

THESIS

PAVEMENT, PESTS, & PARASITOIDS, OH MY! ELM HERBIVORES AND THEIR
NATURAL ENEMIES IN THE URBAN FOREST

Submitted by

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ABSTRACT

PAVEMENT, PESTS, & PARASITOIDS, OH MY! ELM HERBIVORES AND THEIR NATURAL ENEMIES IN THE URBAN FOREST

Urban areas are the fastest growing habitat type in the world, and an increasing proportion of the United States and global population lives in urban areas. Urban forests provide essential ecosystem services to rapidly expanding urban populations, but their health is threatened by damaging herbivory from non-native, invasive insects. To address this problem, my masters research investigated two critical questions that limit our ability to sustainably manage invasive insects in urban forest ecosystems: (1) How do urban environments impact the density of invasive herbivores in the urban forest? and (2) Are predator and parasitoid natural enemies present, and, if so, what is the level of parasitism? I investigated these questions in the context of the elm-herbivore study system, analyzing a globally distributed host tree and its complex of invasive insect pests in Colorado, USA.

In my first chapter, I address the first question and explore how a variety of environmental factors that vary across urban habitats influence the density of several invasive insects. Specifically, I evaluate how vegetational complexity, distance to buildings, impervious surface, canopy temperature, host availability, and density of co-occurring herbivores impact three invasive pests of elm trees: the elm leaf beetle *Xanthogaleruca luteola* Müller (Coleoptera: Chrysomelidae), the European elm flea weevil *Orchestes steppensis* Korotyaev (Coleoptera: Curculionidae), and the elm leafminer *Fenusa ulmi* Sundevall (Hymenoptera: Tenthredinidae). I found that insect responses to these factors were species-specific, and all environmental factors

were associated with density of at least one pest species except for distance to buildings. Elm leafminer density decreased with higher temperatures and was influenced by an interaction between vegetational complexity and impervious surface. Elm flea weevil density increased with greater host availability, and elm leaf beetle density increased with higher temperatures. Both elm leaf beetle and elm flea weevil density decreased with greater leafminer density, suggesting that insect density is mediated by species interactions. Results of this study can be used to inform future tree planting efforts through the selection of “safe sites”, or locations where trees will be less likely to experience damaging outbreaks of insect pests. Additionally, these results can be used to strategize preventative management on trees that are located in outbreak “hotspots”, or locations where environmental conditions make trees predisposed to insect outbreaks. Finally, results of this study contribute to our knowledge of the dynamic ways in which multiple invasive insects interact in urban environments. This information will be especially valuable as non-native insect introductions continue to increase into the future.

In my second chapter, I narrow my focus to two historically important and particularly damaging pests of elm, the elm leaf beetle and elm flea weevil, to address the second question listed above and explore the complex of natural enemies attacking these two pests. In many areas of these insects’ invaded range, outbreaks severely damage elm hosts. Natural enemies are thought to be important in regulating elm leaf beetle and elm flea weevil populations in other regions, but whether natural enemies are present in Colorado is largely unknown. As such, the aim of chapter 2 was to identify which predators and parasitoids of these pests are present in Colorado, a state with frequent pest outbreaks and where the natural enemy community is almost entirely undescribed. In June – August 2021, I identified predators through field observations and laboratory feeding trials, finding seven species of predators from six arthropod orders that

fed on elm leaf beetle or elm flea weevil. Additionally, I reared 58 elm leaf beetle egg clusters, 539 elm leaf beetle larvae, and 435 elm flea weevil mines to detect parasitoids. Two parasitoids of elm leaf beetle, the egg parasitoid *Oomyzus gallerucae* and the larval-adult parasitoid *Erynniopsis antennata*, are present in Colorado, representing novel records of these species in the state. However, combined parasitism of elm leaf beetle eggs and larvae was low at <3% across the season, with parasitoids nearly absent early in the season and peak parasitism occurring in late summer. I found five families of parasitoid wasps that emerged from leaves containing weevil mines: Chalcididae, Encyrtidae, Eulophidae, Euplemidae, and Pteromalidae. Parasitoids emerged from <20% of leaves containing weevil mines with almost no parasitism early in the season. Given the low parasitism rates and few predators observed in our study, it seems unlikely that predator and parasitoid natural enemies exert effective control over elm leaf beetle and elm flea weevil in Colorado. This finding challenges the assumption that natural enemies are a driving force of elm leaf beetle and elm flea weevil control in Colorado. Additional research is needed to confirm species identifications for parasitoids of the elm flea weevil, disentangle elm leaf beetle and elm flea weevil population dynamics, and establish effective and sustainable control methods amidst frequent pest outbreaks.

Together, these two research projects enhance our knowledge of what triggers outbreaks of the elm leaf beetle *Xanthogaleruca luteola*, the elm flea weevil *Orchestes steppensis*, and the elm leafminer *Fenusa ulmi* in urban areas while also laying the groundwork for a renewed interest in biological control of elm leaf beetle and elm flea weevil. It is my hope that this work can be applied to other invasive insect pests in urban forest ecosystems and make urban forests more resilient in an era when they are increasingly vulnerable to insect attack.

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This work would not have been possible without the support and collaboration of several municipalities along the Front Range of Colorado: Fort Collins, Greeley, Longmont, Loveland, and Windsor. Specifically, I would like to thank Ralph Zentz, Shiloh Hatcher, Brett Stadvold, Jeff Caputo, Ken Kawamura, and their respective staff for their interest in this work and the resources they shared to make this project a success. I would also like to thank Vernon Koehler with the United States Forest Service for working quickly to grant me access to important sampling locations. I enjoyed our chats about insects, and it was heartening to know that others were interested in the same questions that I was researching.

This project benefitted from the work of three superstar undergraduate students and one stellar high school volunteer: Ashley Brackett, Autumn Nicoson, Delaney Young, and Jillian Liu. These budding scientists embarked on their first experience in the field of entomology, braving scorching hot days, tedious data entry, and rapidly evolving field plans. I hope they found the experience rewarding; I know I certainly did. I cannot wait to see what they do next as they continue to blossom in the field of their choosing.

Thank you to my amazing faculty advisor, Dr. Ruth Hufbauer, who gave me the freedom to develop this project and find my niche in the field of urban ecology and landscape entomology. She taught me how to produce good science AND embrace a life outside of my professional endeavors, which is more valuable than we often recognize. Thank you also to my committee members, Dr. Whitney Cranshaw, Dr. Miranda Redmond, and Dr. Jane Stewart as well as my lab mates in the Hufbauer lab for their thoughtful conversations and valuable input.

Dr. Crystal Cooke was absolutely invaluable in identifying parasitoid specimens and contributing to my professional development as an entomologist.

Lastly, I'd like to thank my loving family for their unwavering support and patience as I completed my degree 2,000 miles away from them. To my husband, Eric, my endless gratitude for sitting through practice talks, mounting temperature loggers at the end of long days, expressing genuine interest in this work, and being a shoulder to cry on when times were tough. Thank you for being my partner in life and letting me rope you into our next adventure.

AUTOBIOGRAPHY

Jacqueline Buenrostro grew up as Jacqueline Meyer in New Port Richey, Florida, a small suburb of Tampa, with her mother, Cheryl, father, Jeff, and older sister, Jessica. Her mother, an elementary school teacher who got her degree while raising a family, is Jacqueline's greatest mentor and the hardest-working person she ever met. Her father, a regional service director at Camping World, is the smartest person she ever met and can figure out how everything works, even the minds of his two daughters. Jessica is her very best friend.

Jacqueline graduated from the University of Central Florida in 2018 with a degree in Environmental Science. During her time at UCF, she began working with Dr. Barbara Sharanowski, her earliest mentor in entomology, and Dr. Peter Jacques, who taught her to look at every ecological system from a socio-political perspective. These early mentors helped Jacqueline launch into research as she worked on diverse topics such as parasitoid phylogenetics, crop pests and their natural enemies, and the efficacy of forestry education. It was during this period of early academic discovery that Jacqueline adopted her cat, Coraline Jones, and met her now-husband, Eric.

After graduating from UCF, the three started their next adventure in Colorado. Jacqueline began graduate school at Colorado State University in August 2020 during the COVID-19 pandemic. After graduating, she and Eric are setting off to hike the Colorado Trail, a 485-mile footpath that traverses across the Continental Divide. In August 2022, Jacqueline is moving back to Florida with Eric and Coraline to begin her PhD in Entomology at the University of Florida.

DEDICATION

To those who do not see themselves represented in science. You belong here, so keep fighting. To my family and friends who empowered me to follow my buggy dreams. And to my fluffy, four-legged, one-eyed best friend Coraline Jones. May our home always have that perfect climbing tree.

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CHAPTER 1: URBAN ENVIRONMENTS HAVE SPECIES-SPECIFIC ASSOCIATIONS WITH INVASIVE INSECT HERBIVORES¹

Introduction

Urban areas are the fastest growing habitat type in the world (Faeth et al., 2011), and an increasing proportion of the United States and global population lives in urban areas. Over 80% of the US population resides in urban areas, and at least 70% of the global population will inhabit urban areas by 2050 (Grove et al., 2014; Szulkin et al., 2020). Urban trees and forests are critical for providing ecosystem services to this growing urban population. Urban forests sequester carbon (Nowak et al., 2013), filter air and water (Escobedo & Nowak, 2009; Grote et al., 2016), moderate climate (Akbari, 2002; Edmondson et al., 2016; Loughner et al., 2012), foster community (Jim, 2017), and provide health benefits (Sanesi et al., 2011) to urban residents, who tend to be otherwise isolated from the ecosystem services provided by natural and wilderness areas (Bigsby et al., 2014).

Despite these benefits, urban forests are declining by about four million trees each year (Nowak & Greenfield, 2012), and their biggest threat is damage by invasive insects (Lovett et al., 2016). Insect outbreaks are typically more common in urban areas than they are in surrounding natural areas (Dreistadt et al., 1990; Frank & Just, 2020; Raupp et al., 2012; but see Nuckols & Connor, 1995; Schueller et al., 2019). As international trade hubs, urban areas are important points of entry for invasive insects (Paap et al., 2017; Thomas et al., 2017), and non-native insect introductions are projected to increase in the current era of globalization (Liebhold

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& Kean, 2019). Furthermore, non-native insect establishment is often facilitated by the stressful conditions experienced by urban trees, such as heat and drought, which are likely to worsen due to climate change (Paap et al., 2017; Tubby & Webber, 2010).

Within cities, insect density can be highly variable across different sites, with conspecific trees in close proximity experiencing different densities of insects and, thus, different levels of herbivory (Raupp et al., 2012). While several studies have sought to explain this observed variation (Dale et al., 2016; Dale & Frank, 2014a, 2014b, 2017; Long et al., 2019; Meineke et al., 2013, 2014; Meineke & Frank, 2018; Parsons et al., 2020; Shrewsbury & Raupp, 2006; Speight et al., 1998; Sperry et al., 2001), the existing literature is dominated by studies that focus on a single herbivore species, with particular emphasis on hemipterans and other piercing/sucking feeders. As such, this topic remains largely unexplored. To protect urban forests against damage by invasive insects in an era when globalization and climate change make them particularly vulnerable to attack, we must first understand the factors that promote herbivore density in varied environmental conditions across the urban mosaic.

Here we will address five characteristics of urban environments that are hypothesized to be associated with insect density. First, insect density may be positively or negatively associated with vegetational complexity and the resulting habitat structure it provides. Insects that utilize the ground and surrounding vegetational community for all or part of their lifecycle may respond positively to vegetational complexity (Koivula et al., 2019). At the same time, vegetational complexity is linked to top-down control of herbivore populations in many urban systems due to both greater prey choice for predators and winter refuge for parasitoids (Frank & Shrewsbury, 2004; Raupp et al., 2009; Shrewsbury & Raupp, 2006). As such, vegetational complexity may

decrease insect density through top-down control (Langellotto & Denno, 2004; Raupp et al., 2012).

Second, urban structures may increase insect density by creating conditions that are favorable to insect overwintering. Buildings act as windbreaks and insulate the surrounding area from cold temperatures (Brewer, 1973; Raupp et al., 2009; Speight et al., 1998). Additionally, some urban and structural pests use buildings more directly by overwintering within buildings themselves (Hancock et al., 2019; Inkley, 2012), ultimately increasing winter survival and facilitating greater pest persistence in urban landscapes.

Third, the amount of impervious surface, such as roads, sidewalks, and parking lots, around a tree can influence insect density. Insects that are ground-dwelling for all or part of their life cycle (Philpott et al., 2014) or those that benefit from the microclimate moderation derived from more natural landcover (Otoshi et al., 2015) can be negatively affected by high levels of impervious surface around their host plant. At the same time, impervious surface decreases water availability and induces drought stress, making trees less able to defend against insect herbivory (Gely et al., 2020; Meineke & Frank, 2018; Raupp et al., 2012). As such, impervious surface may also increase insect density by weakening the plant host.

Impervious surface is intimately linked with the canopy temperature in trees, the fourth characteristic we address. The heat retention and low albedo of impervious surface warms the surrounding area in a phenomenon commonly known as the urban heat island effect (Grimm et al., 2008). The urban heat island effect increases the temperatures experienced by insects feeding in urban trees, which can increase or decrease insect density depending on species-specific biology. For example, high temperatures that are within the species' optimal performance range may increase insect density by decreasing development time, increasing fecundity, and

increasing body size (Dale & Frank, 2017; Raupp et al., 2012). Alternatively, high temperatures may also decrease body size (Merckx et al., 2018), lead to asynchrony in key reproductive events (Chick et al., 2019), or be beyond the species' thermal optimum (Meineke et al., 2017; Parsons et al., 2020; Youngsteadt et al., 2017), thus decreasing insect density.

Fifth, insect density may be positively associated with the availability of host trees in the urban environment. Urban areas are often dominated by just a few species of ornamental or landscape trees. Following the resource concentration hypothesis (Root, 1973), this high availability of host plants can facilitate pest outbreaks. The resource concentration hypothesis is often observed in urban areas, as the high availability of a single species or functional group of trees produces ideal conditions for establishment, spread, and subsequent damage by non-native insects (Dreistadt et al., 1990; Poland & McCullough, 2006; Raupp et al., 2006).

In addition to the urban environmental factors described above, herbivorous insects also respond to interactions with other species occurring on the same host. Herbivorous insects may negatively affect each other's density through competition, where multiple species compete for quality host resources while avoiding induced plant defenses (Denno et al., 1995; Kaplan & Denno, 2007). Additionally, the order of herbivore arrival on a host may mediate competition through priority effects, whereby a late colonizing species is negatively affected by induced plant defenses and depleted host resources caused by an early colonizing species (Miller-Pierce & Preisser, 2012). As such, multiple invading herbivores may negatively influence each other's density through competition and priority effects.

The objective of this study is to empirically test several hypotheses to explain variable density of invasive insects in the urban forest. We predict that insect density will (1) increase with greater proximity to built structures and availability of host trees; (2) decrease with greater

density of co-occurring herbivores; and (3) either increase or decrease with greater vegetational complexity, impervious surface, and temperature depending on species-specific biology. While several studies address the effects of urban environments on insect herbivores, the current literature is dominated by research that focuses on a single herbivore species, with particular focus on piercing/sucking feeders. In the present study, we explore a complex of three chewing and mining herbivores that attack an ecologically and economically important host tree with global distribution in urban forest ecosystems. By elucidating the factors underlying density of invasive insects for multiple herbivore species across a patchwork of varied urban sites, results of this study can be used to predict species interactions and inform strategic tree care efforts, making urban forests more resilient in an era where globalization and climate change make them particularly vulnerable to insect attack.

Methods

Study System

Here, we examine the effects of continuous variation in multiple environmental factors on urban forest pests using elms and their herbivores. Elms (*Ulmus* spp.) are important features of the urban forest globally (Zalapa et al., 2008) and are one of the most frequently planted urban trees in the United States (Dreistadt et al., 1990). Native to Asia, Siberian elm (*Ulmus pumila*) is now cultivated in urban forests in both the native and introduced ranges (Li et al., 2018; Zalapa et al., 2010). In the United States, Siberian elm was frequently planted in the Great Plains and semi-arid west for its tolerance to drought and cold and its utility as a windbreak (Frye et al., 1988; Martín et al., 2019; Zalapa et al., 2010). Siberian elm is a preferred host for a complex of damaging invasive insect pests: the elm leaf beetle (*Xanthogaleruca luteola*) (Coleoptera: Chrysomelidae) (Bosu et al., 2007), the elm flea weevil (*Orchestes steppensis*) (Coleoptera:

Curculionidae) (Kirichenko et al., 2019), and the elm leafminer (*Fenusa ulmi*) (Hymenoptera: Tenthredinidae) (Smith & Altenhofer, 2011). The elm leaf beetle (hereafter referred to as the beetle) is a chewing insect that emerges and mates on elm leaves in May and June, completing multiple generations on its host before departing to overwintering locations in August and September. Adults chew shotholes through leaf tissue, while larvae skeletonize leaves by feeding on the outer layers of leaf tissue and avoiding leaf veins (Bekircan et al., 2018; Bosu et al., 2007; Cranshaw, 2018; Dahlsten et al., 1993). The elm flea weevil and elm leafminer (hereafter referred to as the weevil and leafminer, respectively) both emerge from overwintering as adults in April and May and mine through elm leaf tissue in the larval stage, completing one generation per year. Upon emerging from overwintering, weevil adults feed on the underside of leaves, producing small shotholes through leaf tissue that are about 1mm wide (Anderson et al., 2007; Cranshaw, 2010; Radl, 2018). New adults emerge from leaf mines and feed briefly before departing for overwintering locations in July. Leafminer larvae drop from leaf mines in June and enter soil where they pupate and overwinter (Miller & Ware, 2014).

We conducted this study in northern Colorado, USA across four semi-arid, medium-sized cities: Fort Collins, Greeley, Longmont, and Loveland. All sampled trees were publicly managed Siberian elm, and we obtained property owner permission wherever sampling required access to a private yard. One hundred Siberian elm trees were randomly selected for sampling from a database that consisted of approximately 1,700 Siberian elms. Because all environmental variables analyzed were within a 100m radius of each tree, we sampled trees that were at least 100m apart to reduce spatial autocorrelation (Parsons et al., 2020). Throughout the sampling season, some trees were eliminated from the dataset because of limb pruning (12), misidentification (3), or loss of temperature data loggers (16), likely by animals, people, or wind.

As a result, the final dataset consists of the remaining 69 trees (26 in Longmont, 25 in Loveland, 5 in Greeley, and 13 in Fort Collins). All trees were sampled every three weeks in June-September 2021 for a total of five sampling periods (June 1-10, June 28-July 2, July 19-23, August 9-13, and August 30-September 3).

Insect Density

At each sampling period, we measured insect density on four branches of each tree, one branch in each cardinal direction (N, S, E, and W). The sampling unit was a 30 cm terminal branch (Dahlsten et al., 1993; Rodrigo et al., 2019), and we assumed equal leaf area per branch. All sampled branches were in the lower canopy up to 3 meters from the ground, and branches that could not be reached from the ground were accessed using a ladder. Sampled branches were haphazardly chosen from a distance where insects were not distinguishable to avoid sampling bias.

On each tree branch, we counted individuals of each observable insect stage: beetle eggs, larvae, and adults (the beetle pupates in cryptic locations such as under bark or in the soil, and thus pupae were not counted); weevil leaf mines and adults; and the number of leaves with leafminer mines. Individual leafminer mines were not counted because adult females lay multiple eggs per leaf, and it is common for mines to merge and become indistinguishable from one another as larvae develop. Thus, it was not possible to count the number of individual mines for this species. Leafminer adults were not counted because this stage had disappeared for the season by the start of the first sampling period. The total number of leaves on each branch was also recorded. In addition to serving as the response variable for our environmental hypotheses, insect density of each species was also used as predictor variables for the co-occurring herbivore hypothesis.

Vegetational Complexity

We measured the structural complexity of the vegetation in a 10 x 10 meter area around each tree following Shrewsbury & Raupp (2000, 2006). Specifically, we sectioned off a 10 x 10 meter area around each study tree and divided this area into one hundred 1 x 1 meter squares. In each of these squares, we recorded five vegetation categories: ground cover (e.g., mulch or turf grass), herbaceous plants (e.g., garden annuals/perennials, tall native grasses), shrubs (e.g., hydrangea, boxwood, barberry), understory trees (e.g., juniper, plum, crabapple, small Siberian Elm), or overstory trees (those with mature canopy including ash, pine, and other elm). One point was awarded for each vegetation type present, resulting in 0-5 points awarded in each square. To quantify complexity of the vegetation in a continuous way, points were summed for all one hundred squares. Thus, each tree received a vegetational complexity score between 0 and 500. See supplemental materials (S1) for examples of trees with a range of vegetational complexity scores.

Building Distance

To assess the local availability of structures for insect overwintering, we measured the distance of each sampled tree to the nearest building as in Speight et al (1998). This was performed digitally using QGIS version 3.10.12 (QGIS Development Team, 2022) and the ESRI Standard Basemap, which displays built structures.

Impervious Surface

Impervious surface data were obtained through the USGS Multi-Resolution Land Characteristics Consortium (Dewitz & US Geological Survey, 2021) on a 30 x 30 meter scale and processed using QGIS version 3.10.12 (QGIS Development Team, 2022). We used the zonal statistics tool to calculate the percentage of impervious surface within a 20 meter buffer

surrounding each sampled tree, which is more predictive of herbivorous insect density than impervious surface at larger spatial scales (Just et al., 2019). Although impervious surface data were not available at a smaller spatial scale, the zonal statistics tool allowed us to obtain an estimate of impervious surface within 20 meters of each tree using 30 x 30 meter data by computing an average impervious surface value based on weighted averages of the extent to which each 30 x 30 meter pixel overlapped with the 20 meter buffer around a tree.

Canopy Temperature

Canopy temperature at each tree was measured every 1.5 hours via the iButton ThermoChron (model DS1921G-F5). Temperature logging began at 7:30AM MST on June 12 and ended at 7:30AM MST on August 25 for a total of 1,185 data points per logger. We placed each logger in a compostable container to prevent contact with direct sunlight and attached them with a zip tie to branches approximately 2-3 meters from the ground. We placed temperature loggers on the east side of the tree wherever possible or on the west side of the tree if a stable eastern location was not available. Despite efforts to minimize contact with direct sunlight, several loggers recorded artificially inflated temperatures. This made mean and maximum temperatures impractical for analysis. We used mean nighttime temperature in the following analyses (7:30PM-7:30AM MST, n=666 measurements per logger) because the urban heat island effect is less variable, occurs more frequently, and is more intense in urban canopies at night compared to the day (Du et al., 2021; Sun et al., 2019).

Host Availability

We measured host availability digitally by counting the number of elm trees within a 100 meter buffer around each tree using QGIS version 3.10.12 (QGIS Development Team, 2022) and a dataset of publicly managed trees provided by municipal forestry departments. We chose a 100

meter radius because significant changes in insect density are detectable for multiple insect species at this spatial scale (Sperry et al., 2001). Although Siberian elm is a preferred host of the insects in this system, other species of elm may also serve as hosts and were thus included in this data set. Following digital assessment, we verified all counts *in situ* to capture any visible privately owned trees and verify that trees in the dataset were still alive and present in the field. Despite efforts to avoid spatial autocorrelation, four trees had 100 meter buffers that overlapped with the buffer of another tree (that is, two locations where two trees had overlapping buffers). Because the maximum overlap was <14% of the buffer area, we retained these trees in our analyses.

Statistical Analysis

To examine the *a priori* hypotheses above and determine the extent to which urban environmental factors (vegetational complexity, building distance, impervious surface, canopy temperature, and host availability) and density of co-occurring herbivores explain insect pest density, we built linear mixed-effects models in R (R Core Team, 2020) and RStudio version 1.4.1103 (RStudio Team, 2021) using the package *lme4* (Bates et al., 2015). To account for variation between tree and cardinal direction of the branches, we included these variables as random intercepts in all models. Environmental factors and density of co-occurring herbivores were modeled as fixed effects, and each insect species was modeled separately. Predictor variables were not strongly correlated with one another (Spearman's rank correlation coefficient $\leq |0.52|$); thus, all predictor variables (vegetational complexity, building distance, temperature, impervious surface, host availability, and density of co-occurring herbivores) were included in the models. We also included interaction terms for impervious surface and temperature, impervious surface and vegetational complexity, and vegetational complexity and temperature.

Although factors endogenous to each tree were not of primary interest in our study, we also included diameter at breast height (DBH), a measure of tree size, in the models to account for the wide range of tree sizes encountered in the field (see Table 1) and differences in tree physiology (such as age or defense) that can be associated with this metric.

We modeled leafminer density with a multivariate normal distribution using the proportion of leaves mined in the first sampling period (calculated as the number of leaves mined divided by the total number of leaves present on the sampled branch) as the response variable. Leafminer larvae, whether few or many in an individual leaf, typically excavate the entire leaf during mining, causing it to drop off the branch. This makes proportion of leaves mined a biologically relevant indication of damage to the tree. Leafminer density was only quantified during the first sampling period because insect larvae had dropped from their mines to the ground by the second sampling period in late June.

We modeled weevil density with a Poisson distribution using the sum of mines (summed by cardinal direction of the branch) sampled over the course of the season as the response variable. Similarly, beetle density was modeled with a Poisson distribution using the sum of eggs and larvae (summed by cardinal direction) sampled over the season as the response variable. Although the beetle model showed evidence of overdispersion and zero inflation, we chose not to use a negative binomial distribution or observation-level random effects due to poor model fit and the tendency of observation-level random effects to maintain or increase model bias at high levels of overdispersion and zero inflation such as those that we detected (Harrison, 2014). Counts of weevil and beetle adults were not included in analyses as they are highly mobile, jumping or flying from tree branches when disturbed. Thus, adults detected in sampling are unlikely to reflect true insect density.

To analyze the resulting models, we performed model averaging using information theory to avoid model uncertainty and reduce model selection and parameter estimation bias (Grueber et al., 2011; Hegyi & Garamszegi, 2011; Symonds et al., 2011). Specifically, we used the *dredge* function to generate models with different combinations of fixed-effect variables, then performed model averaging using the *model.avg* function (*MuMin* package, Bartoń, 2020). We used AIC_c selection criteria (Grueber et al., 2011) to evaluate leafminer and weevil models, and we used QAIC_c selection criteria and corresponding variance inflation factors to evaluate beetle models to address overdispersion (Richards, 2008).

Model assumptions of linearity and normality were checked using plots of model residuals generated with the *DHARMA* package (Hartig, 2022). A calculation of Levene's test modified for linear mixed-effects models with quantitative predictor variables was conducted to test for homoskedasticity. We also tested for overdispersion and zero inflation of model residuals using the *DHARMA* package. To test for spatial autocorrelation, we used a Moran's I test from the *DHARMA* package. Although we found evidence for spatial autocorrelation of model residuals for weevil and beetle density models, removing trees with overlapping 100m buffers and including a spatial dependency structure did not alleviate the autocorrelation. Additionally, these efforts to account for spatial autocorrelation did not appreciably change predictor variable estimates, 95% confidence intervals, or conclusions drawn from the models. As such, we believe that the autocorrelation detected in the model residuals may be a result of model complexity or a biologically important predictor being missing from analysis (Zuur et al., 2010). Reported results are derived from models that include 69 trees without spatial dependency structures.

Results

We found that insect density is associated with the urban environmental factors analyzed as well as density of co-occurring herbivores. Direction and magnitude of environmental effects on insect density are species-specific, and summary statistics for predictor variables are given in Table 1.1. We present results of model averaging below, and full model outputs with coefficients (slope of the relationship with insect density), 95% confidence intervals (CI), standard errors, and z-values (test statistics) for each species are available in supplemental materials (S1.2-S1.4).

Table 1.1. Summary statistics for predictor variables analyzed in linear mixed-effects models of insect density.

	N	Minimum	Median	Mean	SD	Maximum
DBH (cm)	85	6.0	189.0	213.1	142.751	578.0
Vegetational Complexity	85	0.00	65.00	73.05	51.807	213.00
Building Distance (m)	85	2.047	13.520	30.304	59.827	482.90
Host Availability	85	0.00	14.00	16.87	14.236	71.00
Impervious Surface (%)	85	0.00	34.12	34.97	20.216	87.48
Temperature (C°)	69	17.88	19.67	19.60	0.682	20.81

Elm Leafminer

The proportion of leaves mined ranged from 0.0 to 0.712 with a mean of 0.258 (standard deviation = 0.171). Marginal and conditional R^2 values for the leafminer global model were 0.27 and 0.59, respectively. We found that leafminer density increased with DBH (Estimate = 0.0003, 95% CI = 0.0001 – 0.0005, z-value = 3.136) such that larger trees experienced more leaf mining (Figure 1.1A). For approximately every 300 cm increase in DBH, there was a 10% increase in

the proportion of leaves mined. Leafminer density decreased with higher temperatures (Estimate = -0.0771, 95% CI = -0.2277 – -0.0314, z-value = 3.305) such that hotter tree canopies had less leaf mining (Figure 1.1B). An increase in temperature of approximately 1.3C° was associated with a 10% decrease in the proportion of leaves mined. We also found that vegetational complexity and impervious surface had interacting effects on leafminer density (Estimate = 0.00003, 95% CI = 0.000002 – 0.00005, z-value = 2.110), and this interaction is visualized in Figure 1.1 by creating categories of vegetational complexity and impervious surface.

Vegetational complexity was visualized based on definitions of simple and complex vegetation in Shrewsbury & Raupp (2006), and impervious surface was visualized based on the median observed value. Leafminer density increased more strongly with vegetational complexity on trees surrounded by high levels of impervious surface (> 34%) than on trees surrounded by low levels of impervious surface (< 34%) (Figure 1.1C). Additionally, leafminer density decreased with impervious surface in simple habitats (vegetational complexity <125) and increased with impervious surface in complex habitats (vegetational complexity >125) (Figure 1.1D).

Leafminer density was not associated with either building distance (Estimate = -0.0003, 95% CI = -0.0009 – 0.0002, z-value = 1.191) or host availability (Estimate = 0.0008, 95% CI = -0.0014 – 0.0031, z-value = 0.709). Furthermore, leafminer density was not associated with weevil (Estimate = -0.0013, 95% CI = -0.0035 – 0.0009, z-value = 1.174) or beetle (Estimate = -0.0005, 95% CI = -0.0011 – 0.0002, z-value = 1.461) density. We also found no support for interactions between vegetational complexity and temperature (Estimate = 0.0005, 95% CI = -0.0002 – 0.0012, z-value = 1.377) or between temperature and impervious surface (Estimate = 0.0004, 95% CI = -0.0018 – 0.0027, z-value = 0.379).

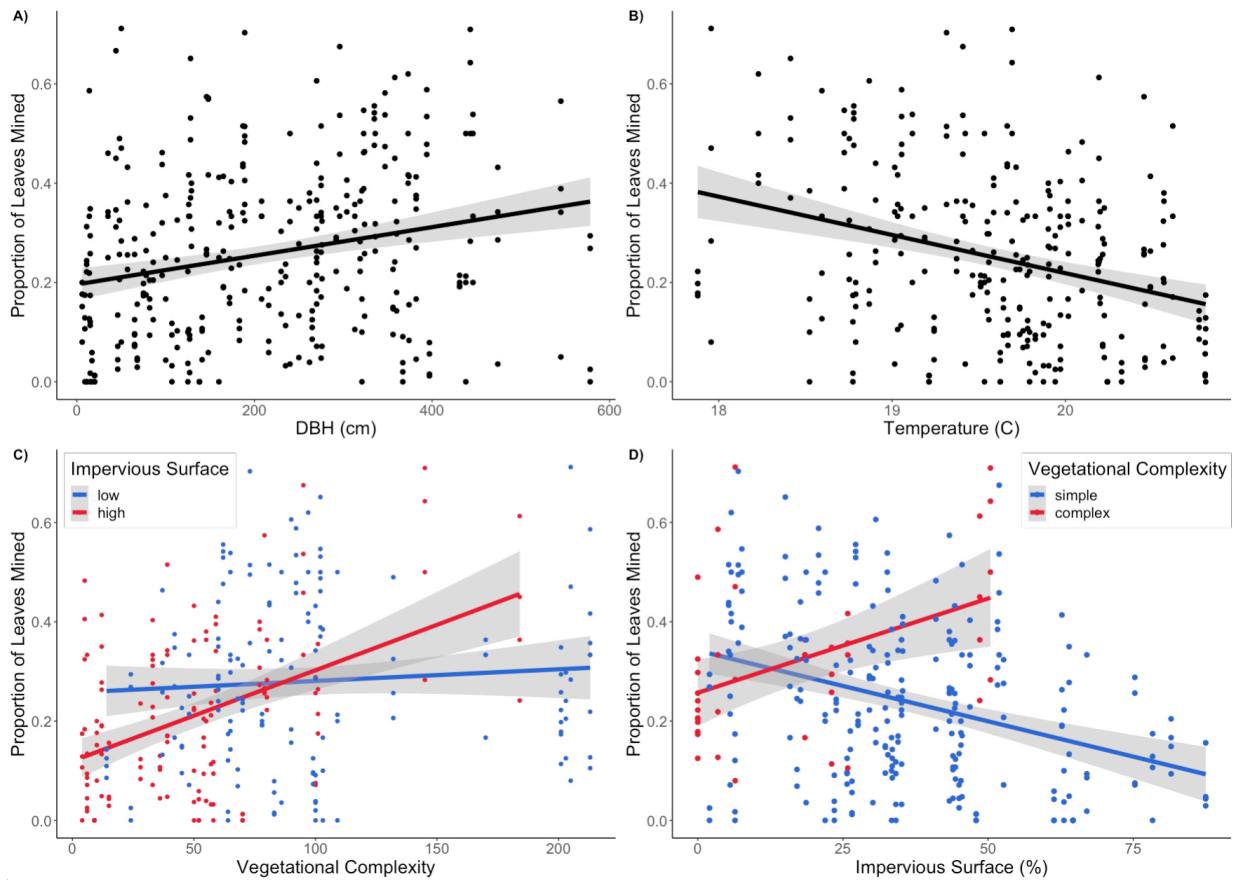


Figure 1.1. The proportion of leaves mined by the elm leafminer **A)** increased with DBH (95% CI = 0.0001 – 0.0005), **B)** decreased with temperature (95% CI = -0.2277 – -0.0314), **C)** increased with vegetational complexity more strongly on trees surrounded by high levels of impervious surface (>34%) than low levels of impervious surface (<34%), and **D)** decreased with impervious surface in simple habitats (vegetational complexity <125) and increased with impervious surface in complex habitats (vegetational complexity >125). Regression lines are displayed with 95% confidence intervals.

Elm Flea Weevil

The sum of weevil mines per branch ranged from 0 to 65 with a mean of 6.21 (standard deviation = 9.56). Marginal and conditional R^2 values for the weevil global model were 0.28 and 0.80, respectively. We found that weevil density increased with DBH such that larger trees experienced more weevil mining (Estimate = 0.003, 95% CI = 0.001 – 0.005, z-value = 3.462, Figure 1.2A). For approximately every 333 cm increase in DBH, there was an increase of 1 mine

per branch. We also found that weevil density increased with greater availability of host elm trees in the landscape (Estimate = 0.015, 95% CI = 0.0007 – 0.030, z-value = 2.049). However, this result should be interpreted with caution because we did not find an association between weevil density and host availability when modeled on a larger sample size (see supplemental materials S1.7 and S1.9, in which a model with 89 trees that did not include temperature did not detect this pattern. This was the one point of difference between weevil models on the smaller dataset with temperature and the larger dataset without temperature). Weevil density decreased with leafminer density such that branches with more leafminer activity experienced less weevil activity (Estimate = -0.711, 95% CI = -1.211 – -0.211, z-value = 2.786, Figure 1.2B). However, we did not find an association between weevil density and beetle density (Estimate = 0.002, 95% CI = -0.0007 – 0.004, z-value = 1.406).

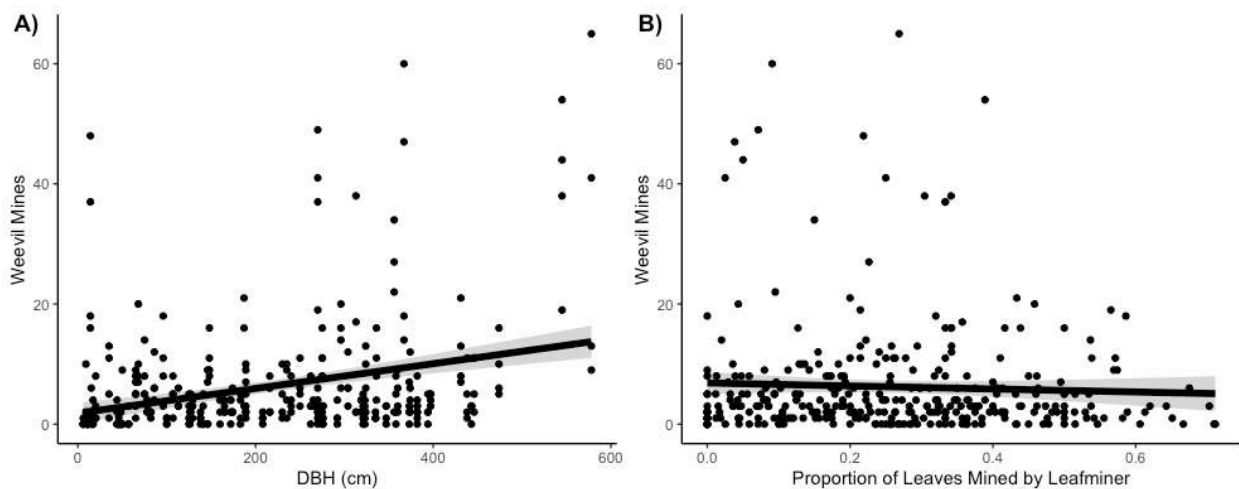


Figure 1.2. Elm flea weevil density **A)** increased with DBH (95% CI = 0.001 – 0.005) and **B)** decreased with leafminer density (95% CI = -1.211 – -0.211). Regression lines are displayed with 95% confidence intervals.

We did not find evidence that weevil density was associated with vegetational complexity alone (Estimate = 0.037, 95% CI = -0.049 – 0.123, z-value = 0.846) or temperature alone (Estimate = 0.265, 95% CI = -0.481 – 1.011, z-value = 0.695). However, we did find that weevil density was influenced by an interaction between vegetational complexity and temperature (Estimate = -0.004, 95% CI = -0.007 – -0.0021, z-value = 3.796), and this interaction is visualized in supplemental materials S1.5 by creating categories of vegetational complexity (based on definitions in Shrewsbury & Raupp, 2006) and temperature (based on the observed median value). Weevil density increased weakly with temperature in simple habitats (vegetational complexity <125) and decreased weakly with temperature in complex habitats (vegetational complexity >125). In addition, weevil density increased faster with vegetational complexity in cooler habitats (<19.7 C°) than in warmer habitats (>19.7 C°).

Weevil density was not associated with building distance (Estimate = 0.002, 95% CI = -0.002 – 0.006, z-value = 1.035) or impervious surface (Estimate = -0.099, 95% CI = -0.412 – 0.215, z-value = 0.617). We also found no support for interactions between vegetational complexity and impervious surface (Estimate = -0.0001, 95% CI = -0.0003 – 0.0001, z-value = 1.024) or between temperature and impervious surface (Estimate = 0.012, 95% CI = -0.004 – 0.029, z-value = 1.449).

Elm Leaf Beetle

The sum of beetle eggs and larvae across the season on each branch ranged from 0 to 181 with a mean of 20.99 (standard deviation = 30.42). Marginal and conditional R² values for the beetle global model were 0.32 and 0.98, respectively. We found that beetle density increased with temperature such that trees in hotter areas had more beetle eggs and larvae (Estimate = 0.966, 95% CI = 0.153 – 1.778, z-value = 2.330, Figure 1.3A). For approximately every 1.0C°

increase in nighttime canopy temperature, there was an associated increase in 1 beetle egg or larva per branch. Beetle density was negatively associated with leafminer density such that branches with more leafminer activity experienced less beetle activity (Estimate = -0.59, 95% CI = -0.895 – -0.289, z-value = 3.830, Figure 1.3B). Although we found a positive association between beetle density and weevil density (Estimate = 0.009, 95% CI = 0.002 – 0.015, z-value = 2.634), this result should be interpreted with caution because we did not find an association between beetle density and weevil density when modeled on a larger sample size (see supplemental materials S1.8 and S1.9 in which a model with 89 trees that did not include temperature did not detect this pattern).

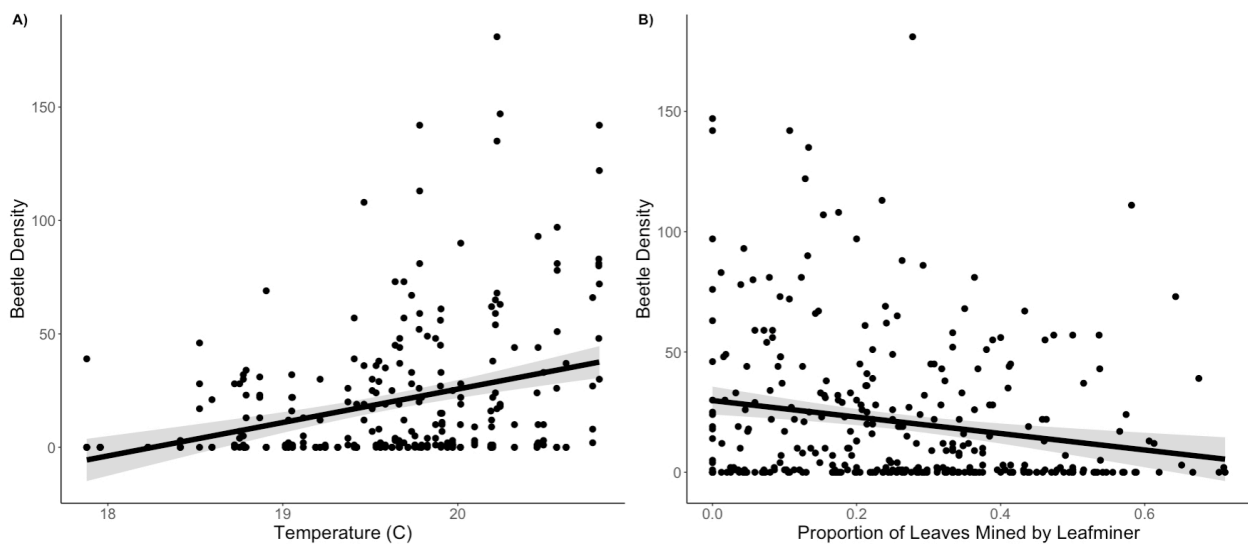


Figure 1.3. Elm leaf beetle density **A)** increased with temperature (95% CI = 0.153 – 1.778) and **B)** decreased with leafminer density (95% CI = -0.895 – -0.289). Regression lines are displayed with 95% confidence intervals.

We did not find evidence that beetle density was associated with vegetational complexity (Estimate = -0.0006, 95% CI = -0.061 – 0.060, z-value = 0.021), building distance (Estimate = 0.003, 95% CI = -0.005 – 0.011, z-value = 0.668), impervious surface (Estimate = 0.030, 95% CI = -0.157 – 0.218, z-value = 0.318), or host availability (Estimate = 0.007, 95% CI = -0.021 –

0.035, z-value = 0.496). We also did not find support for interactions between vegetational complexity and impervious surface (Estimate = 0.0002, 95% CI = -0.0002 – 0.0005, z-value = 0.879), temperature and impervious surface (Estimate = 0.0004, 95% CI = -0.029 – 0.030, z-value = 0.027), or vegetational complexity and temperature (Estimate = -0.0007, 95% CI = -0.010 – 0.009, z-value = 0.144).

Discussion

We found that urban environments have unique associations with three species of invasive insect herbivores on elm trees (Figure 1.4). These variable responses provide insight into the underlying biological mechanisms driving insect density in urban forests while also revealing avenues for future research. We also found that species interactions play an important role in mediating insect density, emphasizing the need for more studies that consider the entire herbivore complex of a host plant.

Insects respond variably to urban environments

Elm leaf beetle density was not associated with vegetational complexity, and elm flea weevil density was not associated with vegetational complexity alone, but this effect was mediated by temperature (see supplemental materials S1.5). On the other hand, elm leafminer density increased in more complex habitats, and this relationship was stronger on trees surrounded by more impervious surface (Figure 1.1C, Figure 1.4). This finding reinforces the importance of a complex vegetative community as protection for the elm leafminer as it overwinters within the soil, especially in areas where vegetation is limited by the dominance of impervious surface. This result is corroborated by studies that find ground-dwelling insects respond positively to vegetative species richness (Philpott et al., 2019) and negatively to vegetative removal (Koivula et al., 2019) in other urban systems.

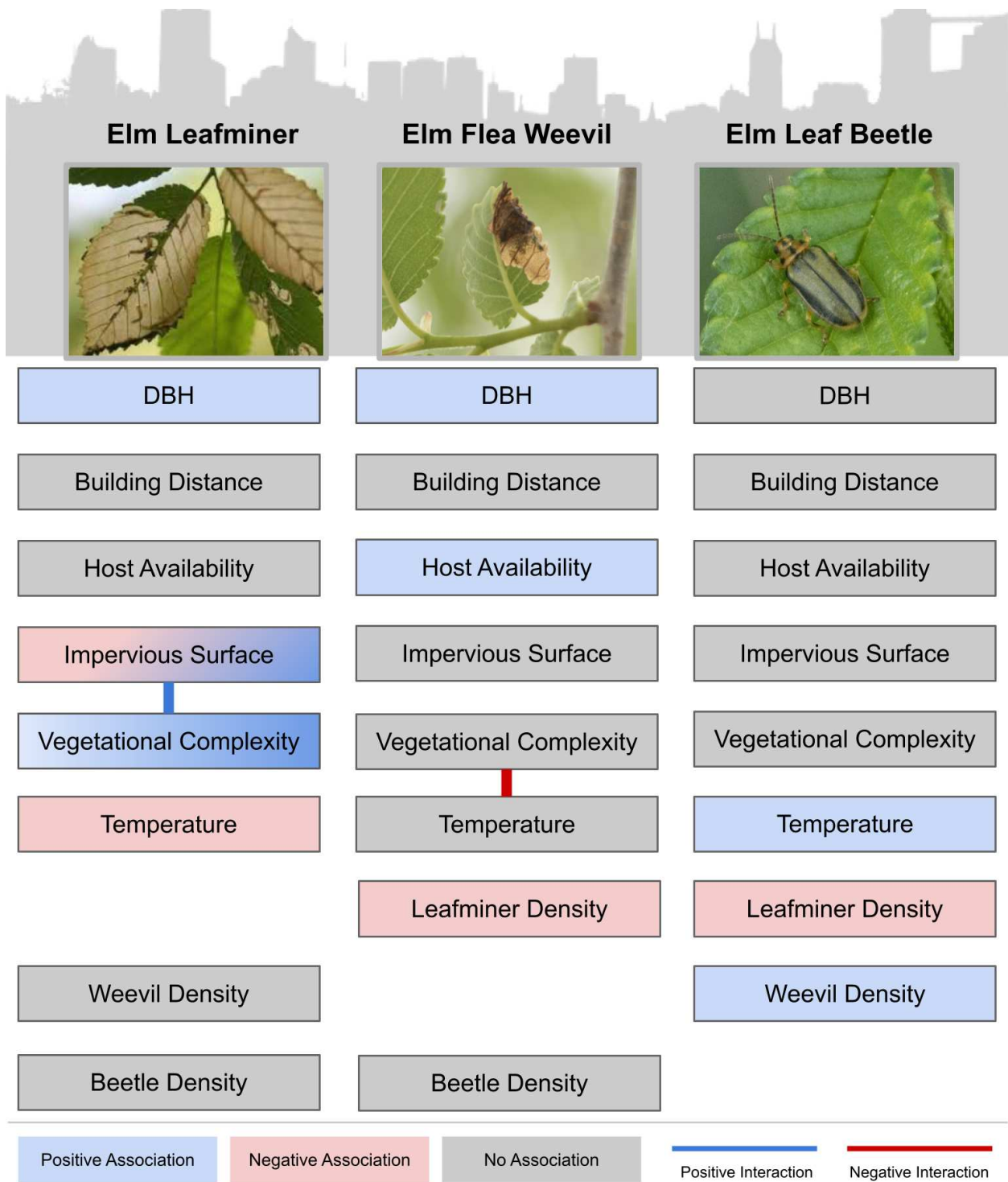


Figure 1.4. Urban environmental factors and co-occurring herbivores that impact the density of elm leafminer, elm flea weevil, and elm leaf beetle. All indicated relationships are for estimates where the 95% confidence interval did not overlap with zero. Elm Leafminer image (UGA2200041) courtesy of Whitney Cranshaw, Colorado State University, Bugwood.org.

Similar to the vegetational complexity results, elm leaf beetle and elm flea weevil density were not associated with impervious surface. However, leafminer density decreased with greater impervious surface in simple habitats and increased with greater impervious surface in complex habitats (Figure 1.1D, Figure 1.4). This finding suggests that on trees surrounded by a complex vegetational community and high levels of impervious surface, the leafminer may retain suitable overwintering habitat while also benefitting from reduced tree defenses and increased nutritional quality that can accompany impervious surface and resulting host water stress (Gely et al., 2020).

For temperature, we found that leafminer density decreased with higher temperatures, beetle density increased with higher temperatures, while weevil density was not associated with temperature alone, but this effect was mediated by vegetational complexity (see supplemental materials S1.5). It is possible that the warm urban temperatures observed in our study are beyond the leafminer's thermal optimum as has been observed with some species of spiders (Meineke et al., 2017), aphids (Parsons et al., 2020), and diverse other insect taxa (Youngsteadt et al., 2017) in urban environments, although there has been no research on the thermal physiology of the elm leafminer. In contrast, laboratory research has demonstrated that elm leaf beetle larvae respond positively to temperature increases up to 28.8 C°, which is similar to the high temperatures recorded in our study region during the months of sampling (Colorado Climate Center, 2022). However, it is unclear from our study whether the observed positive relationship between temperature and beetle density is due to changes in insect physiology (Dale & Frank, 2017; Frank & Just, 2020), changes in tree stress and host quality (Martinson et al., 2020; Moreira et al., 2019), declines in natural enemy communities (Meineke et al., 2014, 2017; Parsons et al., 2020) or something else. In the face of both current and predicted urban warming, further

research is needed to disentangle the biological mechanisms responsible for the observed temperature associations and their ecological implications.

Surprisingly, the distance of a host tree to the nearest building was not associated with insect density for any of the pest species studied. Insects that overwinter on or inside built structures typically have lower winter mortality, and distance to buildings has been an important factor in density of the horse chestnut scale (Speight et al., 1998) and mimosa webworm (Hart et al., 1986) in other urban systems. Research suggests that the elm leaf beetle is chill tolerant but not freeze tolerant during winter diapause. Thus, beetle aggregation in sheltered overwintering locations is important for winter survival in the temperate regions of its range (Soudi & Moharramipour, 2011), and the elm leaf beetle is well known for overwintering in homes, contributing to its historical pest status (USDA Forest Service, 2011). Despite this, the role of overwintering survival in elm leaf beetle population dynamics remains poorly understood. Additionally, other metrics (such as the total area occupied by buildings within an insect's dispersal radius) may provide a more accurate picture of the availability of overwintering habitat. Future research on the dispersal capacity of these and other urban species of interest would allow for the construction of more biologically relevant metrics for availability of overwintering locations.

It was also surprising that the availability of host trees was associated only with elm flea weevil density and not elm leaf beetle or elm leafminer density (though as noted above, we interpret this result for the weevil with caution, see also supplemental materials S1.7 and S1.9). The availability of a host plant can play a large role in the spread of novel invasive insects (Paap et al., 2017; Poland & McCullough, 2006; Raupp et al., 2006) and has been positively associated with density of the horse chestnut scale (Speight et al., 1998), honeylocust plant bug, mimosa

webworm, and honeylocust spider mite (Sperry et al., 2001) in other urban areas. Our results may support the theory that urban landscapes decouple insect density and host availability (Nelson & Forbes, 2014).

Insect density is mediated by species interactions

In this system, we observed three species of insect pests present simultaneously on their host tree. We found that the influence of these co-occurring insects on each other depended on the species. We did not find evidence that leafminer density is affected by either the weevil or the beetle. In contrast, both weevil and beetle density were negatively affected by leafminer density (Figure 1.4). This may be evidence of priority effects because the elm leafminer emerges from overwintering in early spring before the other two species (Miller-Pierce & Preisser, 2012; Stam et al., 2018). During sampling, we observed the leafminer mating and ovipositing on elm leaves prior to the emergence of either the weevil or the beetle, and leafminer larvae still occupied leaf mines when the beetle and weevil emerged to mate and feed on elm leaves. Although we did not directly measure species interactions or competition in this study, our findings may be preliminary evidence of interspecific competition between the non-native species in this system, which can be especially common in interactions between endophytic and free-living herbivores (Denno et al., 1995; Tooker & Giron, 2020).

Conclusion

We live in an increasingly urbanized world. The ability of urban forests to provide ecosystem services is becoming progressively more important as urban populations grow. Urban tree planting programs have been initiated in multiple major cities including Chicago, Denver, Los Angeles, New York, and Philadelphia (Pincetl et al., 2013). However, tree mortality severely limits the success of these and other tree planting efforts in cities (Widney et al., 2016). The

mosaic of environmental stress and disturbance that characterizes urban landscapes exacerbates the damage caused by non-native insects (Hauer et al., 2020; Liebhold et al., 2017; Lovett et al., 2016). To facilitate the resilience of the urban forest and the provision of ecosystem services, it is paramount to understand how urban environments influence pest density on urban trees. Here, we studied the multi-species complex of non-native herbivores on an economically and ecologically important host tree to examine multiple hypothesis for varied insect density in urban forest ecosystems. Using this approach, we find that insects have species-specific associations with urban environments. The direction and strength of these associations reveal important differences based on species' biology and life history while also revealing avenues for future research in this area.

While this research contributes to our understanding of what environmental factors promote pest density in urban forest ecosystems, there is still work to be done to understand the biological mechanisms that underlie the associations we observed. Furthermore, the trends we observed and their biological mechanisms impact organism evolution through both space (different sites within the urban landscape) and time (Ramalho & Hobbs, 2012; Thompson et al., 2021). Understanding the resulting eco-evolutionary consequences will be important for providing more informed urban management and predicting future community responses to urbanization and insect invasion (Des Roches et al., 2021; Steiner, 2016).

Finally, we find evidence that species interactions mediate pest density for multiple non-native insects on a single host. Non-native insect introductions will continue to increase in the current era of globalization and international trade (Liebhold et al., 2017), and cities serve as important entry points for many species of non-native insect pests. As such, pest density on

urban trees may be increasingly mediated by species interactions among multiple non-native insects in the future.

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CHAPTER 2: ARTHROPOD PREDATORS AND PARASITOIDS OF TWO ELM HERBIVORES IN COLORADO²

Introduction

Elm trees (*Ulmus spp.*) are important components of urban forest ecosystems, highly valued for the ecological and cultural value they provide as well as their tolerance to harsh urban conditions (Büchel et al., 2016; Martín et al., 2019). In many urban areas where Dutch Elm Disease eradicated the American elms that once dominated the landscape, Siberian elms (*Ulmus pumila*) and hybrids with Siberian elm parentage were planted to replace them. Although Siberian elm is not native to the North American continent, it is valued for its fast growth, resistance to Dutch Elm Disease, tolerance to drought and cold, and utility as a windbreak, especially in the Great Plains and semi-arid western United States (Frye et al., 1988; Griffin et al., 2017; Martín et al., 2019; Potter & Redmond, 2013; Zalapa et al., 2010).

Siberian elm and its hybrids are attacked by several species of invasive insect pests. The elm leaf beetle *Xanthogaleruca luteola* Müller (Coleoptera: Chrysomelidae) and the European elm flea weevil *Orchestes steppensis* Korotyaev (Coleoptera: Curculionidae, hereafter referred to as “elm flea weevil”) are ecologically and economically important pests that cause aesthetic damage, reduced tree growth and vigor, branch dieback, and tree mortality where pest populations are persistently high (Bosu et al., 2007; Condra et al., 2010; Dreistadt & Puttler, 2016; Leatherman, 2012; Li et al., 2018; Radl, 2018; Rodrigo et al., 2019). Elm leaf beetle completes two generations per year in many parts of its range and damages elm leaves through

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adult shot hole feeding and larval skeletonization (Bosu et al., 2007; Cranshaw, 2018; Dahlsten et al., 1993). Damaged leaves desiccate, shrivel, and often drop from the tree. Elm flea weevil completes one generation per year, and adults also produce shot hole feeding damage to leaf tissue. Immature stages of the weevil mine through leaf tissue in a serpentine pattern that meanders and widens as it reaches towards the leaf margin, eventually terminating as a blotch mine where a single larva develops and pupates (Anderson et al., 2007; Condra et al., 2010; Cranshaw, 2010; Leatherman, 2012; Radl, 2018). Adults and immature stages of these insects can cause up to 100% defoliation twice in a season: once on the first flush of leaves and again after trees produce a new flush later in the season (Bosu & Wagner, 2008; Dreistadt & Puttler, 2016).

Chemical control is not recommended for the populated areas where elm leaf beetle and elm flea weevil are commonly found due to high cost, drift, public concern, secondary pest outbreaks, and non-target effects on other organisms (Dreistadt et al., 1991; Hamerski & Hall, 1988; Rodrigo et al., 2019). Biological control by parasitoid and predator natural enemies may be a viable option for sustainable control of these pests, and natural enemies are often integral in exerting top-down control on invasive herbivores in urban and anthropogenically disturbed environments, where elm leaf beetle and elm flea weevil are most damaging (Frank & Shrewsbury, 2004; Hawkins & Gross, 1992; Moreau et al., 2006; Raupp et al., 2009; Scheirs & Bruyn, 2002).

A long-standing classical biocontrol program for elm leaf beetle took place throughout the twentieth century, and several parasitoids were introduced across the United States including the egg parasitoid *Oomyzus gallerucae* Fonscolombe (Hymenoptera: Eulophidae) (Howard, 1908) and the larval-adult parasitoid *Erynniopsis antennata* Rondani (Diptera: Tachinidae)

(Flanders, 1940). *Oomyzus gallerucae* was released extensively across the eastern United States, but populations from these releases only established in Ohio (Bartlett & Clausen, 1978; Hall & Johnson, 1983). The egg parasitoid was also released in California, and populations established where the parasitoid overwintered successfully (Dahlsten et al. 1998; Dreistadt & Dahlsten 1991). To date, *O. gallerucae* has been found in multiple US states where there is no record of introduction, suggesting successful range expansion of populations that are able to overwinter in the North American invaded range (Dreistadt & Puttler 2016; Puttler & Bailey 2003).

Erynniopsis antennata was also released in multiple states across the country and established in California and Oregon (Dreistadt & Puttler 2016). *Erynniopsis antennata* provides only limited control of elm leaf beetle because its populations generally peak late in the season, failing to suppress early season growth of elm leaf beetle populations (Luck & Scriven, 1976; Rodrigo et al., 2019). In addition to parasitoids, generalist predators have been documented to attack elm leaf beetle in Oklahoma (Eikenbary & Raney 1968) and California (Luck & Scriven 1976), with more recent documentation lacking in the literature. Elm flea weevil natural enemies and biological control agents are largely unknown (Li et al., 2018) due to its recent identification as a species unique from its congeners (Korotyaev, 2016). Several undetermined Pteromalidae and the generalist parasitoid *Eupelmus vesicularis* (Retzius) parasitized flea weevil mines in Utah, Oregon, and Washington (Looney et al., 2012), and the weevil is parasitized by several species in the families Eulophidae and Pteromalidae in its native Chinese range (Li et al., 2018).

Elm leaf beetle and elm flea weevil outbreaks have caused severe damage in Colorado and several other US states in recent years (Condra et al., 2010; Radl, 2018, personal coorespondance with Whitney Cranshaw and the City of Longmont), creating concern among managers and necessitating a renewed interest in sustainable control methods. While natural

enemies are speculated to contribute to regulating populations of elm leaf beetle (Dreistadt & Puttler, 2016) and elm flea weevil (Radl, 2018) there are no field studies evaluating this claim for many parts of the invaded range. The aim of this research was to document the predators, parasitoids, and percent parasitism of elm leaf beetle and elm flea weevil in the Front Range of Colorado where Siberian Elm has been widely planted and suffers outbreaks of both pests. Specifically, we ask (1) What arthropod predators are found with and consume elm leaf beetle and elm flea weevil in Colorado? (2) What elm leaf beetle and elm flea weevil parasitoids are established in Colorado? and (3) How much parasitism occurs, and how does this vary across the sampling season? This research will fill a critical knowledge gap on natural enemy presence in Colorado and help managers evaluate sustainable control options in the face of severe pest outbreaks in the region.

Methods

This research took place in northern Colorado (CO), USA, a semi-arid region in the western Great Plains, where elm leaf beetle has been established since the mid-twentieth century (Brewer, 1973; Eikenbary & Raney, 1968) and elm flea weevil has been established since at least the early 2000s (Looney et al., 2012). Siberian elm is a preferred host species for both pests (Bosu et al., 2007; Kirichenko et al., 2019) and is widely planted in the study region. We sampled insects on Siberian elm trees in three locations known to host both pest species: City of Longmont (Boulder County, CO), Crow Valley Campground in Pawnee National Grassland (Weld County, CO) and the Town of Windsor (Weld County, CO). Longmont and Windsor are medium-sized cities dominated by low to high intensity development and developed open space (Dewitz & US Geological Survey, 2021). Crow Valley Campground is a small area of paved roads and facilities used for medium-intensity recreational activities, such as camping and hiking. While the

surrounding area is dominated by agricultural land and grasslands with few native trees, Siberian elm trees were intentionally planted around the campground and other human settlements within the natural area. Because our goal was to find natural enemies, we concentrated on 15 trees on which abundance of the pests were relatively high (Table 2.1). To capture natural enemies with a range of phenology, we sampled repeatedly throughout the season (June 1-4, June 21- 25, July 12-15, August 2-6, and August 20-25). Trees in Longmont were sampled during all periods, except for one tree that was sampled only in early June because accessible branches were removed after this date; trees in Pawnee National Grassland and Windsor were sampled the latter four periods.

Table 2.1. Locations of surveyed *Ulmus pumila* trees. ^a Sampled five times in early June – August 2021 except for tree 7, which was sampled only in early June. ^b Sampled four times in late June – August 2021.

Location & Tree	Coordinates
City of Longmont ^a	
1	N 40.20389 W 105.2006
2	N 40.15167 W 105.1522
3	N 40.165 W 105.13
4	N 40.17806 W 105.1203
5	N 40.17639 W 105.1097
6	N 40.1675 W 105.1189
7	N 40.17028 W 105.1169
8	N 40.16833 W 105.1147
9	N 40.16944 W 105.1131
10	N 40.17167 W 105.1117
Pawnee National Grassland ^b	
11	N 40.64668 W 104.34343
12	N 40.64674 W 104.34284
13	N 40.64422 W 104.34114
Town of Windsor ^b	
14	N 40.47765 W 104.90070
15	N 40.47897 W 104.89864

Predator Collection & Identification

To determine what arthropod predators are found with and consume elm leaf beetle or elm flea weevil in Colorado, we collected potential predators from trees with pest populations and evaluated consumption in laboratory feeding trials. Specifically, we used a white beat sheet (71 cm²) to dislodge potential predators on four branches (one in each cardinal direction) on each tree during each sampling period. All sampled branches were in the lower canopy and up to three meters from the ground. To evaluate if potential predators would feed on elm leaf beetle or elm flea weevil, we collected all dislodged arthropods, took them back to the laboratory at Colorado State University, and placed them individually in a 14 cm diameter petri dish with the life stages of beetle (egg, larva, pupa, adult) and weevil (leaf mine, adult) that were present in the field at the time of collection. In this way, feeding trials captured a realistic menu of beetle or weevil life stages available to the predator in the field at the time that it was collected. Potential predators were allowed to feed for 48 hours before being retained in ethanol for identification, and any consumed beetles and weevils were recorded. During this period, predators were kept in ambient light and temperature conditions (22.0C° - 24.5C°, mean = 23.18C°). Initial protocol included a 24-hour starvation period before pests were introduced to the predators. However, this was eliminated from the protocol after the second sampling period due to high predator mortality during starvation. In addition to capturing potential predators with a beat sheet, we observed and collected ground-dwelling predators when beetles were pupating in the soil around the host tree.

Predators that consumed any life stage of elm leaf beetle or elm flea weevil either in the field or in laboratory feeding trials were grouped by order or family and identified using group-specific keys (Evans, 1985; Fisher & Cover, 2007; Gordon & Vanderberg, 1991; Hoffman, 1987; Lawson, 1959; Taber, 1998). In addition, insects that did not feed during trials but belonged to

groups previously documented to feed on elm leaf beetle (we are not aware of any documented arthropod predators of elm flea weevil) were also identified using group-specific keys (McPherson, 1982; Strange, 2021). Once identified with keys, specimens were checked for defining characters against reference specimens at the Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins, Colorado USA. All specimens documented herein are deposited in the Gillette Museum of Arthropod Diversity.

Parasitoid Collection & Identification

To survey parasitoids of elm leaf beetle and elm flea weevil in Colorado, we collected beetle eggs, beetle larvae, and weevil leaf mines and reared them in the laboratory for parasitoid emergence. We chose these life stages because they are attacked by parasitoids that are established in other US states (Dreistadt & Puttler, 2016; Looney et al., 2012; Puttler & Bailey, 2003). Specifically, we collected specimens from four 30 cm terminal branches on each tree (one in each cardinal direction) during each sampling period; branches sampled for parasitoids were different from those sampled for predators. During collection, we retained the leaves on which egg clusters were laid and mines were developing, and we collected extra leaves for larval feeding. After collecting insects, we brought them to the laboratory at Colorado State University for rearing. All specimens were reared in lidded plastic containers; egg clusters and larvae were reared under a photoperiod of 16:8 (L:D) (Ehler et al., 1987; Rodrigo et al., 2019), and leaf mines were reared by a window under ambient light conditions. Rearing temperatures ranged from 22.0C° to 24.5C° (mean = 23.18C°). To keep leaves fresh, we inserted the petiole of each leaf into a 1.5mL lidded Eppendorf tube filled with water with a hole cut in the top of the tube to allow the petiole to pass through into the water. We checked for insect emergence three to four times per week, replenishing water in Eppendorf tubes and providing fresh leaves for larval

feeding as needed. We reared insects for four weeks, until beetle or weevil individuals emerged, until parasitoids emerged, or until the specimen was compromised by mold. Late in the season, *Erynniopsis antennata* attacks elm leaf beetle larvae that pupate and develop into adult beetles. The parasitoid then overwinters within elm leaf beetle adults and emerges the following spring (Dreistadt & Dahlsten 1990; Flanders 1940). As such, we retained elm leaf beetle adults reared from second generation larvae to dissect them for *E. antennata*. Parasitoids were stored in ethanol for identification, and we identified elm leaf beetle parasitoids using keys from de V. Graham (1985) and Tschorsnig & Herting (1994). Parasitoids that emerged from leaves containing weevil mines were identified to family- and genus-level using Gibson et al. (1997) and then sent to experts for confirmation and species-level identification. Pending these confirmations, we report family-level identifications for parasitoids emerged from leaves containing weevil mines.

We calculated percent parasitism of beetle eggs, beetle larvae, and weevil mines overall, at each location, and in each sampling period. For each of these values, we estimated both “low” and “high” percent of parasitism. The low parasitism estimate was calculated as (the number of parasitoids) / (all beetles or weevils reared), and the high parasitism estimate was calculated as (the number of parasitoids) / (the number of beetles or weevils reared excluding those that died from unknown causes unrelated to parasitism). To compare percent parasitism of the different locations sampled, we used Fisher’s Exact Test in R (R Core Team, 2020) and RStudio version 1.4.1103 (RStudio Team, 2021).

Results

Through observation and laboratory feeding trials, we found seven species of arthropod predators that consumed elm leaf beetle or elm flea weevil. Over the course of the sampling

season, we also collected 58 beetle egg clusters, 539 beetle larvae, and 435 weevil mines to rear them for parasitoids. Of these, 37 beetle egg clusters, 210 beetle larvae, and 119 leaves containing weevil mines successfully produced either a parasitoid, elm leaf beetle, or elm flea weevil; the remainder of the specimens experienced mortality during rearing due to mold or unknown causes. From these specimens, we found parasitoids of both elm leaf beetle and elm flea weevil, and we believe these to be new state records of parasitoid species for these pests in Colorado.

Predators

Six species representing five orders and six families of arthropod predators attacked various stages of elm leaf beetle (Figure 2.1 A – F). These predators were collected from all Windsor and Pawnee sites and two sites in Longmont. The multicolored Asian lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) was the most abundant predator we sampled, and we collected *H. axyridis* from multiple sites in mid-July through early August. Through laboratory feeding trials, we found that both *H. axyridis* adults and late-instar larvae consumed entire beetle egg clusters, while only *H. axyridis* adults consumed beetle larvae. In late June, an unidentified species of *Phyllobaenus* Dejean (Coleoptera: Cleridae) was present on elm trees, and it consumed beetle eggs and early-instar larvae in feeding trials. *Parasteatoda tepidariorum* (Araneae: Theridiidae) was also present in late June and consumed late-instar beetle larvae in laboratory feeding trials. We observed the western harvester ant *Pogonomyrmex occidentalis* Cresson (Hymenoptera: Formicidae) actively foraging beneath elm trees and attacking beetle larvae on the ground in mid-July. The European earwig *Forficula auricularia* Linnaeus (Dermaptera: Forficulidae) was also active on the ground beneath elm trees in mid-July and consumed beetle pupae in laboratory feeding trials. In late August, we observed a fourth

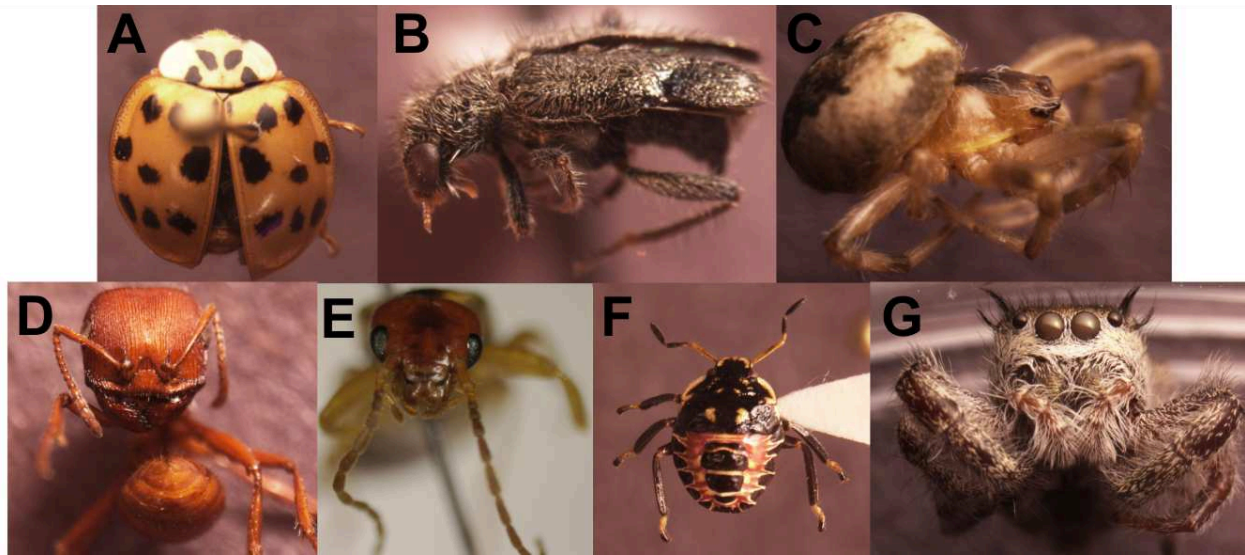


Figure 2.1. Predators found with and consuming elm leaf beetle (A-F) or elm flea weevil (G) in Colorado. A) *Harmonia axyridis* (Coleoptera: Coccinellidae), B) *Phyllobaenus* sp. (Coleoptera: Cleridae), C) *Parasteatoda tepidariorum* (Araneae: Theridiidae), D) *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae), E) *Forficula auricularia* (Dermaptera: Forficulidae), F) *Podisus placidus* (Hemiptera: Pentatomidae), G) *Phidippus audax* (Araneae: Salticidae).

instar nymph of the predatory stink bug *Podisus placidus* Uhler (Hemiptera: Pentatomidae) carrying and feeding on a deceased beetle adult. Another *P. placidus* nymph was also collected from an elm tree in early August, although it did not consume any live stages of elm leaf beetle in laboratory feeding trials. To our knowledge, *Pogonomyrmex occidentalis*, *Phyllobaenus* sp., and *Parasteatoda tepidariorum* belong to families that are newly documented to consume elm leaf beetle.

We found one species, the bold jumping spider *Phidippus audax* Hentz (Araneae: Salticidae), that readily consumed elm flea weevil adults in laboratory feeding trials (Figure 2.1 G). This *P. audax* individual, a gravid female, was collected from elm leaves in late-June at Crow Valley Campground and deposited her egg sac during the feeding trial. We did not collect or observe any arthropods that consumed mining stages of elm flea weevil. Larger images of all predators in dorsal, lateral, and frontal views are available in Appendix B.

Parasitoids

Through rearing elm leaf beetle eggs and larvae, we found the egg parasitoid *Oomyzus gallerucae* Fonscolombe (Hymenoptera: Eulophidae) and the larval-adult parasitoid *Erynniopsis antennata* Rondani (Diptera: Tachinidae) are present and attacking elm leaf beetle in Colorado. Both findings represent new state records for these parasitoids. Over the whole season and across all trees sampled, the combined percent parasitism of beetle eggs and larvae was 1.17% - 2.83% (low parasitism estimate – high parasitism estimate calculated as described above).

The total percent parasitism of beetle eggs by *O. gallerucae* was 5.17% - 8.11%. However, the percentage of eggs parasitized differed by location (Table 2.2). Egg parasitism was higher in Pawnee National Grassland than Longmont or Windsor ($P = 0.005$ for low parasitism estimate, $P = 0.031$ for high parasitism estimate). In fact, egg parasitism was entirely absent from Longmont and Windsor (Figure 2.2A). Across all locations sampled, no egg clusters were parasitized in the first three sampling periods (June 1 – July 15), and egg parasitism peaked in the final sampling period (August 20 – August 25) at 25.0% - 28.57% (Figure 2.2B). This did not synchronize with either the first- or second-generation peak in beetle egg clusters collected, which occurred in June and early August, respectively.

The total percent parasitism of elm leaf beetle larvae by *E. antennata* was 0.74% - 1.90%. We did not find evidence that larval parasitism was different among locations ($P = 0.059$ for low parasitism estimate, $P = 0.095$ for high parasitism estimate), although Pawnee National Grassland was the only location where we did not find parasitized larvae (Table 2.2, Figure 2.3A). Although larval parasitism remained low throughout the study, it peaked during the fourth sampling period (August 2 – 6) at 1.67% - 3.57% (Figure 2.3B). This did not synchronize with the peak in the number of larvae collected (corresponding to the first larval generation), which

occurred in the second sampling period (June 21 – June 25). However, it did align with when second-generation larvae were most abundant in the field, although the peak in second-generation larvae was roughly 1/6 of the peak in first generation larvae.

Table 2.2. Low and high parasitism estimates for elm leaf beetle eggs, elm leaf beetle larvae and elm flea weevil mines by location and sampling period. A single value indicates that the low and high parasitism estimates were equivalent.

Location, Sampling Period	Egg Parasitism (Egg Clusters Reared)	Larval Parasitism (Larvae Reared)	Mine Parasitism (Mines Reared)
Longmont	0.0 % (29)	1.19 – 2.44 % (84)	2.48 – 9.89 % (363)
June 1-4	0.0 % (13)	N/A (0)	0.34 – 1.33% (297)
June 21-25	0.0 % (5)	1.25 – 2.56 % (80)	13.11 – 50.0% (61)
July 12-15	0.0 % (3)	0.0 % (1)	0.0% (5)
August 2-6	0.0 % (7)	0.0 % (1)	N/A (0)
August 20-25	0.0 % (1)	0.0 % (2)	N/A (0)
Pawnee National Grassland	27.27 – 30.0 % (11)	0.0 % (282)	9.76 – 26.67 % (41)
June 21-25	0.0 % (3)	0.0 % (197)	3.33 – 8.33% (30)
July 12-15	0.0 % (1)	0.0 % (30)	27.27 – 100% (11)
August 2-6	20.0% (5)	0.0 % (23)	N/A (0)
August 20-25	100.0% (2)	0.0 % (32)	N/A (0)
Windsor	0.0 % (18)	1.73 – 4.17 % (173)	29.03 – 69.23 % (31)
June 21-25	0.0 % (6)	0.88 – 2.5% (114)	29.63 – 66.67% (27)
July 12-15	N/A (0)	4.76 – 7.14 % (21)	25.0 – 100% (4)
August 2-6	0.0 % (7)	2.78 – 5.56 % (36)	N/A (0)
August 20-25	0.0 % (5)	0.0% (2)	N/A (0)

A diverse parasitoid community emerged from leaves containing elm flea weevil mines. Because genus- and species-level identifications are pending confirmation by taxonomic experts, we report family-level identification for these parasitoids below followed by discussion of our tentative genus-level identifications. The total percent parasitism of elm flea weevil mines

across all locations and sampling periods was 5.06% - 18.49%. Of the emerged parasitoids, roughly 40% of individuals belonged to the family Pteromalidae and 36% of individuals belonged to the family Eulophidae. The remainder of the parasitoid community consisted of 14% Eupelmidae individuals and 5% each of Chalcididae and Encyrtidae individuals. The percent

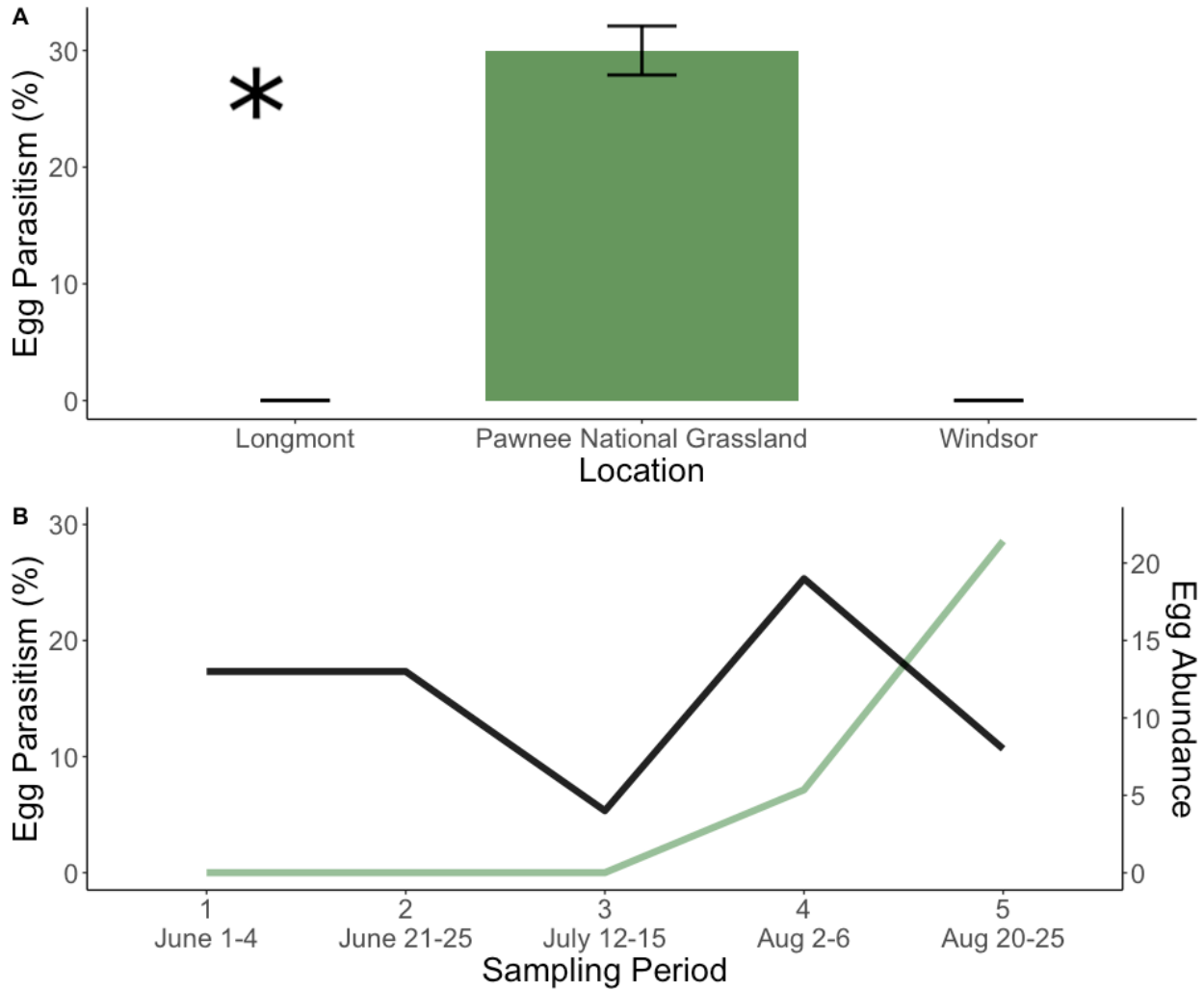


Figure 2.2. Parasitism of elm leaf beetle egg clusters by *O. gallerucae* **A)** was higher in Pawnee National Grassland than Longmont or Windsor ($P = 0.031$), error bar depicts standard error; and **B)** peaked in the final sampling period (August 20 – August 25) as depicted with the green line. This did not synchronize with the peak in total abundance of egg clusters collected as depicted with the black line. High parasitism estimates are shown for simplicity; these patterns are consistent for low parasitism estimates.

parasitism of leaves containing weevil mines differed by location ($P = 7.50 \times 10^{-7}$ for low parasitism estimate, $P = 8.09 \times 10^{-6}$ for high parasitism estimate). Specifically, parasitism was highest in Windsor followed by Pawnee and Longmont (Table 2.2, Figure 2.4A). Interestingly, we did not find the family Pteromalidae in weevil mines collected in Pawnee, while the families

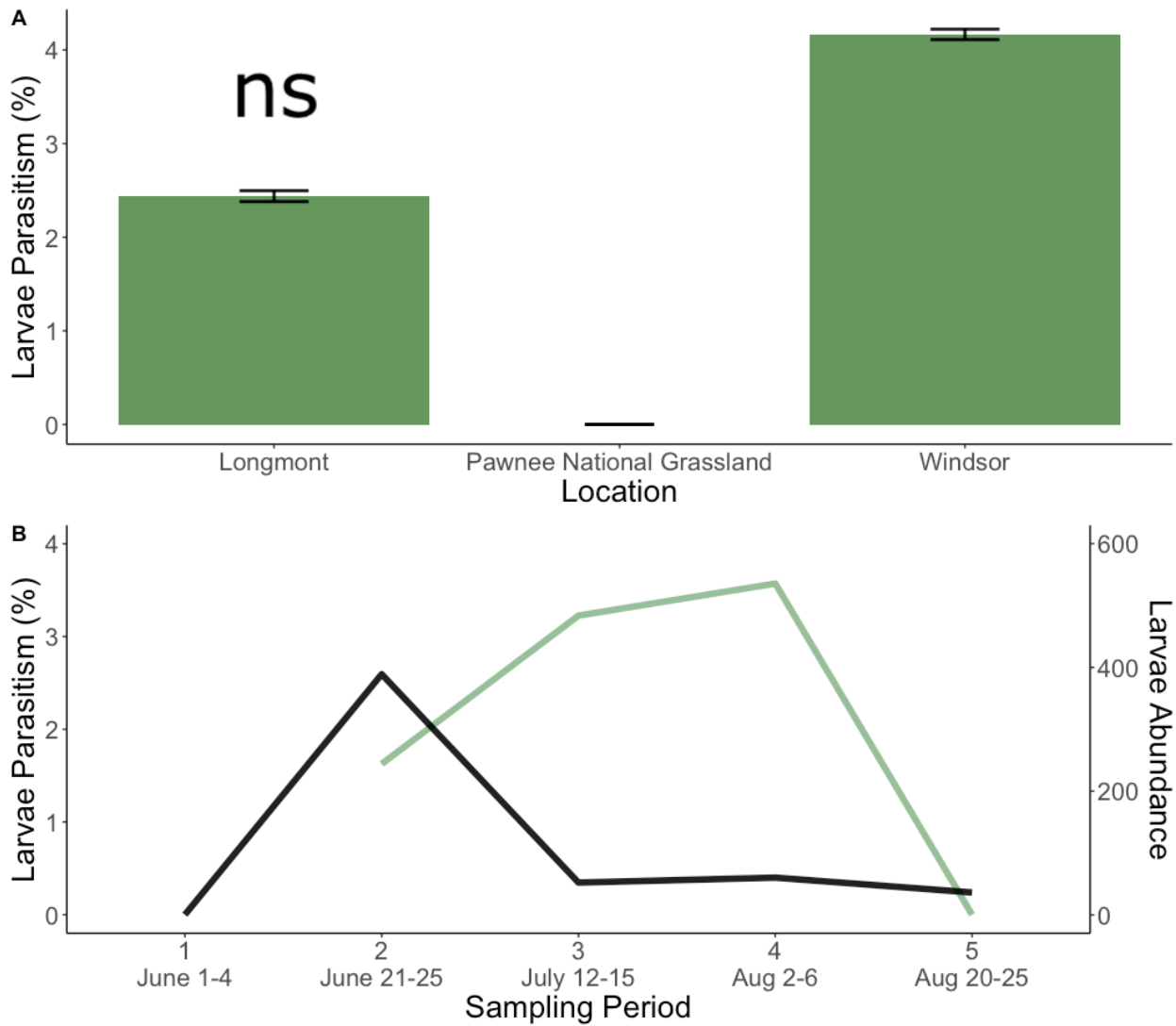


Figure 2.3. Parasitism of elm leaf beetle larvae by *E. antennata* **A**) was not significantly different in Longmont, Pawnee National Grassland, or Windsor ($P = 0.095$), error bar depicts standard error; and **B**) peaked in the fourth sampling period (August 2 – August 6) as depicted with the green line. This did not synchronize with the peak in total abundance of larvae collected as depicted with the black line. High parasitism estimates are shown for simplicity; these patterns are consistent for low parasitism estimates.

Chalcididae and Encyrtidae were only reared from mines collected in Pawnee. We found the family Eupelmidae only in Longmont, and the family Eulophidae was present in all three locations (Figure 2.4A). Across all locations sampled, mine parasitism peaked in the third sampling period (July 12 – 15) at 20.0 – 100%, and this was driven by parasitoids in the families Eulophidae and Encyrtidae (Figure 2.4B). All other parasitoid families reached their peak during the second sampling period (June 21 – 25). No parasitoid family synchronized with the peak in the number of mines collected, which occurred in the first sampling period (June 1 – 4). Because the elm flea weevil has one relatively short generation per year, no mines were present on elm leaves in the final two sampling periods (August 2 – 27).

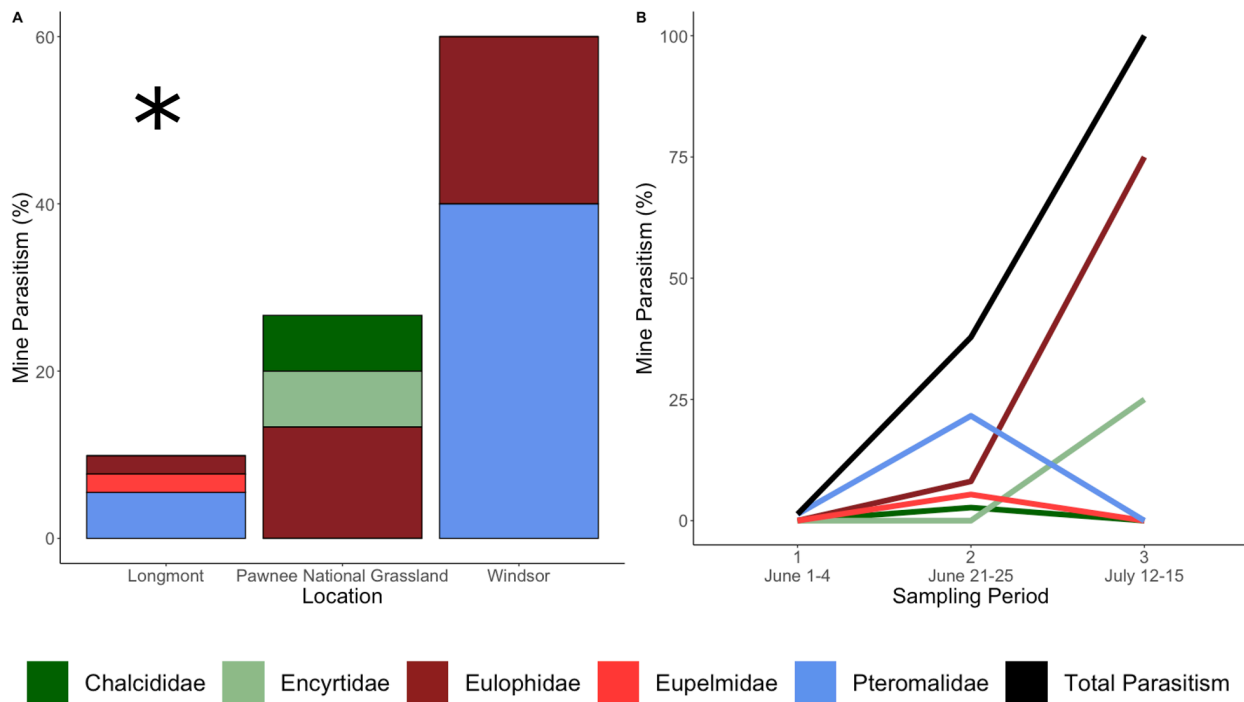


Figure 2.4. A diverse parasitoid community emerged from leaves containing elm flea weevil mines. The total percent parasitism A) differed by location and was highest in Windsor followed by Pawnee and Longmont ($P = 8.09 \times 10^{-6}$) and B) peaked in the third sampling period (Jul 12 – July 15). High parasitism estimates are shown for simplicity; these patterns are consistent for low parasitism estimates.

Discussion

In this study, we provide novel information regarding the predators and parasitoids of two elm pests in Colorado, a state experiencing severe outbreaks, using observation, laboratory feeding trials, and insect rearing. Additionally, we quantify the percent of parasitism to provide an initial evaluation of the level of control provided by natural enemies in this system. Below, we highlight several findings that have important management implications for the control of elm leaf beetle and elm flea weevil by predators and parasitoids.

Predators

In this study, we provide updated documentation of elm leaf beetle predators in the state of Colorado. While we believe *Pogonomyrmex occidentalis*, *Phyllobaenus* sp., and *Parasteatoda tepidariorum* belong to families that are newly documented to consume elm leaf beetle, our results also corroborate earlier reports of insects that consume elm leaf beetle. Earwigs are previously documented to be important predators of the beetle (USDA Forest Service, 2011), and we confirmed the presence of and predation by the European earwig *Forficula auricularia*. In Oklahoma, Eikenbary and Raney (1968) report predation of elm leaf beetle adults by late instar nymphs of the *Podisus* genus of predatory stink bugs. Here, we confirm the presence of *Podisus placidus* in Colorado and its consumption of a deceased elm leaf beetle adult by a fourth instar nymph. Additionally, we collected two specimens of Neuropteran larvae in the genus *Chrysoperla*, which is documented to consume elm leaf beetle eggs and larvae in California (Luck & Scriven, 1976) and Oklahoma (Eikenbary & Raney, 1968). *Chrysoperla* sp. larvae did not consume any stage of elm leaf beetle in our laboratory feeding trials, but we believe this is because both specimens pupated shortly after trials began. Furthermore, *Chrysoperla* sp. and

other arthropods that did not feed during our trials may have been prevented from feeding due to the unnatural conditions of a laboratory.

In Oklahoma, Eikenbary & Raney (1968) documented the convergent lady beetle *Hippodamia convergens*, a native species, feeding on elm leaf beetle eggs and larvae in June and July. Although we did not find *Hippodamia convergens* consuming elm leaf beetle in Colorado, the non-native multicolored Asian lady beetle *Harmonia axyridis* was the most abundant predator we collected. In contrast to the early-season control of elm leaf beetle by *Hippodamia convergens* documented in Eikenbary & Raney (1968), we found that *Harmonia axyridis* was not present on elm branches until mid-July, with the majority of sightings in August. Intentionally introduced in California in the early twentieth century to provide biological control of crop pests, *Harmonia axyridis* is now established throughout the United States (Roy et al., 2016). Despite its utility as a biological control agent in many cropping systems (Koch & Galvan, 2008), *Harmonia axyridis* tends to suppress native lady beetle species, including *Hippodamia convergens*, through intraguild predation and competition (Michaud, 2002; Snyder et al., 2004). Colorado hosts approximately 70 species of native lady beetles, which are common in urban and garden settings; *Hippodamia convergens* is even known to aggregate in the Front Range of Colorado (Cranshaw, 2014; Simpson & Welborn, 1975). Given the absence of other native lady beetle species in our sampling, our results suggest that *Harmonia axyridis* may be replacing native lady beetles as the dominant species in the region while also failing to provide early-season predation of elm leaf beetle.

While all developmental stages of elm leaf beetle (egg, larva, pupa, and adult) were consumed by at least one predator in our study, we did not find any arthropod predators of the mining stages of elm flea weevil. As a leaf mining insect, the weevil is naturally shielded from

the higher levels of predation to which free-living and externally feeding insects are susceptible (Tooker & Giron, 2020). Additionally, predation of elm flea weevil by arthropods may not be as prevalent as predation by birds. In fact, predation of the weevil by several species of birds has been previously documented in Colorado (Leatherman, 2012), and bird predation is important in mediating herbivory by leafmining insects in several European cities (Kozlov et al., 2017).

We acknowledge several limitations of our sampling that may have hindered our ability to capture and identify predators of elm leaf beetle and elm flea weevil. First, using a beat sheet to sample predators from tree branches did not capture many flying insects, such as wasps, or ground foraging insects, such as other species of ants, that might feed on elm leaf beetle and elm flea weevil that have fallen to the ground. Furthermore, our sampling occurred during daylight hours, limiting our ability to detect arthropods that forage primarily at night. Sampling in the lower canopy also limited our ability to investigate the arthropod community that dwells in the upper canopy of elm trees.

Even so, we found that predators of elm leaf beetle and elm flea weevil were uncommon in the Front Range of Colorado. Throughout the sampling season, we collected one individual each of *Parasteatoda tepidariorum*, *Phyllobaenus* sp., and *Phidippus audax*; 2 nymphs and 1 adult of *Podisus placidus*; and 3 adults and 3 larvae of *Harmonia axyridis*. *Pogonomyrmex occidentalis* and *Forficula auricularia* typically live in concealed colonies, and so their numbers were not evaluated. In comparison, Eikenbary & Raney (1968) collected more than 500 predator specimens over the course of two years in Oklahoma. Thus, our findings suggest that predation by arthropod natural enemies plays a relatively smaller role in the control of elm leaf beetle and elm flea weevil in Colorado compared to other areas.

Parasitoids

Both pest species experienced parasitism during this study, and our results reveal new state records of the egg parasitoid *Oomyzus gallerucae* and the larval-adult parasitoid *Erynniopsis antennata*. While it is likely that these parasitoids have been present in the state for some time, under-sampling for parasitoids in Colorado may have prevented previous detection. Furthermore, *O. gallerucae* and *E. antennata* are established in Colorado despite there being no documented introductions of these biological control agents in the state. *Oomyzus gallerucae* has been detected in several mid-western states where there is no record of release, including Illinois, Iowa, Kansas, Missouri, Nebraska, and Oklahoma (Puttler & Bailey, 2003); prior to this study, there were no established populations of *E. antennata* recorded outside California and Oregon (Dreistadt & Puttler, 2016). Therefore, our results may indicate a successful range expansion of these biological control agents into Colorado. Additionally, it is possible these parasitoids entered the state via human transportation of parasitized elm leaf beetle.

We found a diverse complex of parasitoids in the families Pteromalidae, Eulophidae, Eupelmidae, Chalcididae and Encyrtidae that emerged from elm leaves containing flea weevil mines, and these are the first parasitoids of elm flea weevil documented in the invaded range outside the Pacific Northwest. While genus-level identifications are currently pending confirmation by taxonomic experts, we discuss these tentative identifications below. The dominant genus that emerged from leaves containing weevil mines was *Ablaxia* (Pteromalidae). The hosts of this parasitoid genus are mostly unknown in the Nearctic region; however, *Ablaxia* has documented associations with concealed Curculionids in Europe (Gibson et al., 1997). We also found several specimens that we suspect belong to the genus *Eupelmus* (Eupelmidae), which typically parasitizes insects in concealed locations, such as leafminers (Gibson, 2011). We found

one specimen belonging to the genus *Zagrammosoma* (Eulophidae), which is used in the biological control of leafmining pests in the orders Lepidoptera, Diptera, and Coleoptera (Perry & Heraty, 2021). The host records of these genera provide promising evidence that they are parasitoids of elm flea weevil.

However, we also found several specimens whose host records are less consistent with our proposed association with elm flea weevil. We found one specimen belonging to the family Encyrtidae, and this family includes secondary parasitoids of other Chalcidoidea (Gibson et al., 1997) as well as parasitoids of leafminers (Paiva & Yamamoto, 2015). As such, this specimen may be a hyperparasitoid of a primary parasitoid that attacks elm flea weevil, or a primary parasitoid of the weevil itself. We also found several specimens that we suspect belong to the genera *Galeopsomyia* and *Eprhopalotus* (Eulophidae), which are typically parasitoids of gall-making insects in the families Cecidomyiidae and Cynipidae (Gibson et al., 1997). While it is possible that these specimens emerged from cryptic galls that were present but undetected on the elm leaves from which we reared insects, some species of *Galeopsomyia* have also been documented to switch hosts onto leafmining insects (LaSalle & Pena, 1997). Furthermore, host-switching in parasitoids may be more common than previously thought, especially for hosts in an expanded or invaded range (Lee, 2020). Therefore, this result, if confirmed, may provide additional evidence of a host switch from gall-making to leaf-mining hosts in some species of *Galeopsomyia* and *Eprhopalotus*. Species confirmations and additional rearing from elm flea weevil mines will be essential in drawing further conclusions about parasitoid complex associated with this insect.

Percent parasitism of beetle eggs, beetle larvae, and weevil mines in Colorado were low, and this contrasted with the high levels of parasitism recorded in other states with no record of

parasitoid introduction (Puttler & Bailey, 2003). In our study, elm leaf beetle egg parasitism by *O. gallerucae* was 5.17% - 8.11% over the season, and larvae parasitism by *E. antennata* was <2% overall and never exceeded 14% on a single tree. While parasitoid emergence from leaves containing weevil mines was higher at 5.06% - 18.49%, this level was not high enough to achieve control of elm flea weevil. Out of the three locations sampled, we found parasitized egg clusters only in Pawnee National Grassland; weevil parasitoids in the families Chalcididae and Encyrtidae were only found in Pawnee, as well. The other two locations, Longmont and Windsor, are cities dominated by low to high intensity development, with open space and natural areas present but comparatively less prevalent. In contrast, our sampling location at Crow Valley Campground in Pawnee is situated within an area of federally managed grasslands encompassing over 200,000 acres. Although the campground where our sampling took place contains paved surfaces, facilities, and intentionally planted Siberian elm trees, development is of low intensity and relatively uncommon in the surrounding grasslands (USDA Forest Service, 2022).

Compared to developed or disturbed landscapes, natural areas and complex habitats have been shown to promote biological control of pests by providing parasitoids with winter refuge, a favorable microclimate, and alternative floral and nectar resources (Landis et al., 2000; Langellotto & Denno, 2004). Furthermore, research suggests that proximity to semi-natural habitats and unmanaged vegetation promotes egg parasitism of the introduced pest *Halyomorpha halys* (Mele et al., 2022). On the other hand, parasitoids tend to be highly susceptible to habitat destruction and fragmentation, with decreased top-down control resulting in pest outbreaks in disturbed areas (Kruess & Tschardtke, 1994; La Salle & Gauld, 1991). Our results raise the possibility that the egg parasitoid *O. gallerucae* and some parasitoid families associated with elm

flea weevil may be limited within cities and other disturbed ecosystems in Colorado. More extensive sampling would help investigate this possibility further.

In this study, we found that early-season parasitism of elm leaf beetle and elm flea weevil was almost entirely absent, and peaks in parasitism did not correspond with when elm leaf beetle eggs, elm leaf beetle larvae, or elm flea weevil mines were most abundant in the field. *Oomyzus gallerucae* did not parasitize any egg clusters collected in early June through mid-July, and parasitism was highest on eggs collected in late August. This peak in egg parasitism did not align with when first- or second-generation egg clusters were most abundant in the field, which occurred in June and early August, respectively. Likewise, larval parasitism by *E. antennata* remained low throughout the study and peaked in early August; this did not align with when larvae were most abundant in the field during their first generation in June, although it did align with a smaller peak in larvae during their second generation. However, the first-generation peak in larvae was more than six times higher than the second-generation peak in larvae. As such, this late-season larval parasitism is likely to be less effective in controlling elm leaf beetle. Early-season absence of both egg (Dahlsten et al., 1994; Dreistadt & Dahlsten, 1991) and larval (Luck & Scriven, 1976; Rodrigo et al., 2019) parasitism is a commonly documented barrier to effective control of elm leaf beetle, and our results support the presence of this barrier in Colorado. This suggests that spring and early summer are time periods that could be targeted with a novel biological control agent, which might enhance control while reducing the potential for competition with parasitoids already established in the state.

Parasitoid emergence from leaves containing elm flea weevil mines peaked in mid-July, and this did not align with when weevil mines were most abundant in early June. Additionally, parasitoid emergence was segregated taxonomically, with the late-season parasitoid community

was dominated by the families Eulophidae and Encyrtidae. Given the uncertainty of host association for these individuals, it is possible that the late-season peak we detected may not be related to control of elm flea weevil. In contrast, weevil parasitism by individuals in the families Pteromalidae and Eupelmidae peaked earlier in the season, closer to the peak in abundance of weevil mines, and host records of individuals in these families provides stronger evidence of their association with elm flea weevil. Due to their association and synchrony with the weevil host, *Ablaxia* (Pteromalidae) and *Eupelmus* (Eupelmidae) may be promising candidates for biological control.

Conclusion

In this study, we present new state records for the egg parasitoid *Oomyzus gallerucae* and the larval-adult parasitoid *Erynniopsis antennata* in Colorado and provide updated documentation of arthropod predators of the elm leaf beetle *Xanthogaleruca luteola*. Additionally, we report preliminary findings of the parasitoid community hosted by elm flea weevil, the first such report in the invaded range outside the Pacific Northwest region. Although parasitoids of elm leaf beetle and elm flea weevil are present in Colorado, parasitism was low and did not synchronize with when hosts were most abundant and damaging in the field. While the presence of natural enemies is promising, our results suggest that they are unlikely to provide effective control over elm leaf beetle and elm flea weevil in Colorado. We recognize that these results are based on a single year of data, and additional research will help us gain a more accurate picture of beetle and weevil control by natural enemies in the state. Furthermore, the identification of parasitoids associated with elm flea weevil is an ongoing area of research. In addition to providing new information on the parasitoid complex of elm flea weevil, these

identifications will contribute to the broader field of parasitoid ecology in a region that is historically under-sampled.

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APPENDIX A: CHAPTER 1 SUPPLEMENTARY MATERIAL

Vegetational Complexity Examples



B





S1.1. The range of vegetational complexity conditions observed in our study ranged from 0 to 213. A) A vegetational complexity score of 0. This tree was located in a parking lot, where the cement reached to the base of the trunk. Dead grass and sticks were not counted in the vegetational complexity score. B) A vegetational complexity score of 100. This tree was located in an urban park and was surrounded by turfgrass and a mulch ring. C) A vegetational complexity score of 213. This tree was located in an urban natural area. Ground cover and herbaceous plants covered the site with several understory and overstory trees.

Global Model Outputs

To determine the extent to which urban environmental factors (complexity of vegetation, building distance, impervious surface, canopy temperature, and host availability) and density of co-occurring herbivores explain insect pest density, we built linear mixed-effects models in RStudio using the package *lme4* (Bates et al., 2015). Site and cardinal direction are modeled as random intercepts. Environmental factors and density of co-occurring herbivores are modeled as fixed effects. We modeled leafminer density with a multivariate normal distribution using the proportion of leaves mined in the first sampling period (number of leaves mined divided by the total number of leaves present on the sampled branch) as the response variable. We modeled weevil density with a Poisson distribution using the sum of mines sampled over the course of the season in each direction as the response variable. We modeled beetle density with a Poisson distribution using the sum of eggs and larvae sampled over the season in each direction as the response variable. To analyze the resulting models, we performed model averaging using information theory (Grueber et al., 2011). Specifically, we used the *dredge* function to generate models with different combinations of fixed-effect variables, then performed model averaging using the *model.avg* function (*MuMin* package, Bartoń, 2020). We chose AICc selection criteria for the leafminer and weevil (Grueber et al., 2011) and QAICc for the beetle to account for overdispersion (Richards, 2008). Conditional model averaged estimates (slope of the relationship with insect density), 95% confidence intervals (CI) for the estimates, standard errors, and z-values (test statistics) for each species are reported below. For the leafminer global model (S1.2), conditional and marginal R^2 values were calculated using the *MuMin* package (Bartoń, 2020). For the weevil (S1.3) and beetle (S1.4) global models, conditional and marginal R^2 values were calculated using the *piecewiseSEM* package (Lefcheck, 2016). See main text for additional details on methods and statistical analyses.

S1.2. Conditional model averages for elm leafminer density. Marginal and conditional R^2 for the global model are 0.27 and 0.59, respectively. Variables in bold indicate estimates where the 95% confidence interval does not overlap with zero.

Variables	Estimate (95% CI)	SE	z-value
Intercept	1.425 (-0.0353 – 2.8850)	0.744	1.913
DBH	0.0003 (0.0001 – 0.0005)	0.0001	3.136
Vegetational Complexity	0.0008 (0.0001 – 0.0015)	0.0004	2.279
Impervious Surface	-0.0021 (-0.0039 – -0.0004)	0.0009	2.378
Temperature	-0.0771 (-0.2277 – -0.0314)	0.023	3.305
Vegetational Complexity * Impervious Surface	0.00003 (0.000002 – 0.00005)	0.00001	2.110
Vegetational Complexity * Temperature	0.0005 (-0.0002 – 0.0012)	0.0004	1.377
Impervious Surface * Temperature	0.0004 (-0.0018 – 0.0027)	0.001	0.379
Building Distance	-0.0003 (-0.0009 – 0.0002)	0.0003	1.191
Host Availability	0.0008 (-0.0014 – 0.0031)	0.001	0.709
Weevil Density	-0.0013 (-0.0035 – 0.0009)	0.001	1.174
Beetle Density	-0.0005 (-0.0011 – 0.0002)	0.0003	1.461

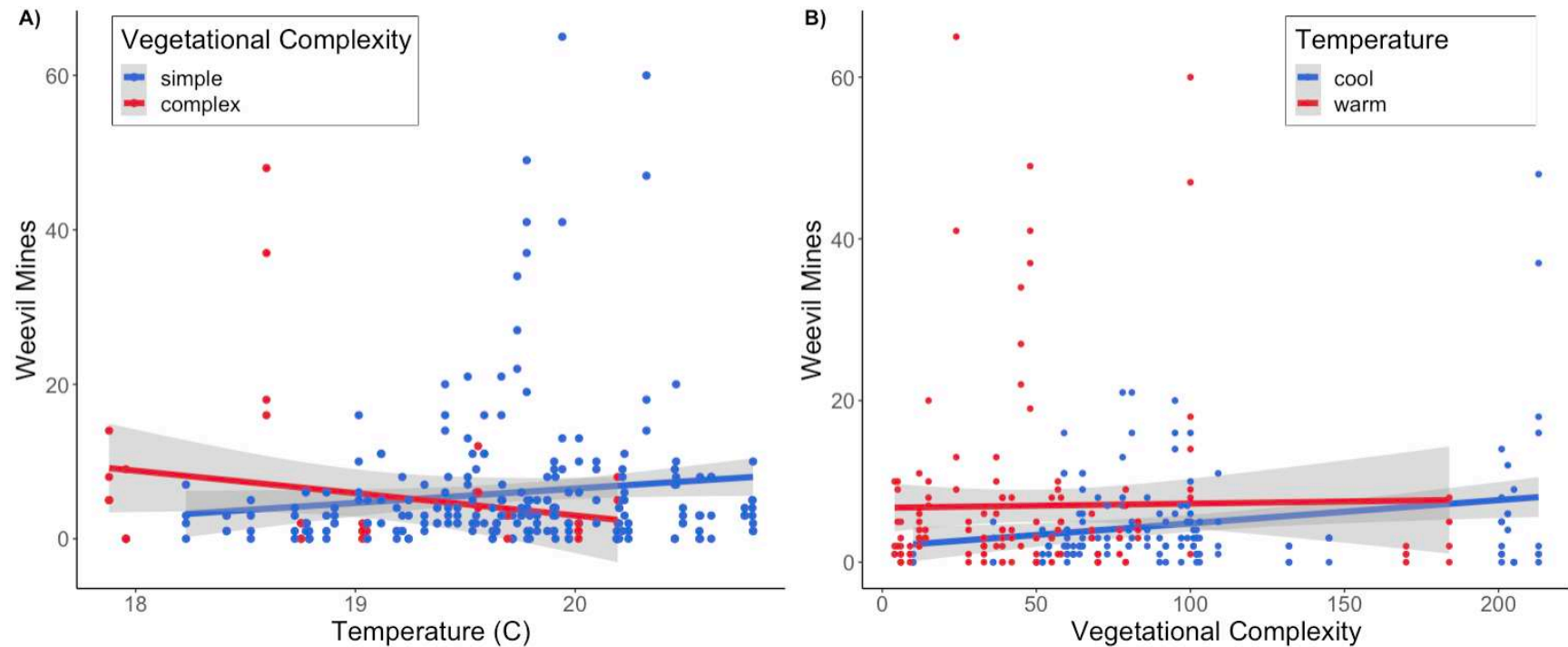
S1.3. Conditional model averages for elm flea weevil density. Marginal and conditional R^2 for the global model are 0.28 and 0.80, respectively. Variables in bold indicate estimates where the 95% confidence interval does not overlap with zero.

Variables	Estimate (95% CI)	SE	z-value
Intercept	-2.781 (-15.697 – 10.136)	6.59	0.422
DBH	0.003 (0.001 – 0.005)	0.0008	3.462
Vegetational Complexity	0.037 (-0.049 – 0.123)	0.044	0.846
Impervious Surface	-0.099 (-0.412 – 0.215)	0.160	0.617
Temperature	0.265 (-0.481 – 1.011)	0.381	0.695
Vegetational Complexity * Impervious Surface	-0.0001 (-0.0003 – 0.0001)	0.0001	1.024
Vegetational Complexity * Temperature	-0.004 (-0.007 – -0.0021)	0.001	3.796
Impervious Surface * Temperature	0.012 (-0.004 – 0.029)	0.009	1.449
Building Distance	0.002 (-0.002 – 0.006)	0.002	1.035
Host Availability	0.015 (0.0007 – 0.030)	0.007	2.049
Leafminer Density	-0.711 (-1.211 – -0.211)	0.255	2.786
Beetle Density	0.002 (-0.0007 – 0.004)	0.001	1.406

S1.4. Conditional model averages for elm leaf beetle density. Marginal and conditional R^2 for the global model are 0.32 and 0.98, respectively. Variables in bold indicate estimates where the 95% confidence interval does not overlap with zero.

Variables	Estimate (95% CI)	SE	z-value
Intercept	-5.378 (-25.726 – 14.970)	10.38	0.518
DBH	-0.00002 (-0.003 – 0.003)	0.002	0.014
Vegetational Complexity	-0.0006 (-0.061 – 0.060)	0.031	0.021
Impervious Surface	0.030 (-0.157 – 0.218)	0.096	0.318
Temperature	0.966 (0.153 – 1.778)	0.414	2.330
Vegetational Complexity * Impervious Surface	0.0002 (-0.0002 – 0.0005)	0.0002	0.879
Vegetational Complexity * Temperature	-0.0007 (-0.010 – 0.009)	0.005	0.144
Impervious Surface * Temperature	0.0004 (-0.029 – 0.030)	0.015	0.027
Building Distance	0.003 (-0.005 – 0.011)	0.004	0.668
Host Availability	0.007 (-0.021 – 0.035)	0.014	0.496
Leafminer Density	-0.59 (-0.895 – -0.289)	0.155	3.830
Weevil Density	0.009 (0.002 – 0.015)	0.003	2.634

Weevil Interaction Effects



S1.5. There is a negative interaction between vegetational complexity and temperature such that **A)** weevil density increased weakly with temperature in simple habitats (vegetational complexity <125) and decreased weakly with temperature in complex habitats (vegetational complexity >125), and **B)** weevil density increased faster with vegetational complexity in cooler habitats (<19.7 C°) than in warmer habitats (>19.7 C°). Regression lines are displayed with 95% confidence intervals.

Modelling Outputs for Alternative Sample Size

Throughout the sampling season, some trees were eliminated from the original dataset of 100 trees because of limb pruning (12) or misidentification (3). Temperature data was available for 69 out of remaining 85 sampled trees. To verify that this smaller sample size did not impact results, we also constructed models excluding temperature on the full set of 85 trees versus the 69 trees for which temperature data was available. Models were built using the package *lme4* (Bates et al., 2015), and we performed model averaging using the *dredge* and *model.avg* functions (*MuMin* package, Bartoń, 2020). We report conditional model averaged estimates, 95% confidence intervals (CI), standard errors, and z-values. We chose the AICc selection criteria for the leafminer and weevil models (Grueber et al., 2011) and QAICc for the beetle models to account for overdispersion (Richards, 2008).

For the leafminer, modeling with 69 or 85 trees did not change which predictor variables were associated with leafminer density (S1.6). For the weevil, both leafminer density and DBH were associated with weevil density when modeled with 69 and 85 trees. Host availability was associated with weevil density with n=69 trees but not n=85 trees (S1.7). As such, we are skeptical of the association between weevil density and host availability in the global model with n=69 trees (including temperature) and speculate that it is a result of the reduced sample size. For the beetle, the intercept, impervious surface, and leafminer density were associated with beetle density when modeled with 69 and 85 trees. There is evidence of an association between weevil density and beetle density when n=69 but not when n=85 (S1.8). As such, we are skeptical of the association between weevil density and beetle density in the global model with n=69 trees (including temperature) and speculate that it is a result of the reduced sample size. Results from all model sets (n=69 with temperature, n=69 without temperature, and n=85 without temperature) for each insect species are summarized in S1.9.

S1.6. Elm Leafminer conditional model averages from models excluding temperature with n=69 trees and n=85 trees. For n=69 trees, marginal $R^2 = 0.19$, conditional $R^2 = 0.58$. For n=85 trees, marginal $R^2 = 0.18$, conditional $R^2 = 0.54$. Variables in bold indicate estimates where the 95% confidence interval does not overlap with zero.

Variables	N=69			N=85		
	Estimate (95% CI)	SE	z-value	Estimate (95% CI)	SE	z-value
Intercept	0.252 (0.196 – 0.308)	0.029	8.835	0.275 (0.193 – 0.358)	0.042	6.528
DBH	0.0003 (0.00009 – 0.0005)	0.0001	2.701	0.0003 (0.00009 – 0.0005)	0.0001	2.801
Vegetational Complexity	0.0009 (0.0003 – 0.001)	0.0003	2.981	0.0008 (0.0002 – 0.001)	0.0003	2.818
Impervious Surface	-0.002 (-0.004 – -0.0008)	0.0008	3.006	-0.002 (-0.004 – -0.001)	0.0007	3.585
Vegetational Complexity * Impervious Surface	0.00003 (0.000002 – 0.00005)	0.00001	2.086	0.00003 (0.000007 – 0.00006)	0.00001	2.520
Building Distance	-0.00005 (-0.0006 – 0.0005)	0.0003	0.157	-0.0002 (-0.0008 – 0.0004)	0.0003	0.596
Host Availability	0.0002 (-0.002 – 0.003)	0.001	0.199	0.0006 (-0.001 – 0.003)	0.001	0.574
Weevil Density	-0.001 (-0.004 – 0.0008)	0.001	1.262	-0.001 (-0.003 – 0.0009)	0.001	1.153
Beetle Density	-0.0006 (-0.001 – 0.00004)	0.0003	1.818	-0.0005 (-0.001 – 0.00006)	0.0003	1.739

S1.7. Elm Flea Weevil conditional model averages from models excluding temperature with n=69 trees and n=85 trees. For n=69 trees, marginal $R^2 = 0.24$, conditional $R^2 = 0.80$. For n=85 trees, marginal $R^2 = 0.24$, conditional $R^2 = 0.82$. Variables in bold indicate estimates where the 95% confidence interval does not overlap with zero.

Variables	N=69			N=85		
	Estimate (95% CI)	SE	z-value	Estimate (95% CI)	SE	z-value
Intercept	0.576 (-0.231 – 1.383)	0.411	1.4	0.464 (-0.343 – 1.270)	0.411	1.127
DBH	0.003 (0.001 – 0.004)	0.0008	3.420	0.003 (0.002 – 0.005)	0.0007	4.227
Vegetational Complexity	0.003 (-0.003 – 0.009)	0.003	0.927	0.003 (-0.003 – 0.009)	0.003	1.030
Impervious Surface	-0.003 (-0.019 – 0.014)	0.008	0.306	-0.002 (-0.018 – 0.015)	0.008	0.193
Vegetational Complexity * Impervious Surface	-0.0001 (-0.0003 – 0.00005)	0.0001	1.440	-0.0001 (-0.0003 – 0.00006)	0.0001	1.410
Building Distance	0.002 (-0.001 – 0.006)	0.002	1.255	0.003 (-0.0009 – 0.006)	0.002	1.457
Host Availability	0.016 (0.002 – 0.030)	0.007	2.186	0.014 (-0.0002 – 0.028)	0.007	1.935
Leafminer Density	-0.720 (-1.2191 – -0.221)	0.255	2.828	-0.405 (-0.781 – -0.028)	0.192	2.108
Beetle Density	0.002 (-0.0006 – 0.004)	0.001	1.468	0.0006 (-0.002 – 0.003)	0.001	0.559

S1.8. Elm Leaf Beetle conditional model averages from models excluding temperature with n=69 trees and n=85 trees. For n=69 trees, marginal $R^2 = 0.27$, conditional $R^2 = 0.98$. For n=85 trees, marginal $R^2 = 0.26$, conditional $R^2 = 0.98$. Variables in bold indicate estimates where the 95% confidence interval does not overlap with zero.

Variables	N=69			N=85		
	Estimate (95% CI)	SE	z-value	Estimate (95% CI)	SE	z-value
Intercept	1.710 (0.018 – 3.402)	0.863	1.981	1.854 (0.224 – 3.484)	0.831	2.229
DBH	0.00009 (-0.003 – 0.003)	0.002	0.060	0.0007 (-0.002 – 0.003)	0.001	0.526
Vegetational Complexity	-0.004 (-0.014 – 0.006)	0.005	0.793	-0.005 (-0.014 – 0.004)	0.005	1.090
Impervious Surface	0.035 (0.015 – 0.056)	0.010	3.400	0.003 (0.014 – 0.052)	0.010	3.452
Vegetational Complexity * Impervious Surface	0.0002 (-0.0002 – 0.0005)	0.0002	0.921	0.0002 (-0.0002 – 0.0005)	0.0002	1.008
Building Distance	0.001 (-0.006 – 0.009)	0.004	0.359	0.001 (-0.006 – 0.009)	0.004	0.373
Host Availability	0.010 (-0.017 – 0.037)	0.014	0.701	0.011 (-0.013 – 0.034)	0.012	0.883
Leafminer Density	-0.596 (-0.899 – -0.293)	0.155	3.857	-0.451 (-0.708 – -0.194)	0.131	3.443
Weevil Density	0.009 (0.002 – 0.015)	0.003	2.649	0.0008 (-0.005 – 0.006)	0.003	0.281

S1.9. Summary of results for the global models with all predictor variables on n=69 trees (“Global”), the models excluding temperature on the same n=69 trees (“N=69”), and the models excluding temperature on n=85 trees (“N=85”). Blue indicates a positive association, red indicates a negative association, grey indicates no association, and crossed through variables were not included in the model. Associations are indicated for variables where the 95% confidence interval estimate does not include zero.

	Elm Leafminer			Elm Flea Weevil			Elm Leaf Beetle		
	Global	N=69	N=85	Global	N=69	N=85	Global	N=69	N=85
DBH	Blue	Blue	Blue	Blue	Blue	Blue	Grey	Grey	Grey
Vegetational Complexity	Blue	Blue	Blue	Grey	Grey	Grey	Grey	Grey	Grey
Impervious Surface	Red	Red	Red	Grey	Grey	Grey	Grey	Blue	Blue
Temperature	Red	Crossed	Crossed	Grey	Crossed	Crossed	Blue	Crossed	Crossed
Veg. X Imp.	Blue	Blue	Blue	Grey	Grey	Grey	Grey	Grey	Grey
Veg. X Temp.	Grey	Crossed	Crossed	Red	Crossed	Crossed	Grey	Crossed	Crossed
Imp. X Temp.	Grey	Crossed	Crossed	Grey	Crossed	Crossed	Grey	Crossed	Crossed
Building Distance	Grey	Grey	Grey	Grey	Grey	Grey	Grey	Grey	Grey
Host Availability	Grey	Grey	Grey	Blue	Blue	Grey	Grey	Grey	Grey
Leafminer Density	Crossed	Crossed	Crossed	Red	Red	Red	Red	Red	Red
Weevil Density	Grey	Grey	Grey	Crossed	Crossed	Crossed	Blue	Blue	Grey
Beetle Density	Grey	Grey	Grey	Grey	Grey	Grey	Crossed	Crossed	Crossed

APPENDIX B: CHAPTER 2 SUPPLEMENTARY MATERIAL

A



B



C



S2.1. *Harmonia axyridis* adults consumed elm leaf beetle eggs and larvae, and *H. axyridis* larvae consumed elm leaf beetle eggs. A) Dorsal view B) Lateral view C) Frontal view.

A



B





S2.2. *Phyllobaenus* sp. consumed elm leaf beetle eggs and larvae. A) Dorsal view B) Lateral view C) Frontal view.

A



B



C



S2.3. *Parasteatoda tepidariorum* consumed elm leaf beetle larvae. A) Dorsal view B) Lateral view C) Frontal view.

A



B



C



S2.4. *Pogonomyrmex occidentalis* was observed carrying an elm leaf beetle larvae while foraging underneath a Siberian elm tree. A) Dorsal view B) Lateral view C) Frontal view.

A



B



C



S2.5. *Forficula auricularia* consumed elm leaf beetle pupae. A) Dorsal view B) Lateral view C) Frontal view.

A



B



C



S2.6. A fourth instar *Podisus placidus* nymph was observed feeding on a deceased elm leaf beetle adult. A) Dorsal view B) Lateral view C) Frontal view.

A



B



C



S2.7. *Phiddipus audax* consumed elm flea weevil adults. A) Dorsal view B) Lateral view C) Frontal view.