *H. halys* was as high as 60% of surveyed individuals at one site in New York. *Nosema maddoxi* has been recorded in *H. halys* populations in Michigan (J.K. Wilson, unpublished), but its distribution within Michigan populations of *H. halys* and its role in suppressing this pest is currently unknown. In *H. halys*, *N. maddoxi* is demonstrated to be at its peak prevalence in populations in the spring, with one study demonstrating infection prevalence levels at 50-60% of individuals emerging from overwintering habitat (Preston, Agnello, & Hajek, 2020). In consequence, emerging populations may suffer from reduced fecundity or larval development. Preston et al. (2020) report that only 26.5% of infected *H. halys* nymphs successfully developed into adults. Thus, if colder springs increase opportunity for spread of *N. maddoxi* and expand the period of infection, *H. halys* populations may be significantly hindered early in the season.

On the other hand, the trend of higher average spring temperatures yielding high annual population abundances poses a concern for the potential opportunity for range expansion. Climate projection estimates for Michigan suggest that in the next 10 years, spring temperatures will continue to rise (Frankson et al., 2022, Gutiérrez Illán et al., 2022). Warming spring temperatures may drive range expansion and increase population abundance of *H. halys* at Northern sites in the future (Gutiérrez Illán et al., 2022). Continued monitoring of *H. halys* populations across this region would provide valuable information on how population abundance may change in response to these changing conditions.

Unexpectedly, spring frosts did not yield any notable change in annual population abundance. *Halyomorpha halys* can tolerate conditions below freezing in some experimental studies due to cold tolerance induced by metabolic changes during diapause (Ciancio et al., 2021;

Lowenstein & Walton, 2018). The effects of diapause have been noted to linger beyond the period in which populations are subjected to consistent adverse conditions (Ciancio et al., 2021; Cira et al., 2018). As a result, brief periods of freezing temperatures in the spring may not provide a significant threat to populations as residual cold tolerance protects individuals transitioning out of diapause.

High precipitation averages and extreme precipitation events (>25 mm in 24 h) early in the growing season were correlated with reduced trap totals (Fig. 2.7). This observation contrasts with one known study that found no relationship between precipitation events and *H. halys* population abundance (Kamiyama et al. 2021). We anticipate extreme precipitation events could facilitate increased mortality directly through injury or indirectly by impeding dispersal, encouraging extended confinement, or contributing to the spread of disease. Dispersal has been noted to be greatest in the spring, as adults come out of diapause and use their last nutrient reserves to disperse (Lee & Leskey, 2015). We anticipate dispersing populations may be more susceptible to extreme rain events than more stationary periods of their life cycle. Our study suggests that precipitation may be an overlooked factor in changes in stink bug populations and should be considered in future research to evaluate the mechanisms that may drive interactions between precipitation and *H. halys* population abundance.

Mid-Season Trends

In the middle of the growing season (June 1st-July 31st), *H. halys* oviposit eggs and offspring begin to emerge and develop. This is considered the most sensitive period in development for *H. halys*; however, our study recorded no trends between either temperature or precipitation variables and annual population abundance (Fig. 2.7). This may be attributed to the ideal climate in Michigan for nymphal development. All days in these periods were within the

development threshold, with few to no occurrences of extreme highs or lows recorded at the sites in the four years of monitoring. Sites received few to no occurrences of days that reached a temperature maximum above 35 °C, so we lowered our standard and examined days where the average daily temperature exceeded the upper range of the development threshold at 30 °C. Since we did not observe a relationship, this supports lab-based developmental models and suggests that this range of temperatures is still ideal for stink bug development. Simaz et al. (2021) demonstrate temperatures beyond 30 °C led to increasing rates of egg mortality, with 0% survival under temperature conditions over 35 °C. Furthermore, some experimental evidence shows nymphs may actively seek out shaded areas in high temperatures (Lee et al., 2014). This may grant populations some level of resiliency to temperature extremes in this period, but more research is needed to demonstrate precisely how this may improve survivorship. Because of the mild and consistent temperatures that fall within the optimal range of *H. halys* development, temperatures may be of interest to investigate in a state or country that exhibits more prevalent extreme heat events to understand any potential effect.

Precipitation averages and extremes in this period also did not present any significant interaction with annual population abundance (Fig. 2.7). This was the only timeframe in the growing season in which precipitation had no influence on annual population abundance. Fisher et al. (2021) analyzed the impact of relative humidity on *H. halys* development and concluded that the effect is dependent on temperature and life stage. The mixed effect of precipitation at specific times of the year on annual population abundance may exhibit a similar pattern in our study. It may be of interest for future studies to investigate how different life stages may directly respond to variables like precipitation.

Late Season Trends

At the end of the growing season (August 1st-September 30th), nymphs enter the late stages of development and begin transitioning into adults. This period is marked by the beginning of dispersing populations and often exhibits peak abundance (Amarasekare & Link, 2023; Nielsen & Hamilton, 2009). Like the early growing season, years with more days of temperatures within the developmental threshold in the late growing season were correlated with higher annual population counts. Colder periods in the late growing season did not yield any notable difference, perhaps because adult populations begin entering diapause and increase their cold tolerance (Ciancio et al., 2021; Cira et al., 2018). Early-frost events did not occur within this period for the duration of our study and subsequently did not contribute to changes in annual population abundance.

Unlike the early growing season, populations were more abundant in years when the late growing season had extreme precipitation events and higher precipitation averages (Fig. 2.7). Increased precipitation may yield better, more quality food resources to sustain populations as they complete development and prepare nutrient reserves for overwintering. However, there is a limit to this benefit, as wetter conditions may also promote decreased quality of fruiting resources. Ultimately, more information is needed to understand how precipitation influences population dynamics of pests, especially regarding *H. halys*. Our study highlights the importance of seasonal and life-stage differences in mediating the response of populations to weather variables. It is notable that extreme precipitation events in the spring seem to adversely affect populations, while fall extreme precipitation events have the opposite effect. To elucidate the cause of this, future studies should be designed to collect real-time data on population responses to weather events as they happen.

Entering Diapause

Between the fall equinox and winter solstice (September 23rd-December 21st), the day length shortens, and *H. halys* begin to enter diapause as they seek overwintering habitat. Higher temperatures in this period were associated with higher population abundances in the following year. We anticipate this could improve population conditions in three ways. First, high temperatures as stink bugs enter diapause could extend the range of time for dispersal to overwintering sites and be more forgiving to stragglers. Second, it could extend the activity period to acquire nutrients before colder periods to come. This may enable better nutrient reserves to sustain populations over the winter, and in their initial activity in the springtime. Lastly, this may reduce the amount of time stink bugs spend aggregating and subsequently reduce *N. maddoxi* infections. Preston et al. (2020) note that the time of inoculation is important for determining the strength of infection. Earlier infections allow more time for the fungus to multiply in the body of the host. Aggregating overwintering populations are likely ideal opportunities for *N. maddoxi* to spread horizontally between individuals, so expanding the time of activity may reduce incubation length for the fungus.

Like the late growing season, early frost events had no effect on populations as they sought overwintering habitat. As mentioned previously, adults entering diapause in the fall exhibit lower mortality rates than adults exiting diapause in the spring when exposed to low temperatures. This may be attributed to improved nutrient and weight status of individuals entering diapause (Ciancio et al., 2021; Skillman et al., 2018). Furthermore, populations may already be in overwintering habitat at the time of the frost events in this period.

Overwintering

Between the winter solstice and spring equinox (December 21st-March 22nd), as *H. halys* overwinter, uncharacteristically warm days were correlated with higher population abundances in the following year. This was surprising as we anticipated warm days in the winter may trigger activity, which could reduce fitness by depleting nutrient reserves. However, it is possible that the uncharacteristically warm days fell within the latter end of this period of the year, in March, and thus are representing the ideal spring conditions for populations to begin emerging safely from overwintering habitat and terminating diapause. In a future study, this could be accounted for by splitting the winter into briefer periods that strictly reflect the coldest period of the year.

Extreme cold events ($<-15^{\circ}\text{C}$) during the overwintering period yielded no observed effect on annual population abundance. While some studies report high mortality rates at temperatures below -13.5°C , *H. halys* has been demonstrated to withstand conditions as low as -20°C (Scaccini et al., 2020; Sibayan, 2018). While this resiliency is important to note, it is more likely that most of the population is harbored in protected areas that have some degree of thermal protection like sheds and houses.

Conclusions

It is evident that some proportion of annual abundance of the invasive *H. halys* is driven by weather patterns. One unexamined interaction in our study is how weather may influence *H. halys* trapping. This would be useful for disentangling any relationships that may be obscured by the effectiveness of traps under certain weather conditions. Trends between annual *H. halys* abundance and weather metrics were dependent on the period of the year in which they occurred. For example, the occurrence of extreme precipitation events ($>25\text{ mm in }24\text{ h}$) in the early season (April 1st-May 31st) were associated with decreased annual abundance, while the same

metric in the late season was associated with increased annual abundance. Michigan summers seem to possess ideal conditions for nymphal development, while spring and fall conditions had variable effects depending on the year. Our study supports the hypothesis that susceptibility to weather conditions is dependent on life stage, but more research is needed to understand real-time population responses to weather events. Furthermore, *H. halys* distribution in Michigan is likely constrained by unsuitable climate conditions at higher latitudes, however, this has the possibility to change as temperatures warm, and growing periods lengthen in Northern regions in response to climate change.

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