Harnessing the power of data-driven models to improve management and detection of emerald ash borer

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Dedication

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Dissertation Abstract

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is an invasive beetle in North America. All North American species of ash (*Fraxinus* spp.) are susceptible to this beetle such that widespread mortality to ash is occurring as the beetle spreads. Since the discovery of emerald ash borer in North America in the early 2000s, much research has been devoted to improving management efforts that target this species. Here, I study the cold tolerance of *Spathius galinae* Belokobylskij & Strazanac (Hymenoptera: Braconidae), a classical biological control agent against emerald ash borer. I forecast the ability of this parasitoid to survive winters in the northern range of ash in North America. To improve monitoring and early detection of emerald ash borer, I also evaluate the range of attraction of baited green prism traps using a novel quantitative method. The traps were baited with the host volatile (3*Z*)-hexenol and the sex pheromone (3*Z*)-lactone. Lastly, I model the spread rate of emerald ash borer from its first detection in Michigan to present across North America to quantify anisotropy (i.e., directionality) in the rate of spread. I then determine how environmental factors known to affect the spread and demographics of insects are associated with these variable rates of spread. Collectively, my dissertation furthers improvements in monitoring and management efforts for this devastating invasive species.

Table of Contents

List of Tables

List of Figures

Dissertation Introduction

Introductions of organisms to novel environments beyond their native ranges have been increasing as global trade and the movement of people increases (Westphal et al. 2008, Aukema et al. 2010, Seebens et al. 2017). This increase in introductions is of concern because invasions of non-native organisms are costly. It is estimated that the North American economy has lost US$1.26 trillion between 1960 and 2017 due to costs associated with invasive species (Crystal-Ornelas et al. 2021). In addition to economic costs, invasions by non-native organisms may cause more difficult-to-quantify impacts to biodiversity, ecosystem services and stability, and degrade the aesthetic of natural and urban areas (Simberloff 2000, Pimentel et al. 2005). Understanding how invasions progress and the different management options available at each stage of an invasion is vital to limiting future costs from the introduction of non-native organisms.

Invasions typically progress through three stages: arrival, establishment, and spread (Shigesada and Kawasaki 1997, With 2002). Preventing the arrival of pests in novel locations is the most cost-efficient strategy for reducing their impact as strong pre-arrival measures can reduce arrival rates of pests (Liebhold et al. 1995, Leung et al. 2002). Such measures include phytosanitary import requirements, such as fumigation or sterilization of wood packaging material, and establishing international partnerships that implement clearance protocols for trade goods, such as faster processing for goods that comply with phytosanitary measures (Lovett et al. 2016). In the event that pre-arrival measures fail to prevent arrival of a pest, early detection, rapid-response programs can reduce the likelihood of establishment and spread as eradication becomes increasingly more difficult and costly as a pest establishes. (Myers et al. 2000, Simberloff 2000,

McLaughlin and Dearden 2019). Early detection, rapid-response programs frequently entail quarantining and inspecting imported material, surveillance of high-risk areas, and rapid eradication of any discovered introductions (Hulme et al. 2008, Crall et al. 2012, Lovett et al. 2016). These programs may be employed on the leading edge of the range of an established pest, where slower spread rates can lower the cost of management, ameliorate costs over a longer time period, and, in some instances, eradicate the organism (Sharov et al. 2002, Simberloff 2002, Mercader et al. 2011, Hope et al. 2021).

Non-native forest insects and diseases are a significant threat to urban and forest trees. Introductions of these organisms to novel locations have been occurring at a rate of 2.5 introductions per year since 1860 (Aukema et al. 2010). In general, most introductions do not result in established populations and only some established populations of introduced insects cause significant damage (Williamson and Fitter 1996). Occasionally, however, an introduced organism causes out-sized damage that may result in the near complete removal of their host species from the landscape. The introduced fungi *Ophiostoma ulmi* (Buisman) Nannf and *Ophiostoma novo-ulmi* Brasier, which cause Dutch Elm Disease, is one example of such an organism. These fungi have caused extensive mortality of elm trees (*Ulmus* spp.) since the spread into Europe and North America from their native range in Asia in the early 1900s (Brasier 1990, Shukla et al. 2012). In North America, nearly 95% of elms have been killed by these fungi (Shukla et al. 2012).

One of the most damaging forest insect pests in North America to date is the emerald ash borer (*Agrilus planipennis* Fairmaire) (Herms and McCullough 2014). Significant time and resources have been spent attempting to control and understand the

spread of emerald ash borer. Emerald ash borer is an invasive beetle (Coleoptera: Buprestidae) in North America. This beetle is native to eastern Asia (northeastern China, North and South Korea, and eastern Russia) (Orlova-Bienkowskaja and Volkovitsh 2018). The larvae of this beetle feeds on the phloem of ash trees (*Fraxinus* spp.), eventually girdling and killing infested trees. To date, millions of ash trees in North America have been killed (Klooster et al. 2014). This beetle was likely introduced to North America via wood packaging material used in shipping, which is a common introduction pathway for wood-boring beetles (Cappaert et al. 2005, Meurisse et al. 2019).

Since its introduction near Detroit, Michigan, USA, emerald ash borer has spread across much of the eastern USA and into Canada, and as far west as Colorado (Ward et al. 2020, Hope et al. 2021). Eggs are laid in late spring and early summer in bark crevices of ash trees (Jennings et al. 2014). After hatching, larvae burrow through the bark into the phloem layer, where they feed over the course of the summer. They progress through four instars, typically overwintering as pre-pupae (Wang et al. 2010). Generally, emerald ash borer populations are univoltine, but in colder regions or areas with high competition a single generation may take two years (Cappaert et al. 2005, Jones et al. 2020). The biology of this pest has made controlling its spread difficult. By the time infested ash trees begin to show symptoms (such as epicormic sprouts and crown dieback), several generations of beetles likely have developed and adults will have dispersed locally, making eradication difficult (McCullough, Poland, and Cappaert 2009, Poland et al. 2011). Furthermore, emerald ash borer adults tend to colonize trees starting in the crown, which makes visual surveys for exit holes difficult. Some of the most effective methods

for detecting emerald ash borer when populations are low are to girdle a trap tree in the spring and check under the bark in the fall (Mercader et al. 2013, Siegert et al. 2017, McCullough 2020) or to look for woodpecker holes in the upper canopy (Fahrner et al. 2017, McCullough 2020). Traps baited with green leaf host volatiles and a short-range sex pheromone are also used to monitor emerald ash borer populations and are used with comprehensive surveys to monitor spread and population growth (Tobin et al. 2021).

In an effort to slow the population growth and spread of emerald ash borer, four parasitoids native to emerald ash borer's host range have been approved for release in North America as part of a biological control program (Duan et al. 2018). Three of these parasitoids attack the larval stage of emerald ash borer: *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), *Spathius agrili* Yang (Hymenoptera: Braconidae), and *Spathius galinae* Belokobylskij & Strazanac (Hymenoptera: Braconidae). The fourth, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), attacks eggs laid on the bark of ash trees. *Tetrastichus planipennisi*, *S. agrili*, and *O. agrili* were the first three parasitoids approved for release in the United States (Federal Register 2007). Initially, *S. agrili* was released across the USA, but it was later found that populations of *S. agrili* were not establishing in areas north of 40° latitude. This failure is likely due to a phenological mismatch between *S. agrili* and its host induced by colder temperatures further north. *Spathius galinae*, which is native to the Russian Far East (Belokobylskij et al. 2012), is now being released north of the 40th parallel. Climate matching suggests that *Spathius galinae* is well-suited for winter climates north of the 40th parallel, as it is native to the Russian Far East where it experiences similar climatic situations (Federal Register 2015a). However, while matching potential biological control agents to climates

similar to their native range provides guidance on where populations may establish, it is not sufficient for quantifying survival (Stiling 1993). In the case of surviving winter conditions, delimiting the cold hardiness of the potential biological control agent may be necessary to produce accurate forecasts of survival (Hopper 1998, Hoelmer and Kirk 2005, Kenis et al. 2017).

Where climate plays a role in the mortality of insect populations, it also plays a role in the spread of insects as demography is intrinsically linked with spread (With 2002, Hastings et al. 2005, Morin et al. 2009, Lantschner et al. 2014). Spatial and/or temporal heterogeneity in abiotic or biotic factors (e.g. climate, resource availability, predators and competitors) affect the spread of invasive insects (Hastings et al. 2005, Melbourne et al. 2007, Lustig et al. 2017, Lutscher and Musgrave 2017). These effects may manifest as changing rates of spread through time or across the invaded range of an introduced insect (i.e. anisotropic spread). Modeling how abiotic and biotic factors in the novel environment affect the rate of spread of an invasive insect can provide predictions on the arrival of the insect pest to novel locations within its invaded range, which in turn can help management agencies target efforts to control the pest. Several studies have evaluated the spread of emerald ash borer and factors linked with this spread (BenDor et al. 2006, Prasad et al. 2010, Evans 2016, Ward et al. 2020), although to-date none of these studies have included data across the entire range of emerald ash borer in North America or focused on how these spread rates vary through time or across space.

The goal of this dissertation is to improve our understanding of the emerald ash borer system and, in turn, provide information to managers that may prove useful when making management decisions. In chapter 1, we evaluated the cold tolerance of *S.*

galinae in both the laboratory and under field conditions to produce forecasts of its overwintering survival across the range of ash in North America. Chapter 1 is published as "Forecasting overwintering mortality of *Spathius galinae* in North America" in the journal *Biological Control* (Wittman, Aukema, et al. 2021). To improve the efficacy of traps used in detecting emerald ash borer, we studied the range of attraction of the baits used in green prism traps, which is described in Chapter 2 and is published as "Optimizing early detection strategies: defining the effective attraction radius of attractants for emerald ash borer *Agrilus planipennis* Fairmaire" in the journal *Agricultural and Forest Entomology* (Wittman, Silk, et al. 2021). Chapter 3 of this dissertation describes modeling efforts wherein we estimate the rate of spread of emerald ash borer across North America and associate changes in the rate of spread with heterogeneity in the environment. Both chapters 1 and 3 improve on existing modeling techniques and may be employed with future insect pests to improve their management.

The chapters of this dissertation were prepared for publication in peer-reviewed journals. I am the lead author, but the work of the remaining chapters is the combined results of multiple authors, hence my use of the plural voice in these sections. Each chapter may have some redundancy, which is included to preserve the integrity of each chapter as a stand-alone unit.

Chapter 1

Forecasting overwintering mortality of *Spathius galinae* in North America

Chapter Synopsis

Evaluating the cold tolerance of biological control agents is often necessary to optimize their release and performance. We used field and laboratory assays to determine the cold hardiness of the parasitoid *Spathius galinae* Belokobylskij & Strazanac, an approved classical biological control agent of emerald ash borer (*Agrilus planipennis* Fairmaire) in North America. Supercooling points and lower lethal temperature of mature (cocooned) *S. galinae* larvae were measured in controlled cooling assays in the laboratory. Most *S. galinae* larvae died after reaching their supercooling point, which occurred at -25.0°C on average. Several larvae, however, initiated freezing but later eclosed, suggesting *S. galinae* may be partially freeze tolerant. Supercooling points were not affected by chilling rate. In the winter of 2019 – 2020, we monitored development of mature *S. galinae* larvae in ash segments above and beneath the snow in three locations in Minnesota, USA. Nearly 100% of *S. galinae* larvae died after air temperatures reached -29°C in Minnesota. Using models developed from our data, we forecast eclosion rates of *S. galinae* based on minimum winter temperatures across the range of ash (*Fraxinus* spp.) in North America. Our results indicate that *S. galinae* populations may suffer high overwintering mortality in areas where winter temperatures regularly decrease below -28°C, but a small portion of the population may be able to survive lower temperatures.

Introduction

One important component in the success and optimization of a biological control program is identifying how well-suited a potential biological control agent is to the environment into which it will be introduced (Hance et al. 2007, Heimpel and Mills 2017). Typically, climate matching is used to compare a suite of abiotic factors between a potential biological control agent's native range and the proposed range of introduction to delineate novel locations in which these agents may perform well (Robertson et al. 2008). Failure of a biological control agent to establish a persistent population due to a climate mismatch is thought to be the main factor in 34.5% of attempted introductions (Stiling 1993). However, climate matching methods alone are not sufficient to predict success or establishment (Stiling 1993, Hart et al. 2002, Bauer et al. 2015). More specifically, insect adaptation to climate, such as the cold tolerance of a potential biological control agent should be examined as part of this evaluation (Stiling 1993, van Lenteren et al. 2006), especially if releases are intended in northern latitudes. Evaluating the cold tolerance of a potential biological control agent provides information that can be used in selecting optimal release locations while also reducing the risk of non-target effects (Hopper 1998, Hoelmer and Kirk 2005, Kenis et al. 2017).

Evaluating the cold hardiness of the parasitoid *Spathius galinae* Belokobylskij & Strazanac (Hymenoptera: Braconidae) is of particular interest for the optimization of the classical biological control program for emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. *Spathius galinae* is one of four parasitoids that have been approved for release against emerald ash borer in North America (Duan et al. 2018). Three are larval parasitoids: *Tetrastichus planipennisi* Yang (Hymenoptera:

Eulophidae), *Spathius agrili* Yang (Hymenoptera: Braconidae), and *Spathius galinae*. The fourth, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), is an egg parasitoid. *Spathius galinae* was the parasitoid most recently approved for release in 2015 (Federal Register 2015b), while the other three insects were approved in 2007 (Federal Register 2007). *Spathius galinae* is an idiobiont ectoparasitoid that attacks third and fourth instars of emerald ash borer. Larvae of *S. galinae* develop through five instars and overwinter as a cocooned fifth instar underneath the bark of ash trees. The overwintering stage of *S. galinae* does not enter a diapause (Chandler et al. 2020). Larvae of *S. galinae* will resume development once temperatures reach approximately 15°C. In the spring, *S. galinae* larvae complete development and emerge as adults.

Spathius galinae has unique features that may improve biological control of emerald ash borer. For example, *S. galinae* has a longer ovipositor than *T. planipennisi* so it should be able to reach emerald ash borer larvae deeper beneath the bark than *T. planipennisi* (Murphy et al. 2017). Additionally, *Spathius agrili* did not establish well in northern climates likely due to a phenological mismatch with emerald ash borer (Hooie et al. 2014, Jennings et al. 2016, Gould et al. 2020). In New York, USA, *S. agrili* emerged a month later than *T. planipennisi* and *S. galinae*, by which time there were fewer parasitoid-susceptible emerald ash borer larvae (Jones et al. 2020). As such, releases of *S. agrili* have since been restricted to south of the 40th latitudinal parallel. *Spathius galinae* may not suffer from this phenological mismatch in part because it is native to the Russian Far East (Belokobylskij et al. 2012). Climate matching suggests *S. galinae* is well suited to regions north of the 40th parallel, where it will complement established populations of *T. planipennisi* (Federal Register 2015a). *Spathius galinae* may have up to three or four

generations per year in the northeastern and midwestern USA (Duan et al. 2014, Watt et al. 2016). The cold hardiness of *S. galinae* has not been fully evaluated to date.

Cold temperatures can cause both metabolic injury or sub-lethal effects to insects (Storey and Storey 1988, Tussey et al. 2018), as well as mechanical injury when fluids inside the insect body freeze (Denlinger and Lee Jr 2010). However, many insects have evolved various mechanisms or strategies to avoid freezing or control where freezing occurs (Zachariassen 1985, Turnock and Fields 2005, Toxopeus and Sinclair 2018). For example, some insects can reduce the freezing temperature of fluids inside their body by producing cryoprotectant polyols such as glycerol. The temperature at which these insects begin to freeze is termed the supercooling point. Other strategies for surviving subzero temperatures include removing ice nucleating agents, lowering body water content, producing thermal hysteresis proteins, or selecting favorable overwintering locations (Baust and Rojas 1985, Zachariassen 1985, Sinclair 1999, Bale 2002). Insects that tolerate freezing may freeze at higher temperatures than those that avoid freezing (Sinclair 1999). Laboratory assays with a controlled rate of cooling are often used in conjunction with field studies to evaluate supercooling point, lower lethal temperature (the minimum temperature to which an insect can survive exposure), and lower lethal time (the length of time an insect can survive exposure to a particular temperature) (Sinclair et al. 2015).

Understanding the cold hardiness of *S. galinae* will aid in identifying regions where it may not perform well. To date, two studies have evaluated localized cold tolerance and overwintering mortality of *S. galinae* (Chandler et al. 2020, Duan et al. 2020). Chandler et al. (2020) evaluated the supercooling point and overwintering survival

of *S. galinae* at sites in Massachusetts, Connecticut, Rhode Island, and Delaware, USA. *Spathius galinae* demonstrated the ability to lower its supercooling point throughout the winter as it acclimated to lower temperatures (Chandler et al. 2020). Duan et al. (2020) took advantage of the extreme cold temperatures due to a polar vortex in January 2019 to compare mortality of *S. galinae*, *T. planipennisi*, and emerald ash borer populations in Michigan and Connecticut. In Michigan, where temperatures reached as low as -26°C, *S. galinae* populations displayed as much as 50% mortality, whereas in Connecticut, where temperatures only reached -18°C, the highest mortality observed was 7.3%. No study has yet evaluated the overwintering survival of *S. galinae* in the upper Midwest region of the United States where winters are generally colder than the locations in the aforementioned studies. In this paper, we describe experiments carried out to evaluate the ability of *S. galinae* to survive winters in Minnesota, USA in USDA Plant Hardiness Zones that are colder than those used in previous studies. We also investigate the supercooling point and lower lethal temperature of *S. galinae* in the laboratory and study how different cooling rates affect the supercooling point. We compare predictions from lab assays on lower lethal temperature with observed field mortality at three locations in Minnesota. Finally, we develop geographically explicit forecasts from these experiments to predict winter mortality across the USA based on minimum winter temperatures.

Materials and Methods

Lower lethal temperature assays

All *S. galinae* larvae used in these assays originated from a colony established in 2010 from approximately 100 individual cocoons collected from the Russian Far East. For these assays, these parasitoids were reared on late-instar emerald ash borer larvae

infesting green ash (*Fraxinus pennsylvanica* Marsh) logs at the United State Department of Agriculture (USDA) Beneficial Insects Introduction Research Unit in Newark, DE. The green ash logs containing late instars of emerald ash borer larvae for rearing *S. galinae* were produced according to methods described in Duan et al. (2013). Green ash logs, freshly cut from trunks of naturally growing trees, were artificially infested with emerald ash borer eggs (~10 eggs per log, each log ~ 7 cm in diameter x 20 cm long) and then incubated in an environmental chamber at 30°C for approximately 5 weeks so that most EAB larvae would have reached late instars suitable to *S. galinae* attacks. These green ash logs containing late instars of EAB larvae were then exposed for 7 days to gravid females of *S. galinae* (along with some males) in ventilated-clear polystyrene crisper boxes (each 17.6 by 12.6 by 10 cm, Tri-State Plastics, Latonia, KY) in an environmental chamber (Percival Scientific, Perry, IA) at 25°C (±1°C), with 65±10% relative humidity and a photoperiod of 16:8 L:D h). Parasitoid-exposed logs were then maintained in the same environmental chamber for approximately 7 more days to allow the development of immature parasitoids to mature (cocooned) larval stages (Duan et al. 2014). The logs were then cold acclimated for a week at 1.7°C. Late-instar *S. galinae* larvae were dissected from ash logs and placed into Petri dishes with moist paper towels.

The insects were shipped overnight to Saint Paul, MN, where they were held at 4°C until used in laboratory assays. A bath of silicon 180 oil (A40; Thermo Fisher Scientific, Waltham, Massachusetts) was used to control temperatures in these laboratory assays. Insects were placed in 1.5 ml microcentrifuge tubes before a plastic dowel fitted with an O-ring was placed in the opening of each tube. A 1.27-mm diameter (36 AWG) type-T copper-constantan thermocouple was threaded through the plastic dowel so that

the end of the thermocouple was in contact with the insect (Stephens et al. 2015). Each microcentrifuge tube was placed into an 18 x 150 mm Kimax glass test tube in a plastic rack in the silicon oil bath. Temperature was recorded every 0.5s using TRACERDAQ PRO software (Measurement Computing, Bourne, MA, USA).

To determine the lower lethal temperature and supercooling point, insects were chilled in 33 batches of 20 larvae at one of three rates, as cold hardiness metrics may vary with the rate at which the insects are cooled (Miller 1978, Wang and Kang 2005, Terblanche et al. 2007). We chose cooling rates of 1°C/minute, 0.5°C/minute, and 0.1°C/minute. Cooling at 1°C/min is a common laboratory standard (Salt 1966), but others have argued that such a fast cooling rate is not ecologically relevant (Bale 1986, 1987, Sinclair et al. 2003). The 0.1°C/minute cooling rate closely matches the average rate of cooling observed between the daily high temperature and the following daily low temperature in our field studies, which was 0.015°C/minute. Three insects in each batch were designated as control insects and left at room temperature during the duration of the assay. The remaining 17 insects in a batch were randomly assigned a temperature between 0°C and -32°C inclusive, in two-degree increments. Initially, insects were to be cooled as low as -40°C, however the silicon bath had difficulties cooling below -32°C. Insects that had been designated to cool lower than -32°C were instead pulled from the bath at -32°C. There were 16 insects cooled to each temperature, except -32°C, which had a sample size of 73 insects. In total, 329 late-instar larvae were used in these assays.

Each insect was removed from the chiller bath once its corresponding thermocouple recorded the previously designated low temperature, even if an exotherm (the release of heat that occurs when water freezes) was observed prior to reaching the

designated temperature, and placed on ice until the end of the batch. The insects were then returned to storage at 4°C for three days. Insects were stored in their microcentrifuge tubes with a small piece of moist cotton added to prevent desiccation. During this storage period, larvae were checked daily for signs of discoloration. After three days, larvae were transferred to incubators held at 25°C with a 16:8 L:D cycle. Humidity was not held constant in these incubators due to mechanical issues and as a result, relative humidity in the incubators mirrored the ambient relative humidity in the incubator room. After an additional four weeks, larvae were checked to record how many had successfully developed to the adult life stage, which we will refer to throughout as successful eclosion. Supercooling points of *S. galinae* were estimated by visual inspection of plots of the temperature recordings from the lower lethal temperature assays for evidence of an exotherm, and the lowest temperature observed prior to the exotherm was recorded as the supercooling point.

Overwintering field study

All insects used in these field studies were reared in the same manner as those used in the laboratory study. After cold acclimation, the green ash bolts were shipped overnight from Delaware on 12 December 2019 in a cooler on an ice pad to Saint Paul, MN. These bolts were placed in 4°C storage until they were deployed in the field on 16 – 17 December 2019. Six bolts were immediately placed into incubators at 25°C and 16:8H L:D cycle as a control without exposure to the cold. Additionally, six bolts were placed in an outdoor open-air insectary at the USDA Beneficial Insects Introduction Research Unit in Newark, DE as a control. The number of insects in each treatment group was not even

across all treatments due to the inability to identify the number of larvae in log segments without removing the bark.

Bolts were placed outside in Mullen Woods at the Saint Paul campus of the University of Minnesota (44.98 °N, 93.18 °W) and in small forested areas at the University's Southern Research and Outreach Center in Morris, MN (44.59 °N, -95.87 °W) and Western Research and Outreach Center in Waseca, MN (44.07 °N, 93.53 °W). At each location, half of the bolts were tied around the circumference of a tree trunk at approximately breast height (ca. 1.5m above the soil line) using twine. Trees were chosen on the interior of the stands to limit the effect of direct sunlight. The other half of the bolts were placed nearby on the ground so that they would be insulated by any snow that fell. If snow was already present at the site, the snow was temporarily displaced before placing the bolts on the ground and recovering with snow. *Spathius galinae* that attack emerald ash borer near the base of the tree trunk may overwinter below the snow line if sufficient snowfall occurs, so these bolts on the ground serve as an assessment of how this thermal refuge may affect the survival of these parasitoids. A HOBO data-logger (Onset Computer Corporation, Bourne, Massachusetts) was placed adjacent to each group of bolts to record ambient temperature and relative humidity.

Bolts were retrieved on 25 March 2020 when the mean daily temperature was approximately 2°C in the previous week. We had hoped to leave the bolts in the field until temperatures were regularly warm enough (approximately 15°C) for the insects to continue their development to adults (Watt et al. 2016), but they were retrieved earlier as the University of Minnesota was preparing to restrict employee travel due to the COVID-19 pandemic. Thus the bolts were retrieved to prevent the loss of data if travel restrictions

remained in place past the emergence of *S. galinae* adults. The control segments in Delaware remained outdoors until adult parasitoids emerged in mid-May. Once removed from the outdoors, all log segments were placed in emergence cages in incubators held at 25°C on a 16:8H L:D cycle. Additionally, we placed a saturated sodium nitrite ($NaNO_2$) solution in the base of incubators to hold relative humidity between 60 – 70%, which was recorded with HOBO data loggers (Winston and Bates 1960). Cages were monitored thrice weekly and emerging adults counted. Several weeks after the last emergence, bark was peeled off the bolts to tally any larvae that failed to eclose (i.e. they failed to complete development to the adult life stage) and any adults that failed to emerge (i.e. those that eclosed but failed to exit the bolt). Insects that showed partial adult morphology were recorded as failing to eclose.

Statistical analysis

The primary goals of the laboratory assays were to determine lower lethal temperature (LLT) for *S. galinae*, to find the proportion of insects that froze at sub-zero temperatures, and to see if the rate at which larvae were chilled affected either of these values. Specifically, we wished to estimate LLT_{50} and LLT_{90}, which are the temperatures at which 50% and 90% of the insects tested would die from acute cold exposure. We used both discoloration of larvae 3d post-chilling and eclosion as proxies for insect death. Lower lethal temperature was estimated by using logistic regression. Two logistic regression models were made: one model used discoloration of larvae (yes/no) 3d after chilling as the response variable while other used eclosion as the response. A modified Abbott's correction was applied to adjust for discoloration or failure to eclose in insects in the experimental control that was cooled to 0°C in each chill rate group (Rosenheim

and Hoy 1989). In each model, the rate at which the insects were chilled and the minimum temperature to which the insect was exposed were included as parameters, along with their interaction. If the interaction term was significant, that would indicate that the rate at which insects were chilled may alter the effect of the minimum temperature on the lower lethal temperature outcome. Because no effect of chill rate was found in these experiments, the modified Abbott correction was reapplied using the insects in the control group chilled to 0°C across all chill rates as the control treatment.

We also wanted to estimate the temperatures necessary for 50% and 90% of the insects to reach their supercooling point. To avoid censor bias in our estimates of average supercooling points and the temperatures at which 50% and 90% of the insects froze, only insects that were cooled to the minimum -32°C were used in these calculations (n = 73). To test the effect of chill rate on supercooling points, we fit a mixed effects model with a term for chill rate as the sole explanatory variable and a term for batch as a random effect. Additionally, to estimate the percentage of insects that would freeze at a given temperature, we fit a logistic regression to the cumulative distribution of supercooling points. Model coefficients reported from these models are on the log odds scale. To determine LLT estimates, we used the predict function provided with base-R (R Core Team 2020) to identify the temperature at which the model predicted eclosion or discoloration rates of 50% and 90% and the concomitant confidence interval for these estimates.

For the field assays, we were interested in verifying the lower lethal temperature results of our laboratory work and assessing the overwintering mortality of *S. galinae* in Minnesota. We again constructed logistic regression models to quantify overwintering

mortality. We created two sets of two models: one set used eclosion as the response variable (insects that eclosed were recorded as 1, insects that did not were coded as 0), while the other model used successful adult emergence from the log as the response variable (insects that emerged were coded as 1, insects that did not were coded as 0). These models were fit only to the data from Minnesota. No Abbott correction was applied to data collected from these experiments because there was no analogous control group for such an adjustment. Within each set, the response was treated as a function of one of minimum temperature or average relative humidity; both recorded by the HOBO data loggers. These variables were highly correlated with each other so we did not include these variables in a model together. These models were fit as generalized estimating equations with a unique identifier for brood used as the grouping variable and an exchangeable correlation structure (Lee and Nelder 2004, Yan and Fine 2004, Halekoh et al. 2006). Generalized estimating equations can be used to estimate population-level regression model coefficients when data are correlated within groups. Additionally, we fit generalized estimating equation models to compare rates of eclosion and emergence among the two treatments (i.e., below and above snow). A term for treatment was fit as a categorical variable and the unique identifier for brood was used as the grouping variable. All model residuals were visually assessed to ensure model assumptions of homoscedasticity and normality of residuals were met.

Geographic Forecast

We sought to forecast survival of *S. galinae* across the United States and Canada. We used the models from our lab assays to estimate eclosion rates and the proportion of *S. galinae* that would begin to freeze given a minimum temperature and the model from

our field study to estimate eclosion rates from the minimum temperature recorded. To limit predictions to the distribution of ash in the USA and Canada, we obtained a raster layer of the distribution of *Fraxinus* species in the USA at 250m^2 resolution from Wilson et al. (2013). We also obtained a raster layer of estimated percent species composition of *Fraxinus* species in Canadian forests at 250m^2 resolution (Beaudoin et al. 2014). These two ash raster datasets were combined to approximate the distribution of ash in the USA and Canada. We also obtained raster files from WorldClim containing minimum winter temperatures at approximately 21km^2 resolution across USA and Canada in the years 2013 – 2014 and 2017 – 2018 to use as the predictor variable in the aforementioned models (Fick and Hijmans 2017). These specific years were chosen because 2013 – 2014 included the occurrence of a polar vortex, during which cold air from the Arctic circle caused unusually cold temperatures in much of the northern United States, while the winter of 2017 – 2018 was relatively mild. We then extracted from the minimum temperature rasters only those cells that overlapped a cell from the ash layers with a non-zero value. This step resulted in a minimum temperature layer with temperature values only where ash was present. These minimum temperatures were then used in our three models to calculate the proportion of *S. galinae* larvae that would be expected to freeze or eclose based on the minimum temperature in that cell. These three models were chosen in order to compare the predictions from the laboratory assays with our field observations, as well as other results in the literature (see Results and Discussion).

All analyses were carried out in R v4.0.2 (R Core Team 2020). Logistic regression models were fit using the glm function provided in the stats package (R Core Team 2020). Generalized estimating equations were fit using the package geepack (Yan

2002). Data cleaning and organizing was performed with the packages dplyr and purrr (Wickham 2016, Henry and Wickham 2020), figures were created using the package ggplot2 (Wickham 2016), and multiplot figures were assembled with the patchwork package (Pedersen 2020). All raster processing was done using the raster package (Hijmans 2020).

Results

Lower lethal temperature and supercooling point laboratory assays

The average supercooling point was -25.0°C (95% CI: -24.8°C – -25.2°C). Approximately 50% of *S. galinae* began to freeze at -24.9°C (95% CI: -24.2°C – -25.5°C), while 90% of the insects began to freeze at -26.7°C (95% CI: -26.0°C – -29.1°C) (Fig. 1.**Error! Reference source not found.**). Cooling rate had no effect on d iscoloration (Z = 1.16, P = 0.245) or eclosion of larvae (Z = -1.16, P = 0.244) so the models were refit without chill rate as a predictor. Additionally, the ΔAIC for the full model, which included minimum temperature, cooling rate, and their interaction, compared to the model that included minimum temperature as the only covariate was less than 0.2, suggesting that the addition of the chill rate as a variable in the model did not improve the fit of the model. Supercooling point was also unaffected by the rate of chilling ($F_{2,13}$ = 0.052, P = 0.950).

As temperature decreased, the odds of both appearing normally colored and eclosing as an adult decreased significantly (Table 1.**Error! Reference source not f ound.**). It was not possible to estimate a LLT_{50} or LLT_{90} from the laboratory assay models using discoloration as the response as neither 50% or 90% of the insects became

discolored even after exposure to the lowest temperatures (Fig. 1.**Error! Reference s ource not found.**A). Similarly, it was not possible to estimate the LLT_{90} from the lab assay models using eclosion as the response, as only 70.8% of the insects exposed to the lowest temperature failed to eclose. However, the model of eclosion suggests that 50% of the insects would fail to eclose at -27.0°C (95% CI: -25.1°C – -29.2°C) (Fig. 1.**Error! R eference source not found.**B). While most insects that initiated freezing later failed to eclose, three insects cooled to -30°C and four insects cooled to -32°C exhibited exotherms but later successfully eclosed.

Overwintering field study

The three overall coldest days at each site in Minnesota occurred on 12, 13, and 20 February 2020. Minimum air temperatures averaged across our three sites on those days were -27.0°C, -25.9°C, and -25.4°C, respectively. The coldest air temperature recorded across our three Minnesota sites was -29.5°C on 20 February 2020 at Waseca, MN. Figure **Error! Reference source not found.** displays the ambient temperature at o ur study site in Delaware and averaged across the three Minnesota sites under the snow and in the air, respectively. Temperatures were similar among treatments in sites in Minnesota; the average standard deviation of temperatures under the snow at any time was 1.7°C, while the average standard deviation of temperatures in the air from every time point was 2.4°C. All three MN sites had at least 2.5 cm of snow cover until the second week of March. The average temperature two weeks prior to logs being retrieved from the field was 3.4°C.

Across all sites and treatments, there were 558 larvae in the overwintering portion of the study. Table 1.**Error! Reference source not found.** displays the proportion of *S. g*

alinae that successfully eclosed or emerged in each group. Larvae that were exposed to the ambient air temperature at our field sites in Minnesota were significantly less likely to eclose than those that overwintered underneath the snow (odds ratio = 0.0947, Z = -11356, P = < 0.0001, Table 1.**Error! Reference source not found.**). Similarly, the odds o f eclosing were 0.149 times lower among larvae exposed to the ambient air than those that overwintered under the snow (odds ratio = 0.149, Z = -14.08, P = <0.0001). The difference in air temperature between the Delaware site and each site in Minnesota averaged over time was 12°C. Despite the fact that bolts in Delaware were exposed to temperatures that were on average 12°C warmer than those underneath the snow in Minnesota (Fig. 1.**Error! Reference source not found.**), the probability of eclosion was l ower in Delaware (60.0%, 95% CI: 49.9% – 70.1%) than under the snow in Minnesota (74.7, 95% CI: 69.9% – 79.5%).

The odds of successfully eclosing (Fig. 1.**Error! Reference source not found.**A) o r emerging (Fig. 1.**Error! Reference source not found.**B) decreased significantly as the minimum winter temperature decreased (Table 1.**Error! Reference source not found.**). Based on the eclosion model from the overwintering experiment, we estimate the LLT_{50} for *S. galinae* to be -22.4°C (95% CI: -19.6°C – -25.7°C). Estimates of the LLT_{90} are not available as the model predicts 82.9% mortality at -30°C, which is the lowest temperature observed in the field study. The model of emergence suggests the LLT_{50} may be -14.0°C. The lower 95% confidence limit on this estimate is -17.0°, however, an upper limit cannot be estimated as it would be beyond the range of observed temperatures. The LLT_{90} estimated from the emergence model is -28.6°C. Similar to the confidence limit on the LLT_{50} estimate, it is not possible to estimate a lower bound as that estimate extends

beyond the range of our observed temperatures, but the upper bound on this estimate is -24.6°C. As average relative humidity increased by one unit, we saw the probability that an insect would eclose increased by 11%, while the probability that they would emerge increased by 10% (Table 1.**Error! Reference source not found.**).

Geographic Forecast

Figure **Error! Reference source not found.** displays three different model p redictions of the proportion of *S. galinae* that would be predicted to survive overwintering based on minimum winter temperatures experienced. Each column of maps represents a different proxy for survival. It should be noted that using supercooling points as a proxy for mortality carries the assumption that all insects that freeze will die (see Discussion). Figures 1.**Error! Reference source not found.**A – 1.**Error! Reference so urce not found.**B and Figures 1.**Error! Reference source not found.**C – 1.**Error! Reference source not found.**D display predicted rates of eclosion from the laboratory-based and field-based models of eclosion, respectively. Figures **Error! Reference source n ot found.**E – **Error! Reference source not found.**F display predictions of the proportion of *S. galinae* that would be expected to remain unfrozen based on our laboratory measurements of supercooling point. Maps in the top row of Figure 1.**Error! Reference source not found.** use minimum winter temperatures from a relatively mild northern winter (2017 – 2018 winter) as the predictor variable, while maps in the bottom row of Figure 1.**Error! Reference source not found.** use minimum temperatures from a severe northern winter (2013 – 2014 winter) as the predictor variable.

Both models of eclosion predict that at least some proportion of *S. galinae* will be able to eclose across the range of *Fraxinus* spp. in North America in either winter

scenario. The field model predicts slightly lower rates of eclosion than the laboratory based model at more northern locations. The predictions of both eclosion models begin to move lower along a south-north gradient in Minnesota and Wisconsin which corresponds to USDA plant hardiness zones 4a - 2b and the deciduous forest to boreal forest ecotone (Goldblum and Rigg 2010). There are no noticeable differences in the model predictions of eclosion between the mild and severe winters.

Spathius galinae is unlikely to experience air temperatures that would trigger the onset of freezing across most of the United States, except for the most northern part of Minnesota and a portion of North Dakota in the severe winter scenario. The proportion of insects that might begin to freeze increases as lower minimum temperatures are reached in Saskatchewan, Manitoba, and Ontario than in more southern parts of the continent. There appears to be a slight moderating effect on freezing along the coast of Lake Superior (i.e. northeastern Minnesota, northern Wisconsin, the northern portion of the Upper Peninsula of Michigan, and south central Ontario).

Discussion

We observed extensive mortality of *S. galinae* overwintering in areas with temperatures below the supercooling point of *S. galinae* larvae. We found that the average supercooling point of *S. galinae* in our assays was -25.0 (95% CI: -24.8°C – -25.2°C), although *S. galinae* appears to be able to further reduce its average supercooling point as low as -28°C with prior exposure to colder temperatures than temperatures in our study (Chandler et al. 2020). This lower average supercooling point is within the range of the supercooling points we recorded. These results suggest that *S. galinae* may not exhibit significant mortality where extreme low winter temperatures are > -25°C (up to

USDA Plant Hardiness Zones 4b). Mortality will increase as temperatures drop below -25°C, although our results also suggest that some *S. galinae* may survive temperatures as cold as -32°C (USDA Plant Hardiness Zone 4a). These results suggest that *S. galinae* may be able to survive winters in the northern range of *Fraxinus* spp. and emerald ash borer. In fact, cold acclimation appears to help synchronize *S. galinae* populations with the presence of third and fourth instar emerald ash borer (Ragozzino et al. 2020).

Interestingly, while most of the larvae in the lab study that exhibited exotherms failed to eclose, seven *S. galinae* larvae that exhibited an exotherm when cooled to -30°C or -32°C later successfully completed development. This finding suggests that some proportion of *S. galinae* larvae may be capable of partial freeze tolerance (Baust and Rojas 1985, Sinclair 1999, Morey et al. 2016). Partial freeze tolerance may take several forms, including insects that survive the initial onset of freezing but not complete freezing (Block et al. 1988), the ability to switch between freeze avoidance and freeze tolerance strategies (Duman 1984, Horwath and Duman 1984), or some proportion of an insect population being able to survive a complete freeze event (Todd and Block 1995). It is difficult to estimate the true proportion of *S. galinae* that may exhibit some tolerance to freezing due to mortality observed in our control treatment. The observed percentage of insects that initiated freezing and later eclosed was 1%, while the percentage expected to eclose based on the mortality-adjusted model displayed in Figure 1.2B is approximately 30%. The true percentage of *S. galinae* that may survive partial freezing likely lies somewhere between these two percentages. If most *S. galinae* die when freezing occurs but some proportion of these insects are able to tolerate freezing then we may expect the proportion of *S. galinae* that die due to freezing to fall somewhere between the predicted

proportions displayed in Figure 1.**Error! Reference source not found.**A – 1.**Error! Reference source not found.**D and Figure 1.**Error! Reference source not found.**E – 1.**Error! Reference source not found.**F.

The models fit to eclosion rates in both the laboratory and the field forecast at least 43% and 63% failure to eclose at temperatures below -25°C, respectively. The latter prediction is slightly higher mortality than what was observed in *S. galinae* populations in Michigan after the polar vortex in January 2019 (Duan et al. 2020). Temperatures during this polar vortex reached as low as -26°C, after which cold mortality of *S. galinae* populations ranged between 15 – 50%. The mortality observed in Michigan falls within the range predicted from our supercooling point model (20%) and field eclosion model (63%) at -26°C. While overwintering survival ultimately depends on the complex interaction of factors such as duration of exposure, minimum exposure temperature, and the frequency and length of warming events (Terblanche et al. 2011, Marshall and Sinclair 2014, Cohen et al. 2018), the models of eclosion produced from laboratory assays and the supercooling point model described in this paper appear to approximately bracket observed mortality in Michigan, while the model of eclosion rates in the field appears to slightly overestimate the observed mortality. The *S. galinae* used in the field study in Minnesota overwintered in small logs (~5 cm in diameter) cut from green ash trunks, which likely dried out over the winter, while *S. galinae* in Duan et al. (2020) were sampled from mostly large whole ash trees (diameter at breast height 8 – 21 cm). The dry host tree material may have led to excess desiccation of *S. galinae* larvae, which in turn may have led to mortality in excess of what would have been experienced in a whole tree (Duan et al. 2014). Additionally, winter 2018 - 2019 in Michigan may have overall been

less stressful than winter 2019 - 2020 in Minnesota. Our sites experienced several days with temperatures lower than -20°C and reached a colder absolute low minimum temperature than what was recorded during the polar vortex in Michigan. Alternatively, the insects used in the field study may simply have been less cold hardy than those used in the laboratory experiments or observed in the study in Michigan.

Populations of emerald ash borer in Michigan, in contrast to those of *S. galinae*, exhibited 26.2% mortality after the same polar vortex in 2019. Emerald ash borer appears to be able to survive cold temperatures better than *S. galinae*. Other work has shown that the average supercooling point of emerald ash borer may be as low as -32°C, with some individuals supercooling to even colder temperatures (Venette and Abrahamson 2010, Christianson and Venette 2018). Due to this differential in mortality, there are northern locations where winter temperatures are sufficient to cause severe *S. galinae* mortality without equally impacting emerald ash borer populations, although this difference may be moderated by host effects. In some instances, parasitoids that feed on more cold hardy hosts will tolerate lower temperatures than parasitoids that feed on less cold hardy hosts through the accumulation of host cryoprotectants (Rivers et al. 2000, Li et al. 2015, Amiresmaeili et al. 2020). Additionally, the small number of partially freeze tolerant *S. galinae* we observed in our laboratory assays suggest that variation in cold tolerance strategy may exist within the colony of these parasitoids. Some insect populations exhibit variation in cold hardiness or cold tolerance strategy and this variation is typically correlated with local climate conditions (Mausel et al. 2011, Sinclair et al. 2012, Cira et al. 2016, Zhang et al. 2017). For example, populations of the parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) from the northern region of its range had

lower adult mortality at cold temperatures than populations from more southern regions of its range (Royer et al. 2001). Future work may seek to determine the amount of variation in cold hardiness present in geographically separate populations of *S. galinae* from across its range, as well as the potential for this variation to result in fitness differences in different cold thermal regimes.

Tetrastichus planipennisi populations also displayed higher mortality than emerald ash borer in Michigan during the polar vortex (Duan et al. 2020), but Gould et al. (2020) posit that the reproductive biology of *T. planipennisi* provides a mechanism by which their populations can recover quickly. Populations of *T. planipennisi* exhibit a 3:1 female-biased sex ratio, and females produce on average 57 – 86 progeny in a lifetime. Moreover, *T. planinpennisi* are multivoltine, with up to four generations per year (Liu et al. 2007, Ulyshen et al. 2010, Duan et al. 2011). It remains to be seen if this differential in mortality will negatively affect the ability of *S. galinae* to control emerald ash borer in northern climes, but the reproductive biology of *S. galinae* is similar to *T. planipennisi* (Duan et al. 2014, Watt et al. 2016). A potential avenue for future work would explore demographics of these insects populations in the aftermath of an extreme winter temperature event.

Microclimate refuges, such as those provided by overwintering under the snowline, inside the bark of a tree or different habitat types on the landscape scale, play an important role in the overwintering strategies of many insects by providing thermal buffering or increased humidity, which can increase the survival of insects that overwinter in these locations (Chen et al. 1999, Sinclair et al. 2003, Suggitt et al. 2011, Rozsypal et al. 2013, Tougeron et al. 2016). *Spathius galinae* larvae placed underneath

the snow in our study had higher eclosion and emergence rates than those in the warmer open air insectary in Delaware (Table 1.**Error! Reference source not found.**), despite e xperiencing lower minimum temperatures. These insects also benefit from overwintering underneath the bark, as temperatures underneath the bark of ash trees are between 0 and 4°C warmer than ambient air temperature (Vermunt et al. 2012). Without knowing underbark temperatures, it is possible that our estimates of the lower lethal temperature from the field are slightly high due to the microclimate provided by the bark.

The rate at which our insects successfully eclosed was consistent with or greater than eclosion rates reported in Chandler et al. (2020). However, few *S. galinae* emerged from the bolts used in our field studies, especially compared to emergence typically seen in lab rearing scenarios (Duan et al. 2014). Because emergence was so low across all treatments in the overwintering study, precise estimates of LLT_{50} and LLT_{90} are unavailable. Like the low eclosion rates noted previously, this low emergence may be attributable to the cut bolts drying out over the winter months, making it difficult for the insects to chew out. Low eclosion rates may also be caused by sublethal effects of cold exposure (Hutchinson and Bale 1994, Vladimír Koštál et al. 2019). For example, the production of polyols such as glycerol, which lower the supercooling point of an insect, come at an energetic cost resulting in a reduction in glycogen (Chino 1960). Surviving cold exposure may decrease fat body stores in insects (Chino 1960, Colinet et al. 2006, Colinet and Boivin 2011, Colinet et al. 2018), and preclude the ability to complete development as that requires a minimum fat body lipid content (Nijhout 1975, Mirth and Riddiford 2007, Arrese and Soulages 2010). Sub-lethal effects of cold exposure may explain both the low adult emergence and the small number of partially developed adults

noted in our samples; the cold exposure may have left the insects without sufficient energy reserves to finish development or chew exit holes to facilitate exit from underneath the bark.

While our supercooling point and lower lethal temperatures characterized for *S. galinae* are similar to those found for *S. agrili*, the effect of long term exposure to low temperatures may differ as *S. agrili* has an overwintering diapause while *S. galinae* does not (Hanson et al. 2013, Chandler et al. 2020). Hanson et al. (2013) showed that 50% or less of diapausing *S. agrili* died when exposed to -15°C temperatures for 80 days. Further work could explore the effect of exposure time to low temperatures on *S. galinae* populations.

We found no significant effect of chill rate on the responses measured in our laboratory assays. Much of the literature suggests that cooling at slower, more ecologically relevant rates produces a stronger cold hardiness response (Miller 1978, Bale et al. 1989, Block 1990, Terblanche et al. 2011). Although no effect of cooling rate on supercooling point, discoloration, or eclosion of *S. galinae* was noted in the results, it is possible that subtle effects could emerge with sample sizes greater than the several hundred insects we studied.

Conclusions

Optimizing release of biological control agents requires assessment of the ability of a biological control agent to establish in the target location (Debach and Rosen 1991, Cullen et al. 2011, Fischbein et al. 2019). Cold tolerance and the ability to successfully overwinter are one component of climate matching (Hance et al. 2007). We found

evidence that *S. galinae* exhibits a mixed freeze tolerance strategy, with all but a few insects failing to eclose upon initiating freezing. Results from our laboratory assays suggest *S. galinae* larvae are able to survive temperatures as low as -32°C, although we saw extensive mortality below -25°C in our field studies. This cold hardiness may contribute to the ability of *S. galinae* to survive in northern climates. Research has shown that established *S. galinae* populations are contributing significantly to emerald ash borer mortality; *S. galinae* appears to be playing a strong role in the biological control program in parts of the United States (Duan et al. 2019). While our results suggest that *S. galinae* may survive in USDA cold hardiness zones up to 4a, it remains to be seen if the differential cold mortality documented between emerald ash borer and *S. galinae* in some regions will significantly affect the biological control of emerald ash borer in those regions.

Tables

Table 1.1: Summary of models evaluating the association between minimum temperature and the probability an insect would appear discolored after three days or would eclose. Estimates are presented on the log odds scale, while values in parenthesis are the 95% confidence interval for each estimate. Log odds estimates of slopes greater than zero indicate a positive relationship between response and the predictor (i.e., for every 1°C increase in minimum temperature, the log odds of appearing normally colored increase by 0.16).

Response	Coefficient	Estimate	Z Value	P Value
Normally Colored	Intercept	6.02 (4.4, 8.17)	6.3	0.001
	Slope	0.16 (0.1, 0.23)	4.8	0.001
Eclosion	Intercept	3.84 (3.02, 4.77)	8.6	0.001
	Slope	0.14 (0.11, 0.18)	8.2	0.001

Table 1.2: Proportion of *Spathius galinae* eclosing or emerging after overwintering from 16 December 2019 -- 25 March 2020 at three locations in Minnesota and in Delaware. Larvae in Minnesota either overwintered in bolts underneath the snow or tied at breast height to a tree trunk and exposed to the ambient air. The sample size used in calculating each proportion is listed in parenthesis.

Location	Under Snow		Air	
	Proportion Eclosed	Proportion Emerged	Proportion Eclosed	Proportion Emerged
Newark, DE	-	-	0.6 (91)	0.34 (91)
Morris, MN[a]	0.99 (199)	0.62 (199)	0.02 (49)	0 (49)
St. Paul, MN	0.49 (87)	0.3 (87)	0.85 (48)	0.38 (48)
Waseca, MN	0.72 (43)	0.4 (43)	0 (41)	0 (41)

[a]A small group of bolts that were shipped to Minnesota was placed immediately at 25°C (70% RH). Of the 177 larvae present in these segments, 98% eclosed and 72% emerged.

Table 1.3 Summary of models evaluating the association between minimum temperature or average relative humidity and the probability that *Spathius galinae* larvae would eclose or emerge after overwintering. Estimates are presented on the log odds scale, while values in parenthesis are the 95% confidence interval for each estimate. The intercept in each model can be exponentiated to estimate the odds ratio of eclosing or emerging when temperature is 0°C or relative humidity is 0. A slope coefficient greater than 0 indicates a positive relationship between the predictor variable and the response (i.e. for every 1°C increase, we expect the log odds of eclosion to increase by 0.2.).

Response	Predictor	Coefficient	Estimate	Z Value	P Value
Eclosion	Minimum temperature (°C)	Intercept	4.484 (2.799, 6.169)	27.206	<0.001
		Slope	0.200 (0.124, 0.276)	26.420	<0.001
	Average relative humidity	Intercept	-8.172 (-16.468, 0.124)	3.728	0.054
		Slope	0.100 (0.008, 0.192)	4.540	0.033
Emergence	Minimum temperature (°C)	Intercept	2.127 (0.851, 3.403)	10.671	0.001
		Slope	0.151 (0.085, 0.217)	19.903	<0.001
	Average relative humidity	Intercept	-9.170 (-16.519, -1.822)	5.983	0.014
		Slope	0.097 (0.015, 0.179)	5.428	0.020

Figures

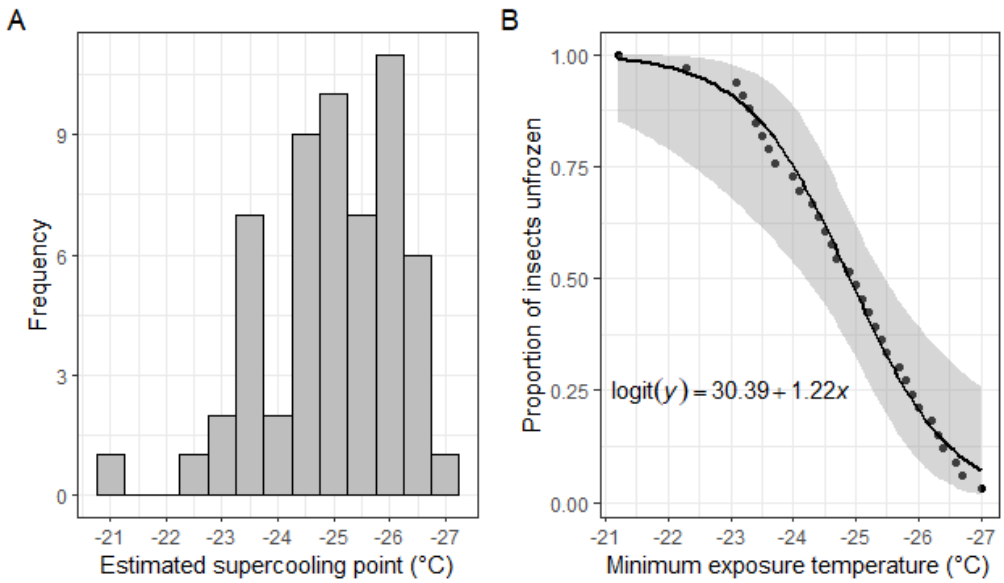

Figure 1.1: Distribution of supercooling points observed in larvae of *Spathius galinae* (*n* = 73) cooled in a silicon cooling bath.

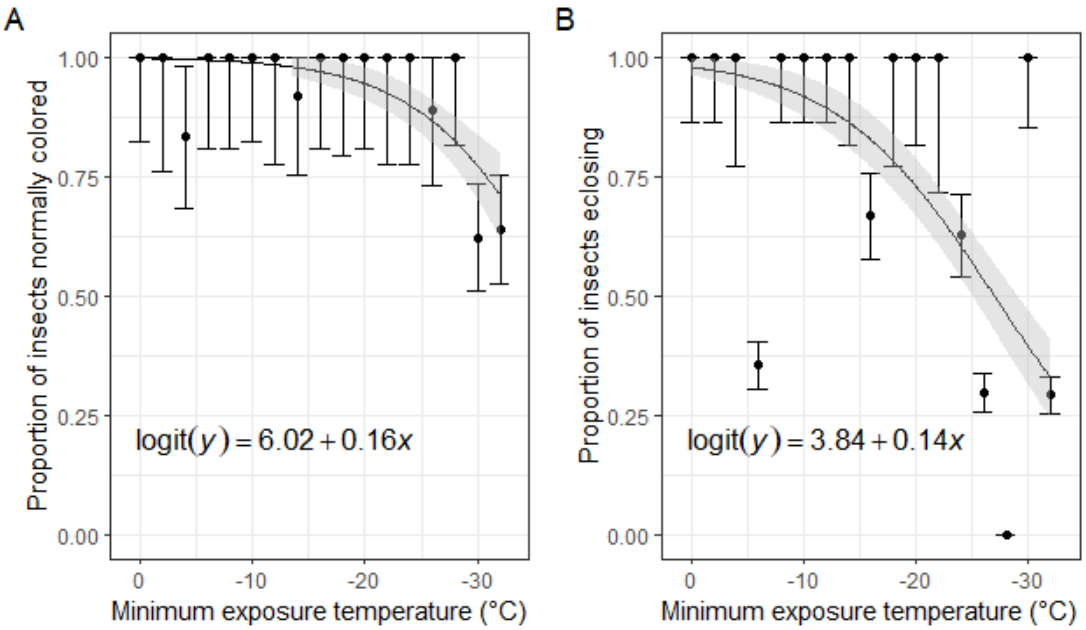

Figure 1.2: Probability that larvae of *Spathius galinae* (*n* = 427) would appear discolored (A) or eclose (B) after being cooled in the laboratory to a sub-zero temperature. Points are the Abbott corrected proportion of *S. galinae* that were normally colored (1 = 100% normally colored, 0 = 0% normally colored) or eclosed (1 = 100% eclosion, 0 = 0% eclosion) at a given temperature, while error bars are ± two standard errors. The solid line are predicted response rates from the models fit to these data. The grey band represents the 95% confidence interval for the fitted line.

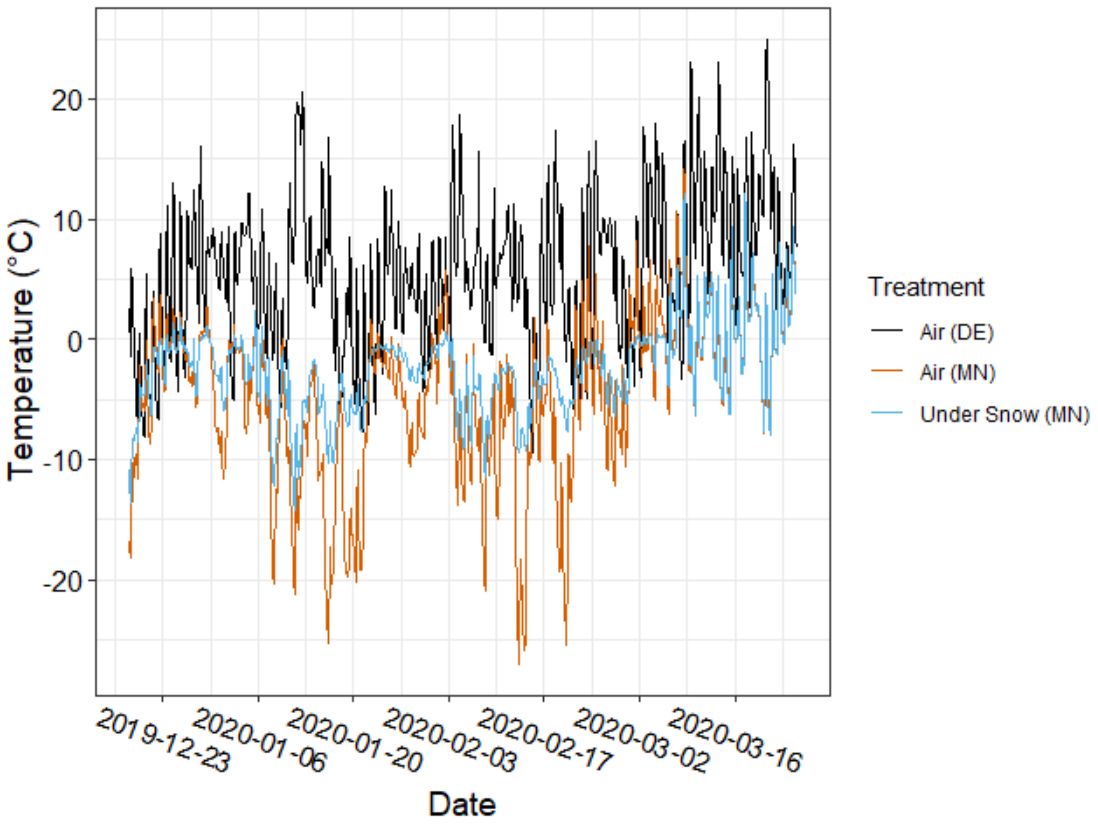

Figure 1.3: Time series of the average ambient temperature recorded near bolts placed at three sites in Minnesota underneath the snow, in the air above the snow, as well as one site in an open air insectary in Delaware. Temperatures were recorded from 16 December 2019 - 25 March 2020 by a HOBO data logger.

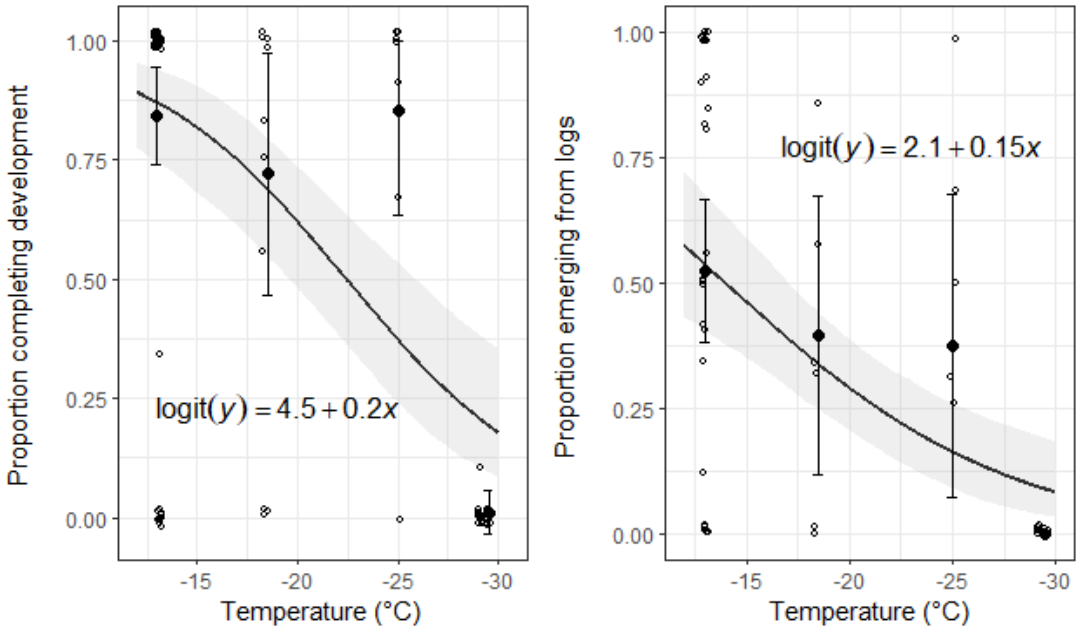

Figure 1.4: Relationship between the probability of eclosing (A) or emerging from underneath the bark (B) for *Spathius galinae* (*n* = 558) and the lowest temperature experienced over the winter of 2019 - 2020. Larvae were overwintering in bolts under the snow or tied to a tree trunk above the snowline in Minnesota, USA. Open points are the proportion of each brood that eclosed (A) or emerged (B) and have been jittered to facilitate viewing. Solid black points are the overall proportion of *S. galinae* eclosing (A) or emerging (B) at a given temperature, while error bars are ± one standard error. The solid line is the fitted population model. Grey bands represent 95% confidence interval for the fitted line.

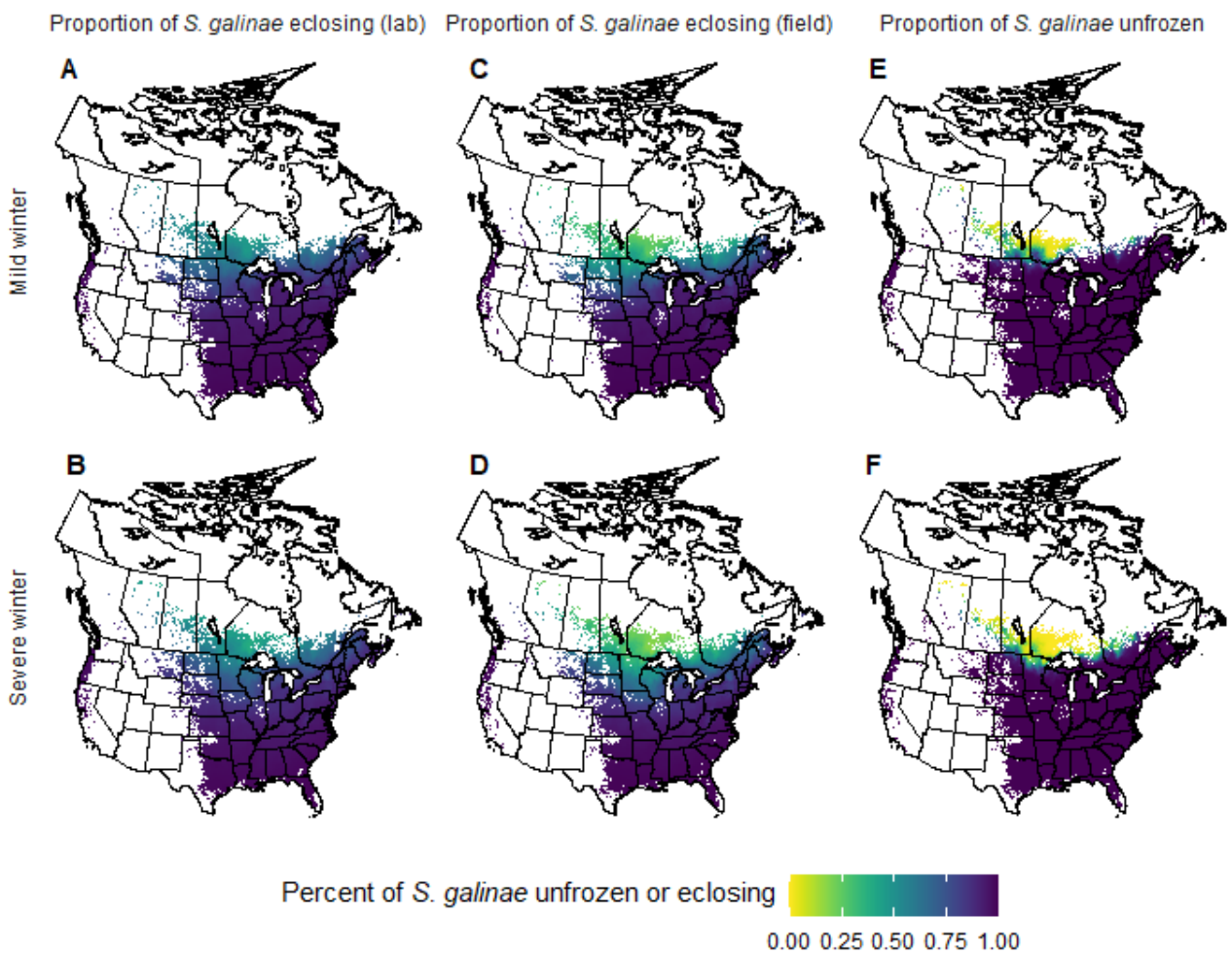

Figure 1.5: Predictions and confidence intervals of the percent of *Spathius galinae* that will eclose or initiate freezing based on minimum winter temperatures. Figures A - C display the lower 95% confidence interval prediction, predicted value, and the upper 95% confidence interval prediction, respectively, for a winter with relatively mild minimum temperatures (2017 - 2018),

while figures D - F represent the same values for a winter with extreme minimum temperatures due to a polar vortex (2013 - 2014).

Chapter 2

Optimizing early detection strategies: defining the effective attraction radius of attractants for emerald ash borer *Agrilus planipennis* Fairmaire

Chapter Synopsis

Adult emerald ash borers are attracted to green prism traps baited with the ash host volatile (3*Z*)-hexenol and the sex pheromone of emerald ash borer (3*Z*)-dodecen-12-olide [(3*Z*)-lactone]. Quantifying the heretofore unknown range of attraction of such traps would help optimize deployment strategies for early detection. Examining trap captures of traps deployed in pairs at variable distances offers insight into the range of attraction. Recent work has shown the range of attraction can be estimated as half the intertrap distance at which trap catch begins to decrease, which should occur when proximate traps overlap their respective attractive ranges. We estimated these traps' attractive range for emerald ash borer using ninety-eight baited dark green prism traps deployed in pairs, one trap per tree, in an urban park in Saint Paul, Minnesota, USA in summer 2020. We estimate attractive range by fitting a logistic model to trap catch data using Bayesian inferential methods and describe advantages thereof. The attractive range of these baited traps was estimated to be between 16 – 73m, with a median of 28m. We recommend that dark green prism traps baited with these semiochemicals be placed 25 - 35m apart near high-risk entry points.

Introduction

Invasive insect pests can cause widespread damage to host plants in their invaded range, which can lead to costly economic and ecological impacts (Aukema et al. 2011, Bradshaw et al. 2016). Detecting invasive insects as they arrive in a new location or spread across their invaded range (i.e. early detection) and responding before the insect can establish or cause extensive damage (i.e. rapid response) reduces the impact these insects may have and tends to be less costly than managing well-established insect populations (Brockerhoff et al. 2010, Lovett et al. 2016, Tobin 2018). In areas where a non-native pest is already established, monitoring helps time and target appropriate population controls (Tobin et al. 2009, McLaughlin and Dearden 2019). Monitoring established populations of insects and detecting newly arrived insect pests is often done using traps baited with semiochemicals such as synthetic pheromones or host volatiles (Elkinton and Cardé 1980, Witzgall et al. 2010, Torres-Vila et al. 2014). These semiochemicals may also be used in mass trapping efforts designed to suppress populations (Weslien 1992, El-Sayed et al. 2006, Yamanaka 2006, Sanchez-Husillos et al. 2015). When new invasive insects are detected, significant research efforts are directed to determine the most effective trap designs, semiochemical combinations and release rates, and trap positions.

The chemical ecology and behavior of emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) has been studied extensively, as it is one of the most costly and destructive invasive forest insect pests in North America (Silk et al. 2010, Aukema et al. 2011, Herms and McCullough 2014, Silk and Ryall 2014). This beetle is native to eastern Asia and arrived in North America in the late 1990s (Cappaert et al.

2005, Herms and McCullough 2014, Siegert et al. 2014). Emerald ash borer larvae feed on the vascular tissue of ash trees (genus *Fraxinus*), which ultimately girdles the host tree leading to tree death (Herms and McCullough 2014). Visual surveys for early detection of emerald ash borer are challenging: woodpecker feeding, for example, can be a good indicator of emerald ash borer activity, but may be hard to detect when leaves are present (Fahrner et al. 2017). Symptoms of infestation such as canopy dieback and epicormic shoots are not apparent until trees are heavily attacked, by which point populations of emerald ash borer in the area are quite high (Poland and McCullough 2006, McCullough, Poland, and Cappaert 2009). Fortunately, emerald ash borers exhibit positive phototaxis to wavelengths of light in the green (540 - 560nm), blue (420 - 430nm , 460nm), and red (640 - 650nm, 670nm) ranges, which has led to the use of both green and purple prism-shaped sticky traps (Francese et al. 2008, Crook et al. 2009, Crook and Mastro 2010, Silk et al. 2019). These traps are often baited with lures composed of volatiles found in ash leaves ((3*Z*)-hexenol) and tree oils, such as manuka oil (from the New Zealand tea tree, *Leptospermum scoparium* J.R. and G. Forst (Myrtaceae)) and phoebe oil (from the Brazilian walnut tree, *Phoebe porosa* Mez (Lauraceae)) (de Groot et al. 2008, Crook and Mastro 2010, Grant et al. 2010, Poland et al. 2011).

Research has shown that female emerald ash borers produce contact pheromones (Lelito et al. 2009, Silk et al. 2009) as well as a short-range sex pheromone, the macrocyclic lactone (3*Z*)-dodecen-12-olide [(3*Z*)-lactone] (Bartelt et al. 2007), that can be used to increase catch in traps baited with (3*Z*)-hexenol (Silk et al. 2011, Ryall et al. 2012, Silk et al. 2020). Prior to the detection of emerald ash borer in North America, there existed only a single published example of any beetle in the Buprestidae family

potentially using a volatile pheromone (Dunn and Potter 1988, Silk and Ryall 2014). The attractive range of traps baited with both the ash leaf volatile (3*Z*)-hexenol and volatile pheromone (3*Z*)-lactone remains to be established. The attractive range of the pheromone-baited trap has been estimated to be at least 25m, but the upper bound of the attraction radius has heretofore been unknown (Parker et al. 2020).

Identifying the attractive range of semiochemical baits (i.e., "the maximum distance over which insects can be shown to direct their movement to the source" (Wall and Perry 1987, Schlyter 1992)) is critical for optimizing trapping programs, as this information helps quantify the area that can be sampled with a set of traps (Kriticos et al. 2007, Manoukis et al. 2014). The shape of a pheromone plume at any given instant is complex (Murlis et al. 1992), but because air currents in the vicinity of the plumes are stochastic, the molecules will disperse into a volume that may roughly approximate to a sphere for analytical purposes (Byers et al. 1989, Schlyter 1992, Byers 2008, 2009). This conceptual model allows the attractive range of a trap to be defined in terms of an attraction radius (Byers et al. 1989, Kriticos et al. 2007, Manoukis et al. 2014). Historically, experimental designs with complex geometric arrangements of many traps were used to determine the attraction radius of a baited trap (c.f. Jactel et al. (2019) for examples).

Jactel et al. (2019) proposed a novel method for determining an attractive radius that involved fewer traps, provided a theoretical justification for this method, and presented results from a field experiment determining the attraction radius of pheromone traps used for monitoring *Monochamus galloprovincialis* Olivier (Coleoptera: Cerambycidae). This new method exploits the principle that interference that occurs

between traps placed short distances apart will reduce trap catch (McMahon et al. 2010, Figueroa-Castro et al. 2016). For example, a trap whose signal overlaps another's may reduce the neighboring trap's potential captures. As the distance between traps increases, they should become independent. By fitting a logistic model to trap catch data, one can then estimate the effective attraction radius (Jactel et al. 2019).

In this paper, we describe a field experiment that uses the method described in Jactel et al. (2019) to evaluate the attraction radius of emerald ash borer traps baited with both the ash leaf volatile (3*Z*)-hexenol and the volatile sex pheromone (3*Z*)-lactone. We expect that the attraction radius of these baited traps is at least 25m, based on our previous work (Parker et al. 2020). Additionally, we advance the methodology of Jactel et al. (2019) by using Bayesian inferential methods. Our findings and the advantages of employing Bayesian techniques are discussed.

Materials and Methods

Field Site

Traps were deployed in Battle Creek Regional Park in Saint Paul, Minnesota, USA (44.9°N, 93.0°W), which consists of 1,840 acres of natural area within a highly developed urban area. The park is comprised of areas of mature forest, prairie, and wetland with numerous green ash trees (*Fraxinus pennsylvanica* Marshall) scattered throughout the park. At the time of the study, most ash in the area were exhibiting some signs of decline (e.g., crown-thinning, epicormic shoots, woodpecker damage) that suggested sufficient numbers of emerald ash borer.

Deployment of traps

Traps used in this study were dark green prism traps (540nm, peak reflectance = 49%, Sylvar Technologies Inc., Fredericton, NB, Canada) pre-coated with Pestick (Synergy Semiochemicals, Burnaby, BC, Canada). All traps were baited with 3.0 mg (3Z)-lactone pheromone pre-loaded on red rubber septa with a release rate of ca. 60 µg per day (Ryall et al. 2015) and (3Z)-hexenol host kairomone (Synergy Semiochemicals) releasing ca. 50m mg/d. Following the design of Jactel *et al.* (2019), we deployed traps in pairs of trees, with a single trap per tree hung ca. 4-8 m high on the south-west aspect in the out mid-canopy (Francese et al. 2008, Lelito et al. 2008) and distances between traps in a pair ranging from 2 m to 94 m. Traps were placed in trees when growing degree day values reached 283, which corresponds to one to two weeks prior to expected adult emergence (i.e., first week of June in 2020). Growing degree day values were taken from the National Phenology Network page for emerald ash borer and were calculated using a base temperature of 10°C and start date of 1 January 2020 (USA National Phenology Network 2020). Traps were removed at the conclusion of the experiment after growing degree day values exceeded 1500, which occurred in the last week of August 2020.

In selecting ash trees for this study, we recorded the location of all ash trees within the park using a handheld GPS unit (Garmin GPSMAP 64). All trees were accessible by paved bike trail or sidewalk. The trees that were chosen also had diameter at breast height measurements greater than 5 cm. We then used a custom R script (R Core Team 2020) to randomly locate pairs of traps throughout the park so that all trap pairs were hung >200m apart from other trap pairs and so that the distances between pairs of trees were approximately evenly distributed between 2 m and 94 m. This script was run iteratively until the aforementioned conditions were met. To account for error in GPS

measurements, we verified in-person that the distance between each tree in a pair was within +/- 50cm of the distance as measured by GPS. If the distance between the trees in a pair exceeded this threshold, another suitable tree nearby was chosen for the pair if available or another pair of trees that was within the threshold was selected. A total of 96 traps, or 48 pairs of traps, were hung in the park. All trees in which traps were hung were located on the edge of stands at either the boundary of the park or adjacent to the wide, paved bike trails that ran through the park. Thus, traps were hung in trees where at least 50% of the area around the canopy of these trees was open.

We checked traps every two weeks after they were deployed. We removed buprestids from the traps and placed them into labeled tubes for transport to the laboratory. If the glue on the traps appeared insufficient for trapping more insects due to insect saturation or otherwise, the traps were replaced but the lures were not. In the laboratory, we identified, sexed, and counted all emerald ash borer present using Paiero et al. (2012).

Statistical analysis

We summed the total number of emerald ash borer caught over the season for each trap pair, hereafter referred to as total paired trap catch or TPTC. We used this value as our response variable in our model. We fit the model in a Bayesian framework using the Stan probabilistic programming language (Stan Development Team 2020a) in R (R Core Team 2020) using the packages rstan (Stan Development Team 2020b) and brms (Bürkner 2017, 2018). The model was a two-parameter logistic model with total paired trap catch as function of the distance (D) between the two paired traps:

$$TPTC_i \sim \text{Poisson}(\lambda_i)$$

$$\lambda_i = \frac{\alpha}{1 + e^{-\beta * D_i}}$$

$$\alpha \sim \text{Half-Normal}(0,\ 100)$$

$$\beta \sim \text{InvGamma}(1,\ 0.01)$$

The parameters of this model offer simple biological interpretations: α represents the maximum number of insects one pair of traps may catch if the two traps are completely spatially independent. This quantity is a function of the background density of insects in the area. The estimated attraction radius (AR) is equal to the distance (D) at which total paired trap catch is 95% of the asymptote divided by two ($\frac{D}{2} = AR$) (Jactel et al. 2019). The attraction radius can thus be estimated by setting the model equation equal to 0.95α, entering the estimated parameter values, and solving the equation for D. Ultimately, the estimate for the attraction radius is equal to $\frac{1.4722}{\beta}$. The indexing variable i simply denotes the trap pair, assuming an integer value between 1 and n = 48.

The priors were chosen to be uninformative while also constraining the parameters to biologically plausible values (i.e. both parameters must be positive and continuous). Because of the inverse relationship between β and the estimated attraction radius, the prior for β had to be chosen carefully. Non-informative prior distributions for parameters are not inherently invariant under transformations (Gelman 2006, Gelman et al. 2008, Dorazio 2016, Lemoine 2019). Indeed, simulations from different prior distributions showed that an uninformative prior distribution for β was equivalent to specifying a strongly informative prior distribution on the attraction radius, and vice

versa (see Appendix A Fig. 1). To remedy this challenge, we searched the literature for estimates of attractive range distances in insects. The longest attractive range estimates reported in the literature for insects in the orders Lepidoptera and Coleoptera, to our knowledge, are 500m and 490m, respectively (Wall and Perry 1987, Schlyter 1992, Jactel et al. 2019). We chose the prior distribution on β such that it translated to a prior distribution on the attraction radius that placed 95% of the prior probability density between 0 and 1000, which is twice the distance reported in the literature. Therefore, this prior is uninformative when considered in light of the scale of possible attraction radius estimates (Lemoine 2019). We assessed model results for sensitivity to prior choices by comparing how parameter posterior distributions differed with different prior distribution specifications (Gelman et al. 2020).

We also tested if the proportion of males caught in a trap changed with the distance between two traps. To do this test, we fit a logistic regression model with proportion males caught in a trap pair as a function of distance between traps. We used uninformative normal distribution priors with mean zero and σ^2 equal to 100 for the intercept and slope coefficients in this model. All parameter estimates are reported with a 95% credible interval.

Results

Field results

We caught 1,817 emerald ash borers over the course of the trapping season. All traps except for two captured at least a single emerald ash borer, while the most caught by one single trap was 55. On average, 92.3% (95% CI: 90.9 – 93.6%) of the beetles

captured in the traps were male. The proportion of males caught did not change as distance between traps increased (slope = -0.00328, but 95% credible interval of -0.01 – 0.003 overlaps zero).

Figure 2.**Error! Reference source not found.** displays the number of emerald a sh borer caught by each trap pair and the distance between the traps in a pair, as well as the fitted line (with 95% credible intervals) from the two-parameter logistic model. A pair of traps that were separated by less than 10m would be expected to catch 30 or fewer emerald ash borers in total, for example. The expected total paired trap catch increases as the intertrap distance increases, although the rate of increase in total paired trap catch decreases as traps are moved farther apart. Pairs of traps spaced more than 50m apart would catch between 40 – 50 emerald ash borers over the course of the flight season.

Figure 2.**Error! Reference source not found.** displays posterior distribution e stimates for the effective attraction radius and the parameters used in the model. We estimate the effective attraction radius as 28.1m (95% CI: 16.1 - 73.0m) (Fig. 2.**Error! R eference source not found.**A). The parameter α was estimated as 46.90 (95% CI: 41.74 - 56.35) and β was estimated as 0.05 (95% CI: 0.02 - 0.09). (Figs. **Error! Reference source not found.**B & **Error! Reference source not found.**C, respectively).

Prior sensitivity

The parameter α demonstrates very little sensitivity to the choice of prior distribution (Fig. 2.**Error! Reference source not found.**). Posterior distributions for α d o not demonstrably change for the variety of priors that we tested. Figure **Error! Reference source not found.** demonstrates how estimates of β and the attraction radius

change with different prior distributions. The parameter β appears to be relatively insensitive to changes in prior distributions. Due to the inverse relationship between β and the attraction radius, small changes in the posterior distribution of β can lead to corresponding larger changes in the posterior distribution of the attraction radius (Fig. 2.**Error! Reference source not found.**). Thus, the prior we chose for β in the base m odel provides a conservative estimate for the attraction radius.

Discussion

The attraction radius is a useful simplification for identifying the spatial area that a set of traps may cover (Byers et al. 1989, Schlyter 1992, Branco et al. 2006, Byers 2008). The results obtained in this study can be used to design efficient trapping systems in areas not yet invaded by the emerald ash borer, which is currently the most damaging and costly forest pest to invade North America (Aukema et al. 2011, Herms and McCullough 2014). Advancing a Bayesian implementation of estimation methodology from Jactel et al. (2019), we were able to estimate a lower, median, and upper bound on the attraction radius of the combined (3*Z*)-hexenol and (3Z)-lactone baits for emerald ash borer. Our previous work suggested that emerald ash borer traps baited with (3*Z*)-lactone and (3*Z*)-hexenol could be spaced approximately 15-20 m apart within 100 m of high-risk introduction points for optimal early detection work (Parker et al. 2020). Our new results, which have quantified the upper bound for attractive range (Fig. 2.**Error! Reference s ource not found.**A), relax our previous suggestions to 25 – 35m spacing, which doubles an area covered with the same amount of resources. Using the upper limit of attraction suggests that spacing even between 50 - 75m may be acceptable and effective in monitoring schemes. Such developments would minimize interference that can occur

when two similarly baited traps are placed too close to each other, while maximizing the spatial sampling area (Schlyter 1992, McMahon et al. 2010).

Recent research has shown that several of the most commonly used trapping schemes (e.g. combinations of different trap types and lure combinations), including the scheme used in this study, catch comparable numbers of emerald ash borers across a range of insect densities and are equally likely to catch at least one emerald ash borer in areas with low insect density (Tobin et al. 2021). The only trap scheme tested that caught significantly fewer insects and had significantly lower probabilities of detecting at least one emerald ash borer was a single purple prism trap baited with (3*Z*)-hexenol. In light of these findings and the results of our study, using our spacing suggestion with dark green prism traps baited with both (3*Z*)-hexenol and (3*Z*)-lactone should maximize the ability to detect emerald ash borer in high-risk introduction areas while minimizing the number of traps required. Future research could evaluate the effective attraction radius of other trapping schemes to determine if other trapping schemes provide better spatial coverage.

The predominant capture of males vs. females in our traps was consistent with previous work (Crook et al. 2009, Francese, Crook, et al. 2010, Domingue et al. 2012, Poland et al. 2019, Parker et al. 2020). Emerald ash borer males use visual cues in conjunction with olfactory cues and contact pheromones to locate mates (Lelito et al. 2007, Lelito et al. 2009, Pureswaran and Poland 2009). The use of just (3*Z*)-hexenol alone in baited traps attracts more males than females, and adding the pheromone (3*Z*)-lactone further increases the proportion of beetles caught that are males (Crook and Mastro 2010, Domingue et al. 2012). Moreover, green traps catch more male beetles than female beetles, perhaps because this wavelength of green characterizes ash foliage and

would represent a location where males could find both mates and food (Rodriguez-Soana et al. 2007, Francese, Crook, et al. 2010). The inclusion of purple prism traps in a double-decker scheme as described by (Poland et al. 2019) would likely increase the number of female beetles caught (Crook et al. 2009, Francese, Fraser, et al. 2010, Francese et al. 2013), although it is unknown how the inclusion of the purple prism trap would affect the effective attraction radius. Previous research had shown that double-decker traps had higher detection rates than single prism traps (Marshall et al. 2010, McCullough et al. 2011, Poland and Mccullough 2014, Poland et al. 2019), although none of the aforementioned studies tested the pheromone (3*Z*)-lactone so direct comparisons are difficult. Tobin et al. (2021) showed that single dark-green prism traps baited with both the pheromone (3*Z*)-lactone and (3*Z*)-hexenol performed as well as green funnel traps baited with the host volatile, single light-green prism trap baited with both compounds, and dark purple/dark purple or dark green/dark purple prism traps baited with just the host volatile.

Dispersion of semiochemicals in the vicinity of a baited trap depends on a number of environmental factors, such as the local structure of the stand and abiotic conditions such as air temperature and wind speed (Lewis and Macaulay 1976, Elkinton et al. 1984, Farrell et al. 2002, Girling et al. 2013). Each of these factors can create substantial variation in attractive range; our median estimate of the attraction radius of the semiochemicals was approximately 28m, but could extend up to 70m based on our 95% credible interval (Fig. 2.**Error! Reference source not found.**A). Quantification of the f ull distribution of these values in a Bayesian analysis captures this variation and offers advantages reflecting biological properties within the experimental design. For example,

while the mathematical abstraction of a simple attractive sphere offers helpful analytical properties (Byers et al. 1989, Byers 2008, 2009), pheromone plumes in the stochastic natural environment are subject to turbulent diffusion and much more complex (Murlis et al. 1992, Koehl 2006, Cardé 2020). Likewise, the park in which we placed our traps was not homogeneous in tree cover. Some traps were placed in ash trees that were on the edge of the park and not near other trees and some traps were placed in trees on the edge of forested stands; varied conditions that likely reflect environments in which early detection/rapid response programs may take place. Summing trap captures over time and deploying trap pairs at random directions contends with some of these environmental factors, while full posterior distributions that can be asymmetric capture remaining variation (Fig. 2.**Error! Reference source not found.**A) and thus can be more useful t han single point-estimates for attractive range values in classical, frequentist analyses. The insensitivity of these posterior distributions to our choices of prior specifications provides confidence that our results are robust and reliable (Dorazio 2016, Lemoine 2019). Using other trap pairing arrangements, future research may look at how attraction radius estimates may vary among different local conditions (e.g. stand edge vs. stand interior).

Costs associated with invasive species introductions are predicted to continue to rise as globalization increases (Simberloff 2000, Liebhold et al. 2012). Early detection can help control damage and costs of managing invasive insect pests (Epanchin-Niell and Hastings 2010, Epanchin-Niell et al. 2014) and monitoring for emerald ash borer with traps is preferable in areas where girdling of trap trees is not practical (Augustin et al. 2012). While this study is only the second to utilize this paired-trap methodology, the

consistency with alternate methods (Parker et al. 2020) suggests that pairing traps at increasing distances may be a useful way to estimate the attraction radius of semiochemical baits for some beetles in the order Coleoptera. In a study examining the accumulation of non-native forest insects in the USA since 1635, Order Coleoptera accounted for 26.2% of the insects with at least one recorded location of establishment in the continental United States (Aukema et al. 2010). Moreover, wood and phloem boring beetles accounted for 56% of new insects established between 1980 and 2006, which coincides with an increase in containerized shipping using solid wood crafting, dunnage, and pallets. More work in diverse groups of beetles will be needed to discern this method's utility across other taxa, especially if wood and phloem boring beetles continue to account for the majority of non-native insect establishments.

Figures

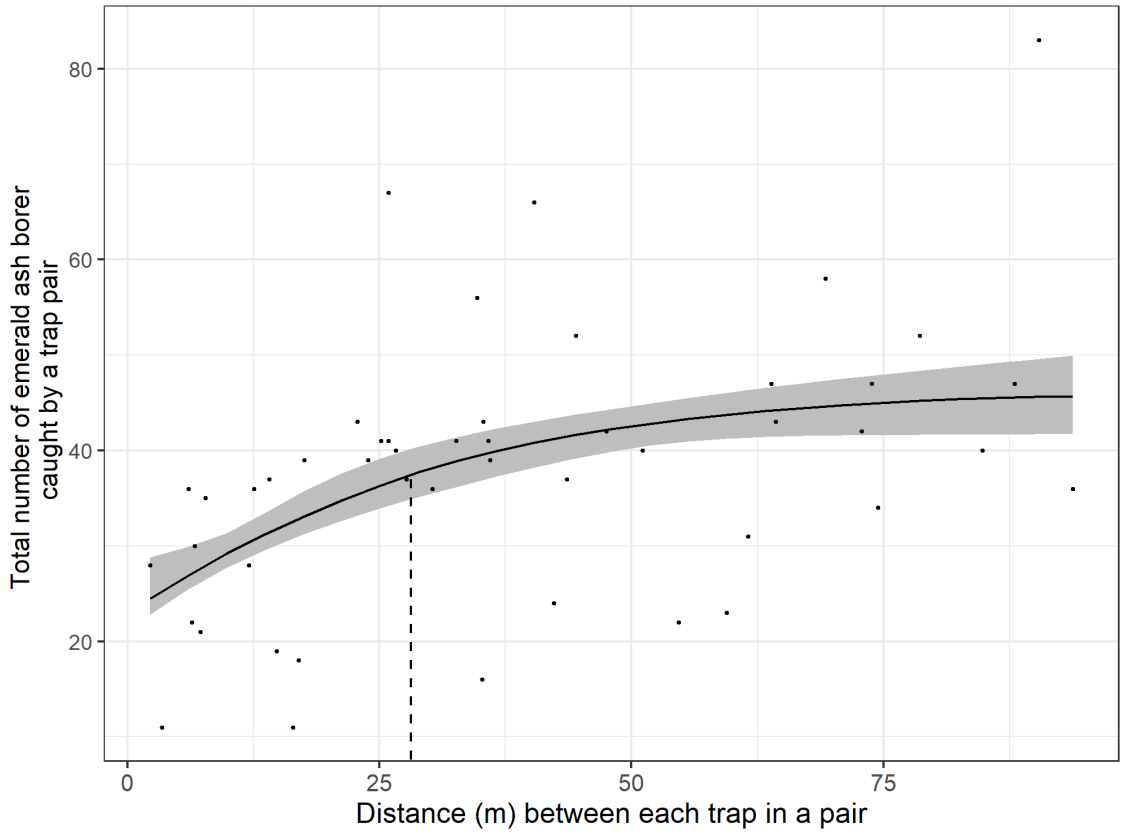

Figure 2.1: Total number of emerald ash borer caught in a pair of traps (*n* = 98) as the distance between the traps in a pair increases. The fitted line is a logistic regression line with two parameters and the grey shaded area represents the 95% credible interval. Dashed vertical line reflects median estimate of the range of attraction.

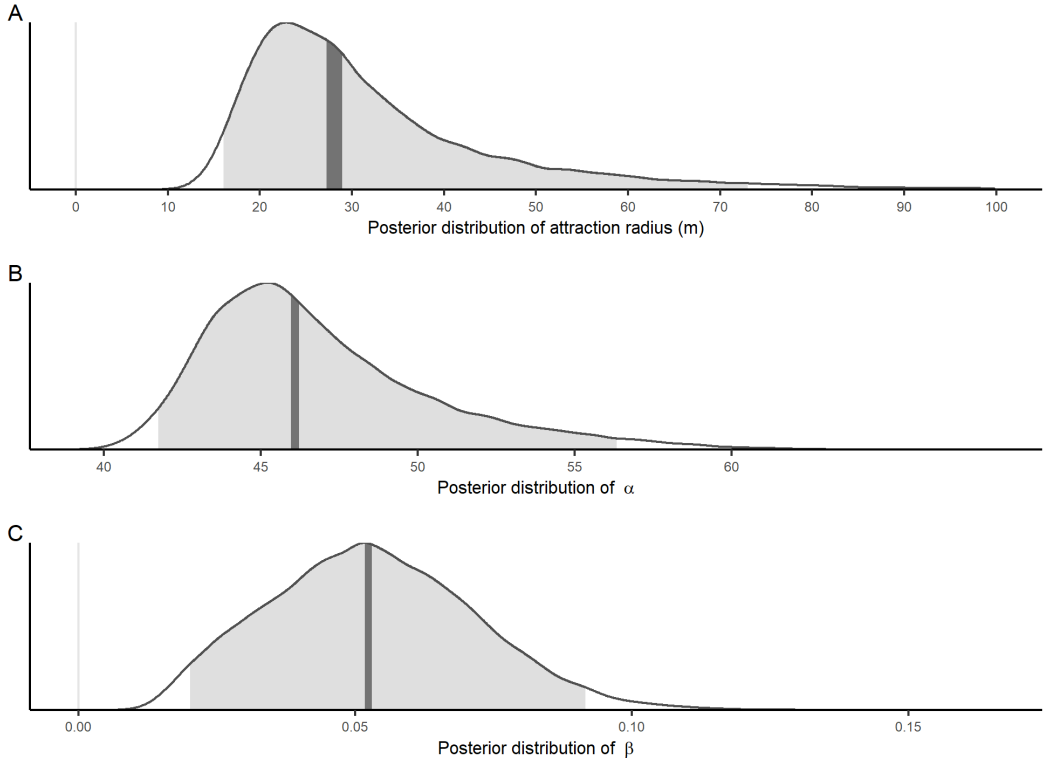

Figure 2.2: Posterior distribution estimates for the (A) attraction radius of traps baited ash host volatile (3*Z*)-hexenol and emerald ash borer sex pheromone (3*Z*)-lactone and the two parameters α (B) and β (C) estimated as part of the logistic regression model fit to trap catch data. The dark grey vertical line represents the median value of the posterior distribution and the lighter grey shaded area is the 95% credible interval.

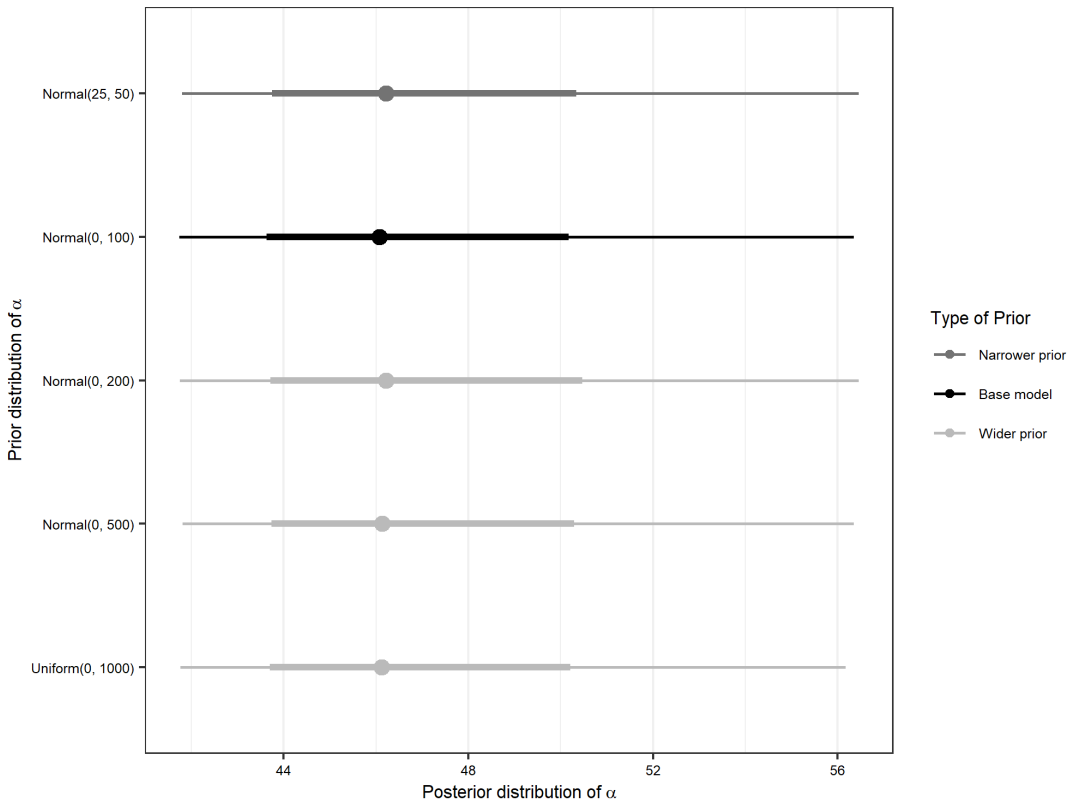

Figure 2.3: Comparison of posterior density estimates for parameter α from the logistic model fit to emerald ash borer trap catch data when different prior probability distributions are used. Each interval represents a posterior density calculated using a different prior distribution, which are listed on the *y*-axis. The point represents the median value of the posterior distribution, the thick line is the 50% credible interval around the median, and the thin line is the 95% credible interval around the point. The base model posterior distribution is the estimate produced from the model described in the Methods section. A prior distribution is considered wider if its 95% credible interval is larger than the 95% credible interval of the prior used in the base model, or narrower if its 95% credible interval is smaller than the 95% credible interval used in the base model.

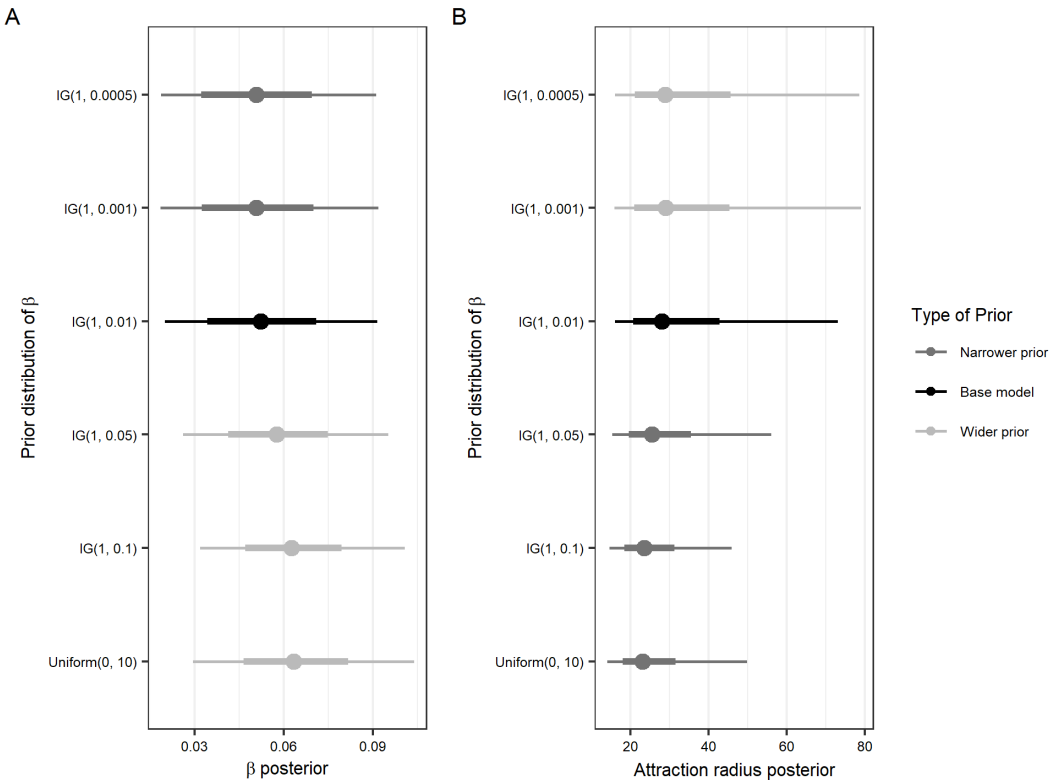

Figure 2.4: Comparison of posterior density estimates for parameter β (A) from the logistic model fit to emerald ash borer trap catch data and the corresponding estimate for the attraction radius (B) when different prior distributions are used. IG represents an Inverse-Gamma prior distribution. The attraction radius is equal to $\frac{1.4722}{\beta}$, so placing a prior distribution on β also acts as placing a prior distribution on the attraction radius. Each interval represents a posterior density calculated using a different prior distribution, which are listed on the *y*-axis. The point represents the median value of the posterior distribution, the thick line is the 50% credible interval around the median, and the thin line is the 95% credible interval around the point. The base model posterior distribution is the estimate produced from the model described in the Methods section. A prior distribution is considered wider if its 95% credible interval is larger than the 95%

credible interval of the prior used in the base model, or narrower if its 95% credible interval is smaller than the 95% credible interval used in the base model. Because of the inverse relationship between β and the attraction radius, a prior distribution that is wider than the prior used for β in the base model will correspond to a transformed prior for the attraction radius that is narrower than what was used in the base model.

Chapter 3

Variation in the spread rate of emerald ash borer *Agrilus planipennis* in North America is associated with environmental factors

Chapter Synopsis

Early work on the theory of biological invasions assumed spread occurs in a homogeneous environment and that the primary drivers of spread are the population growth rate and dispersal. An assumption of homogeneity across the environment, however, is seldom true at the landscape scale and has implications for estimating the spread of invasive organisms. Structured variation in abiotic or biotic factors within a habitat may result in asymmetric spread rates in space and time via effects on behavior or demography. We use historical records of spread of emerald ash borer (*Agrilus planipennis* Fairmaire) to show that the spread rate of emerald ash borer has varied across its invaded range and through time. We also demonstrate that these changes are associated with variation in the environment. Minimum winter temperature had the largest association with changes in spread rates, as an increase in temperature of 1°C was associated with a 1.02 km/year increased rate of spread. Our results provide further evidence that the invasion of emerald ash borer may be entering the saturation phase in eastern North America. These models may be used to help predict spread in other locations invaded by this insect, such as eastern Europe, and to understand how spread of this insect in the future may be impacted by climate change.

Introduction

The rate at which non-native species are being detected outside their native range has increased from the early 1800s to the modern day (Seebens et al. 2017). Much of this increase can be attributed to increases in human travel and trade (Levine and D'Antonio 2003, Westphal et al. 2008, Meurisse et al. 2019). Costs associated with the damage caused by invasive species and their management in North America have reached an estimated $1.2 trillion (USD) from 1960 - 2017 (Crystal-Ornelas et al. 2021). While eradication of invasive species is sometimes possible (e.g. Myers et al. 1998, Hendrichs et al. 2002, Veitch and Clout 2002, Sarty 2007, Suckling et al. 2007, Liebhold et al. 2016), it may be too difficult or expensive to eradicate the entire population if non-native species are not detected early (Bogich et al. 2008). Managing established invasive species might then focus on attempting to slow their spread through quarantines and suppress populations, as through integrated pest management or importation biological control programs (Tobin 2018, McLaughlin and Dearden 2019, Venette and Morey 2020).

The spread of invasive insects emerges from the combination of population growth and dispersal behavior (Kot et al. 1996). This coupling of behavior and demography is used in theoretical models used to understand spread. Early work on the theory of biological invasions assumed that spread occurs in a homogeneous environment and that the primary drivers of spread are the population growth rate and the type of dispersal (Skellam 1951, With 2002). The assumption of homogeneity, however, is seldom true at the landscape scale. Some matches have been found between theorized and observed spread rates in invasive insects, but incorporating heterogeneity may result in models that more closely match observed spread (Andow et al. 1990, Shigesada and

Kawasaki 1997, With 2002). Often, spread is also augmented with inadvertent, human-mediated movement (i.e. long-range dispersal) (Andow et al. 1990, Hastings et al. 2005, Liebhold and Tobin 2008).

Habitat that varies spatially or temporally in terms of abiotic or biotic factors may result in variable spread rates in space and time via effects on behavior or demography (With 2002, Hastings et al. 2005, Schreiber and Lloyd-Smith 2009, Lustig et al. 2017, Lutscher and Musgrave 2017, Crone et al. 2019). Theoretical models have often focused on resource availability and behavior (Shigesada et al. 1986, Jactel et al. 2005, Brockerhoff et al. 2006, Dewhirst and Lutscher 2009, Rigot et al. 2014, Lutscher and Musgrave 2017). Other factors that affect spread may include changes in fecundity and survivorship of the spreading insect (With 2002), densities of predators and competitors (Melbourne et al. 2007), voltinism (Fahrner and Aukema 2018), precipitation (Hartley et al. 2010, Price and Hunter 2015), and temperature (Evans and Gregoire 2007, Morin et al. 2009, Lantschner et al. 2014, Sambaraju et al. 2019). For example, temperatures in the southern range of the invasive defoliator *Lymantria dispar dispar* (L.) (Lepidoptera: Erebidae) in North America often exceed the optimal temperature for the development of larvae (Tobin et al. 2014). These high temperatures are implicated in increased Allee effects along this range margin, leading to variable rates of change in the range from expansion to contraction (Walter et al. 2020).

Much effort has been devoted to understanding the spread of invasive insects to target early detection and rapid-response programs efficiently and mitigate future costs of management and the potential for damage. An understanding of the specific drivers that affect the spread of an invasive insect pest can provide predictions for arrival times. Such

predictions may help natural resource managers direct management efforts (Sadof et al. 2017, Liebhold and Kean 2019). The “Slow the Spread” program targeting *Lymantria dispar dispar* used models of spread for this insect to target management operations along the leading edge of the invasion. This program has slowed spread of *L. dispar* by more than 50% (Sharov et al. 2002). Similarly, information on dispersal abilities of a pest can be used in the creation of “barrier zones,” where suitable host habitat is intentionally removed to prevent the spread of an invasive insect (Li et al. 2020). In 2004, early in the invasion of emerald ash borer (*Agrilus planipennis* Fairmaire Coleoptera: Buprestidae) in North America, an ash-free barrier zone was created in Ontario, Canada but it was unsuccessful due to populations that had already established beyond the barrier zone (Herms and McCullough 2014). Understanding the drivers of spread for individual species may also help early management efforts when similar, related invasive species are later detected (Herms and McCullough 2014).

This study describes an investigation into variability in spread of emerald ash borer across North America. Emerald ash borer is native to eastern Asia. It arrived in North America in the 1990s and was first detected in the early 2000s (Siegert et al. 2014). The larvae of this insect feed on the phloem of ash trees (*Fraxinus* spp), eventually girdling the tree. Emerald ash borer spread can be characterized by stratified dispersal, whereby local diffusive spread by adults through flight is coupled with long-distance dispersal events by all life stages through the movement of infested ash material to locations outside the invasion boundary (Cappaert et al. 2005, Muirhead et al. 2006). Characteristics of the local environment, such as the amount of ash phloem available, affect dispersal on a local scale, with emerald ash borer appearing to prefer to disperse to

areas with high ash density and to stressed ash trees (McCullough, Poland, and Cappaert 2009, McCullough, Poland, Anulewicz, et al. 2009, Siegert et al. 2010) . Most adults in a newly invaded area disperse within 100 meters of the arrival location if ash resources are sufficient (Mercader et al. 2009, 2011, 2016).

Previous research has described spread rates for emerald ash borer. The initial growth of the invasion front of emerald ash borer in the USA was estimated to be approximately 20 km/year from 1998 to 2006 (Prasad et al. 2010). This rate was estimated by combining multiple early data sources detailing ash mortality to delineate invaded areas. The authors assumed it took five years to kill 80 - 100% of ash trees in a region. For example, an area infested in 1998 would have 80 - 100% ash mortality in 2003. Evans (2016) estimated that the spread rate of emerald ash borer in the USA was as high as 57 km/year based on distances measured from the centroid of invaded counties to Detroit, MI from 2003 to 2008. A more recent evaluation of spread of emerald ash borer using records from 1997 to 2018 that the effective range radius, a measure of the area invaded by emerald ash borer, increased in the USA at variable rates through time (Ward et al. 2020). The growth of the effective range radius was estimated to be 13.8 km/year from 1998 to 2002, 31 km/year from 2002 - 2012, and peaking at approximately 55 km in 2015. These range radius increases were estimated based on dendrochronological reconstruction of emerald ash borer spread from 1997 to 2003 and county-detection data after that period. While these studies generally agree on the overall spread of emerald ash borer, we are aware of no studies that have incorporated detection records from both the USA and Canada. Additionally, landscape-scale spread rates have been shown to vary in space for other invasive forest pests (Tobin et al. 2007, Lantschner et al. 2014) and

comparing the rate at which counties become invaded among different states in the USA suggests that emerald ash borer is spreading more slowly in some states than others (Appendix B Fig. 1).

The goals of this study were twofold: use historical records of detection to determine how the rate of spread of this insect has varied through space and time in North America and to quantify how factors known to affect the demography of insect populations (i.e. temperature, precipitation, and host availability) may play a role in geographic variation of spread. To our knowledge, this is the first study that has incorporated detection records from across the entire range of emerald ash borer in North America, which is valuable when addressing invasive species that cross international borders. The findings of this research will provide insight into the past spread of emerald ash borer and may inform forecasts of how quickly emerald ash borer will spread to in newly invaded areas.

Materials and Methods

Emerald Ash Borer Detection Data

We used annual county-level records of detection of emerald ash borer in the United States from 2002 - 2020 compiled by the United States Department of Agriculture, Animal and Plant Health Inspection Service (USDA APHIS) to identify the area invaded by emerald ash borer in the USA. We used data from the Canadian Food Inspection Agency on survey efforts from 2002 - 2020 to generate a comprehensive list of county-level detections in Canada (Canadian Food Inspection Agency 2017, 2021). These data included the locations (latitude, longitude) of emerald ash borer traps

throughout Canada and if emerald ash borer was detected. We converted the Canadian data to the same spatial scale as the USA data (i.e. county-level) by designating a given county as invaded at the earliest year a trap in that county detected emerald ash borer. From the USA and Canadian data, we were able to construct a map of the invaded range of emerald ash borer in North America, which allowed us to estimate historic rates of spread. Because these data are only available at the county-level, they carry the assumption that emerald ash borer is present throughout a county once it is initially detected. Additionally, we assumed that detection efforts are relatively uniform across the uninvaded area and that detection dates reflect the actual arrival of emerald ash borer in the county.

Estimating boundary expansion and spread rates

To characterize the spread of emerald ash borer and identify if spread rates are variable, we build on methods presented in Morin et al. (2009). As an initial exploration of spread, we calculated the geographic centroid of the invaded area each year. Shifts in the location of the centroid of the invaded range may be indicative of asymmetric rates of spread in space. This analysis was done by creating one polygon for each year of all counties with a positive detection up to that year. We created this invaded range polygon using the geographic information system capabilities of the sf package in R (Pebesma 2018) to merge the individual county polygons into one shapefile.

To model the expansion of the invaded boundary, we divided the invaded range into “bearing intervals.” We generated 360 radii spaced every 1° and centered on the centroid for Wayne county, Michigan, USA, where emerald ash borer was first detected. These radii extended across the invaded range of the insect. We then calculated the

distance from the centroid of Wayne county to the edge of the invasion boundary in each year from 2002 to 2020. We binned each radius in 5° increments (e.g., [0°, 5°), [5°, 10°), etc.) to form the bearing intervals (Fig. 3.**Error! Reference source not found.**). We a veraged the distance to the boundary measured along each radius in each year across the five radii in each bearing interval. Boundary displacement was chosen as the metric for spread because it more accurately captures the rate of spread than alternatives when geographic barriers, such as the Great Lakes, are present (Gilbert and Liebhold 2010, Tobin et al. 2015). The average radial distances between successive boundary displacements per year were modeled with a generalized additive model (GAM). Year, bearing interval, and the interaction of year and bearing interval were included as smooths in this model to flexibly model the spread of this insect across its invaded range through time. The use of a cyclic cubic spline forced the smooth for bearing intervals to match at 0° and 360°. Once the GAM for boundary displacement was fit, first derivatives (slopes) of this function with respect to time were estimated in each bearing interval (Ruppert et al. 2003). These derivatives provide estimates of the rate of spread of emerald ash borer. A second GAM was fit that only included a smooth for year to characterize the average rate of spread through time across the entire invaded range. This technique allowed for comparisons between spread rate in any given direction and the overall average rate of spread.

Association between spread rates and environmental variables

The spread rates estimated from the GAM were then used in a second model to assess the association between spread rate and environmental variables. The environmental variables used in this analysis were average minimum temperature of the

coldest month from 1970 - 2000 (Fig. 3.**Error! Reference source not found.**A), average a nnual precipitation from 1970 - 2000 (Fig. 3.**Error! Reference source not found.**B), and the percent of total above ground biomass contributed by *Fraxinus* species (hereafter referred to as percent or proportion ash biomass, Fig. 3.**Error! Reference source not f ound.**C). The rasters for minimum temperature and precipitation were obtained from the WorldClim dataset (variables Bioclim6 and Bioclim12, respectively) at 2.5-minute resolution (Fick and Hijmans 2017). A raster for percent ash biomass in North America was created by combining data from two different sources. A raster of percent ash biomass for forested areas in Canada was obtained from supplemental material in Beaudoin et al. (2014). The rFIA package (Stanke et al. 2020) was used to produce a similar raster for the USA and these two rasters were then merged. The sf package was used to produce areal estimates of the average values of these environmental variables within the polygon created for the invaded area in each bearing-year interval (e.g. the average of Bioclim6 in the areal unit corresponding to year i and bearing interval j).

We then regressed spread rate on each of these variables individually and a full model containing all four variables using a simultaneous autoregressive model (SAR) model. Simultaneous autoregressive models make use of a spatial neighborhood structure to account for additional autocorrelation in models that use areal data. These models were fit with a queen's case (second order) neighborhood. Additionally, because the spread rates used as the response in these models were themselves estimates from a model, we used a bootstrap resampling method to attempt to account for error in the estimates of the spread rates. We resampled the spread rate values for each bearing-year combination to generate 5000 bootstrapped datasets. Bootstrapped spread rate values were drawn from a

normal distribution, centered on the expected spread rate value from the previously mentioned GAM and with variance quantified by the standard error for each estimate. The SAR model was then fit to each of these 5000 datasets using computational resources provided by the Minnesota Supercomputing Institute at the University of Minnesota.

All data preparation, analysis, and plotting were carried out in R v4.0.4 (R Core Team 2020). Generalized additive models were fit using the mgcv package (Wood 2017) and SAR models were fit using the spatialreg package (Bivand et al. 2013). Additional data preparation and plotting were done using the dplyr, purrr, and ggplot2 packages (Wickham 2016, Henry and Wickham 2020, Wickham et al. 2020).

Results

The centroid of the area invaded by emerald ash borer in each year has shifted sporadically over time, often to the south of Detroit, MI (Fig. 3.**Error! Reference source not found.**). The centroid remains in Michigan, Indiana, or Ohio. The largest change in the location of the centroid occurred from 2008 - 2009 as the centroid shifted ca. 487 km to the south. The two smallest changes in the centroid location occurred from 2002 - 2003 and 2004 - 2005, where the centroid moved ca. 46 km to the south-west and 41 km to the south-east, respectively.

The expansion rate of the invasion boundary across the entire range appears approximately constant at ca. 47 km/year until 2005, when it increases from 47 km/year to 58.8 km/year in 2009. After 2009, the average rate of increase in the invasion boundary decreases through time until it is 19.5 km/year in 2020 (Fig. 3.**Error! Reference source not found.**A). The smooth for time in this model was statistically

significant (edf = 4.48, refdf = 5.53, χ^2 = 4368.81, p <0.001, deviance explained = 59.4%). In contrast, the boundary of the invaded area grew at different rates across the invaded range (Fig. 3.**Error! Reference source not found.**B). For example, the fastest i ncrease in the distance to the invasion boundary occurred in the directions between bearings ca. 45° - 90° (northeast - east) and 200° - 250° (southwest). The slowest rates of expansion were seen in the north (ca. 315° - 360° and 0° - 22.5°). In this model, the smooths for year (edf = 4.43, refdf = 4.84, χ^2 = 9248.26, p <0.001), bearing (edf = 16.14, refdf = 18.00, χ^2 = 1093.06, p <0.001), and the interaction of the two (edf = 17.68, refdf = 20.00, χ^2 = 894.06, p <0.001) were statistically significant. The overall deviance explained for this model was 71.9%.

Similar patterns can be observed in the rates of spread estimated from the boundary growth models (Fig. 3.**Error! Reference source not found.**). Several d irections (e.g. ca. 45° - 135°) show a humped-shape spread rate curve, indicating the spread of emerald ash borer increased through time and then decreased. Spread to the northwest, north, and northeast, show nearly constant rates of spread, or initially constant followed by a decrease in the rate of spread. Some directions show spread rates that are faster (i.e. ca. 45° - °135, ca. 225° - 247.5°C) or slower (i.e. ca. 0° - 22.5°, ca. 315° - °360) than the average rate of spread over the entire range. Spread to the northeast, east, and southeast appeared to peak at approximately the same time (ca. 2010) while the rate of spread in the southwest shows a later peak around 2015.

Results of the bootstrapped single-variable regressions and the full multiple regression model coefficients quantifying the relationships between model covariates and spread rate are presented in Table 3.**Error! Reference source not found.**. When all the v

ariables were investigated singularly, all of the variables were statistically significant. Minimum temperature had the largest slope coefficient (median β = 0.52, 95% CI: 0.40 - 0.63). Both the proportion of ash biomass and the average amount of neighboring ash biomass had positive relationships with spread rate, with a 1 percent increase in each variable associated with an increased spread rate of 0.18 km/year (95% CI: 0.14 - 0.23) and 0.24 km/year (95% CI: 0.18 - 0.29), respectively. Precipitation had a small, but non-zero, association with spread rate. A 1 cm increase in total annual precipitation was associated with a 0.058 km/year decrease in spread rate (95% CI: 0.030 - 0.093).

Similar coefficient signs and magnitudes were seen for the coefficients in the full model. Minimum temperature still had the largest association with spread rate as a 1°C increase in the minimum temperature of the coldest month was associated with a 1.02 km/year faster rate of spread (95% CI: 0.840 - 1.21). Annual precipitation had an opposite association with spread rates. Increasing annual precipitation by 1 cm was associated with a -0.23 km/year change in rate of spread (95% CI: -0.28 - -0.18). The percent ash biomass that is in the ash genus was associated with a change in the rate of spread (median β = 0.10, 95% CI: 0.046 - 0.16), but the average proportion of ash biomass in the areas neighboring a given unit was no longer associated with a change of spread (median β = 0.0684, 95% CI: -0.0105 - 0.147).

Discussion

Characterizing the spread of invasive insects may provide insight into how the insect will spread if it is found in new locations globally and provides empirical evidence against which theoretical models of spread can be evaluated (Liebhold and Tobin 2008, Lutscher and Musgrave 2017, Tobin 2018). The spread of emerald ash borer appears to

have gone through both the establishment and expansion phases typical of stratified diffusion (e.g. type 2 expansion *sensu* Shigesada et al. 1995) and has reached the saturation phase, at least in the eastern United States (Ward et al. 2020). Our results demonstrate that emerald ash borer has reached the saturation phase of spread in eastern North America, but it has done so at different times in different directions consistent with differences in environmental heterogeneity, reaching geographic limits of host distribution, and encountering a geographic barrier. The fact that an increase in the rate of spread through time was only seen in some directions also suggests that long-distance dispersal events may have occurred with less frequency to the north than to the east and south.

The slow rates of spread in the northern ranges of the invaded range of emerald ash borer may have been caused by colder winter temperatures. These areas in North America regularly have winters with minimum temperatures as cold or colder than -20°C. Overwintering mortality of this beetle is highest in areas where temperatures reach less than -30 to -35°C, which may limit the northern range of this insect (DeSantis et al. 2013, Christianson and Venette 2018, MacQuarrie et al. 2019), although recent research suggests that emerald ash borer may have sufficient phenotypic plasticity to survive extreme cold events given appropriate prior cold exposure (Duell et al. 2022). Increased mortality due to cold temperatures in the winter may slow population growth, leading to slower spread (Schreiber and Lloyd-Smith 2009). Additionally, portions of emerald ash borer populations take two years to complete development due to cooler climate, lower population densities, or increased host vigor (Liu et al. 2007, Wei et al. 2007, Duan et al. 2013, Orlova-Bienkowskaja and Bieńkowski 2016). Semi-voltinism will result in slower

population growth in these regions which may, in turn, slow the spread. Voltinism plays an important role in the spread of invasive insects as more generations per year are associated with higher rates of spread (Fahrner and Aukema 2018). The geographic barrier presented by the Great Lakes likely also contributes to the slower rate of spread in the north.

In contrast, the faster spread to the east and south is likely due to abundant ash resources, high human population density, and optimal temperatures (Hastings et al. 2005, Duan et al. 2013, Ward et al. 2020). While we did not specifically evaluate the association between spread rates and maximum summer temperatures, temperatures greater than 30°C are suboptimal for the development of eggs and larvae (Duan et al. 2013). Temperatures at the southern edge of the invaded area are often above 30°C and may explain the slowing spread on the southern range margin. Our findings also suggest that climate change may impact the spread of this insect in the future; spread may increase in the north as winters warm until the northern limit of ash is reached, and it may slow as temperatures warm in the south. Liang and Fei (2014) found that climate change may result in a divergence between emerald ash borer and its ash hosts as temperatures in the southern USA become unsuitable for the beetle, resulting in retraction in the southern range of this insect. Temperature has been implicated in variable spread rates in *Sirex noctillio* F. (Hymenoptera: Siricidae) (Lantschner et al. 2014), hemlock wooly adelgid Annand (*Adelges tsugae*, Hemiptera: Adelgidae) (Evans and Gregoire 2007, Morin et al. 2009), and *L. dispar* (Liebhold et al. 1992).

Decreased levels of precipitation may increase the spread rate of emerald ash borer via reduced host vigor, which in turn may increase population growth. In the native

range of emerald ash borer, drought has been shown to increase the susceptibility of Manchurian ash (Villari et al. 2016) and the attraction of buprestids in general to stressed trees is well documented (Barter 1957, Haack and Benjamin 1982, Dunn et al. 1986, Svihra and Koehler 1993, Koricheva et al. 1998). Increased precipitation may aid in host vigor. While ash trees in North America have little to no resistance to emerald ash borer, the insect does perform better in trees that have been stressed (Poland et al. 2015). Increased precipitation has also been associated with slower rates of spread for the emerald ash borer congener *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) in its invaded range in California, USA (Scott et al. 2015).

The association of percent ash biomass with spread rates was small, but the direction of the association is in line with other findings. Basal area of ash was an important predictor of the risk of invasion by emerald ash borer in the USA (Ward et al. 2020) and we anticipate that we may have observed a similar association with spread rate had we been able to incorporate basal area of ash, rather than proportion of ash biomass, into our model. Unfortunately, we are not aware of any data set describing the basal area of ash trees in Canada. The spatial scale of our data may also play a role in determining the strength of the association. At the site-scale, emerald ash borer has been shown to stay in the proximate area (i.e. within ca. 100 m) if enough ash resources are present and otherwise will disperse towards areas with abundant ash resources (Mercader et al. 2009, 2011). The beetle is unlikely to leave areas where ash resources are abundant, and populations may remain below detection levels for longer while ash resources are not abundant (Crooks 2005). Evaluating how the effects of environmental heterogeneity on spread rates change at varying spatial scales may be an avenue for future research.

Additionally, incorporating information on the diversity of trees may prove valuable in future similar models, as increased tree diversity may reduce the availability of host trees or sustain a larger generalist natural enemy population which may, in turn, alter the rate of spread (Brockerhoff et al. 2006, Jactel and Brockerhoff 2007).

The spread of emerald ash borer is additionally driven, in part, by human-mediated means such as the movement of infested firewood, ash nursery stock, or on railroads (BenDor et al. 2006, BenDor and Metcalf 2006, Muirhead et al. 2006, Prasad et al. 2010, Short et al. 2020). While our modeling efforts cannot explicitly attribute changes in spread rate to human-mediated events, these events are impacted by the destination environment to which emerald ash borer are moved. Successful colonization of satellite locations depends on appropriate environmental conditions, available host resources, and sufficient number of invading individuals to overcome any potential Allee effects (With 2002, 2004, Taylor and Hastings 2005, Tobin et al. 2011). Long-distance dispersal events may have found more success to the south and east of the introduction point, where winter temperatures are more amenable to emerald ash borer and ash is abundant.

Our findings have implications for the spread of emerald ash borer in Europe and Asia. Orlova-Bienkowskaja and Bieńkowski (2020) found that temperatures in European Russia may be cold enough to prevent the establishment of emerald ash borer, but not in northern Western Europe. Our study suggests that, though the cold in this region may not prohibit establishment, it should slow the spread and provide longer lead times for management activities related to the invasion (Crooks 2005). At longer time scales, changes in temperatures, precipitation regimes and the frequency of severe weather

events due to climate change may further alter the spread rate of this insect. The models presented in this paper provide a tool for estimating the rate of spread based on environmental heterogeneity and may prove helpful in forecasting the spread of this insect into new locations in light of climate change. We also provide further empirical evidence that environmental heterogeneity contributes to varying rates of spread in invasive insects.

Tables

Table 3.1: Coefficient summaries (95% confidence intervals) of the association of spread rate with environmental variables from bootstrapped simultaneous autoregressive models. The first four rows display the association of a single predictor variable on estimated spread rates, while the last row displays a summary of the multiple regression model containing all four variables. Variables whose 95% confidence intervals do not overlap with zero are considered statistically significant.

Intercept	Minimum winter temperature (°C)	Total annual precipitation (cm)	Percent of ash biomass (%)	Avg. neighboring ash (%)
52.24 (50.94, 53.50)	0.52 (0.40, 0.63)	-	-	-
52.84 (49.99, 56.28)	-	-0.06 (-0.09, -0.03)	-	-
44.60 (43.86, 45.34)	-	-	0.18 (0.14, 0.23)	-
43.61 (42.66, 44.61)	-	-	-	0.24 (0.18, 0.29)
76.60 (70.26, 83.16)	1.02 (0.84, 1.21)	-0.23 (-0.28, -0.18)	0.10 (0.05, 0.16)	0.07 (-0.01, 0.15)

Figures

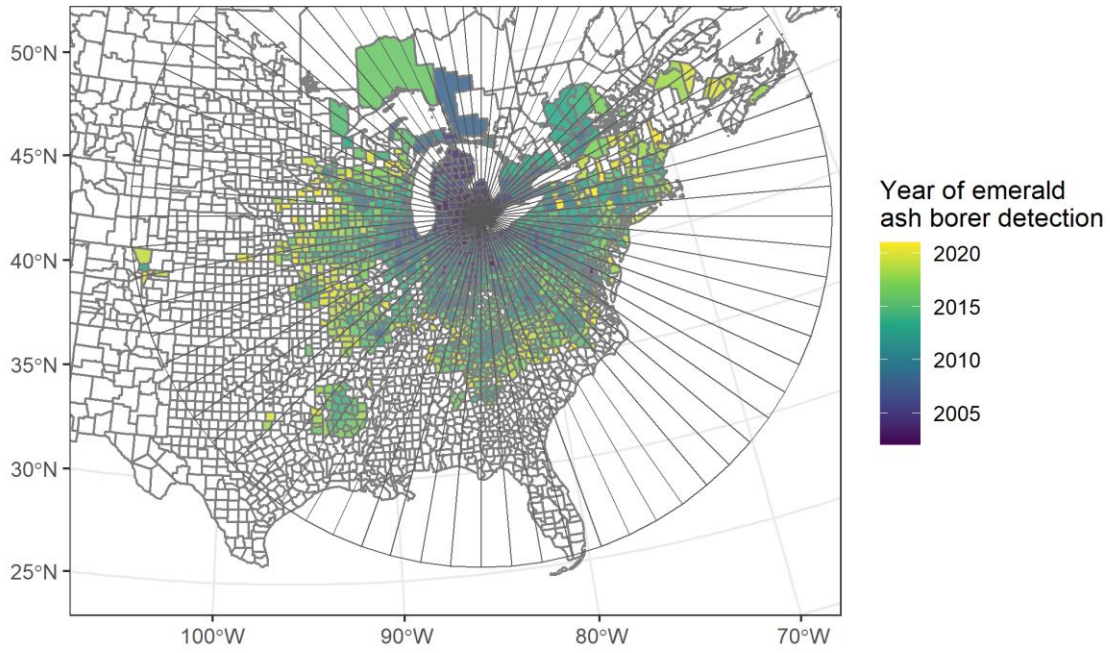

Figure 3.1: Bearing groups used in estimating anisotropic boundary displacement of the emerald ash borer invasion boundary. Wedges are centered on Detroit, Michigan, USA. Each wedge spans 5° of the circle. The average radial distance from the center to the edge of the invaded boundary in each year was calculated and used to model the growth of the invasion boundary through time and across the invaded range.

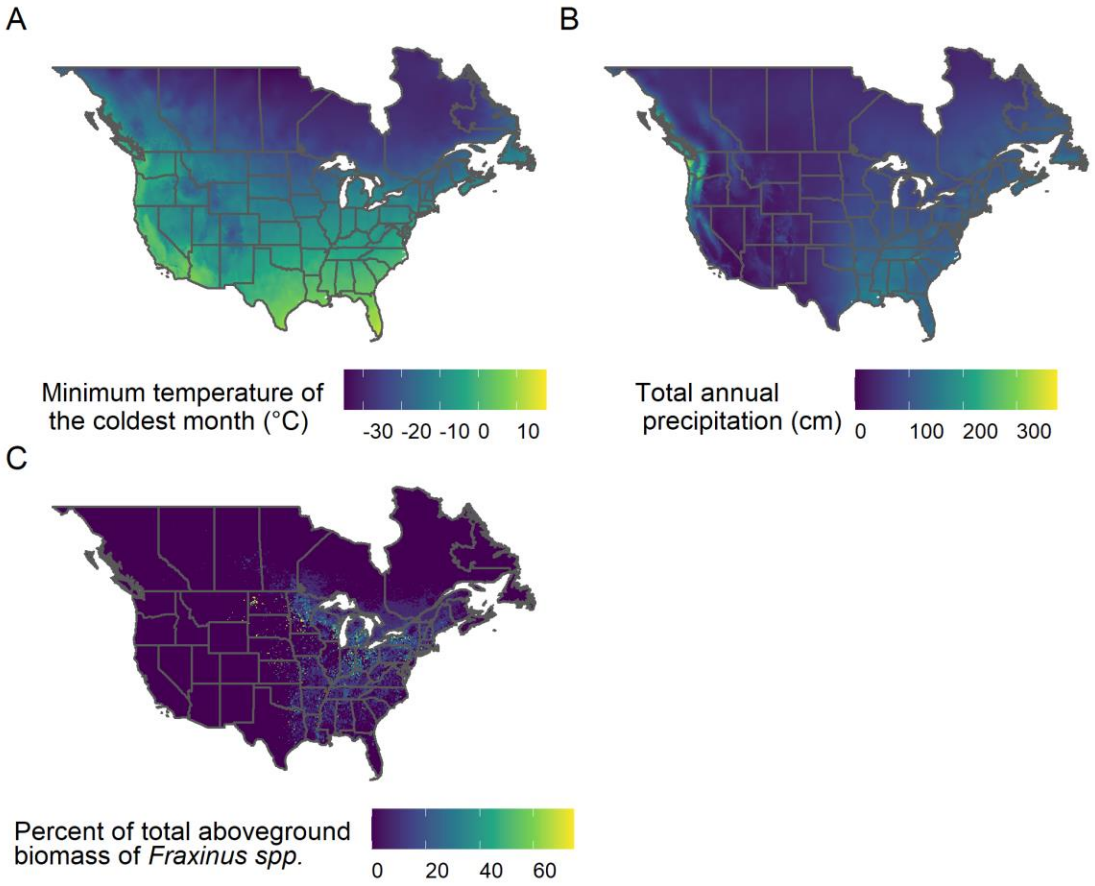

Figure 3.2: Environmental covariates used in the models evaluating the association between these variables and the rate of spread of emerald ash borer: average minimum temperature (°C) of the coldest month in North America (A), average total precipitation (cm) in North America (B), and proportion of total aboveground biomass that is *Fraxinus* spp. (C).

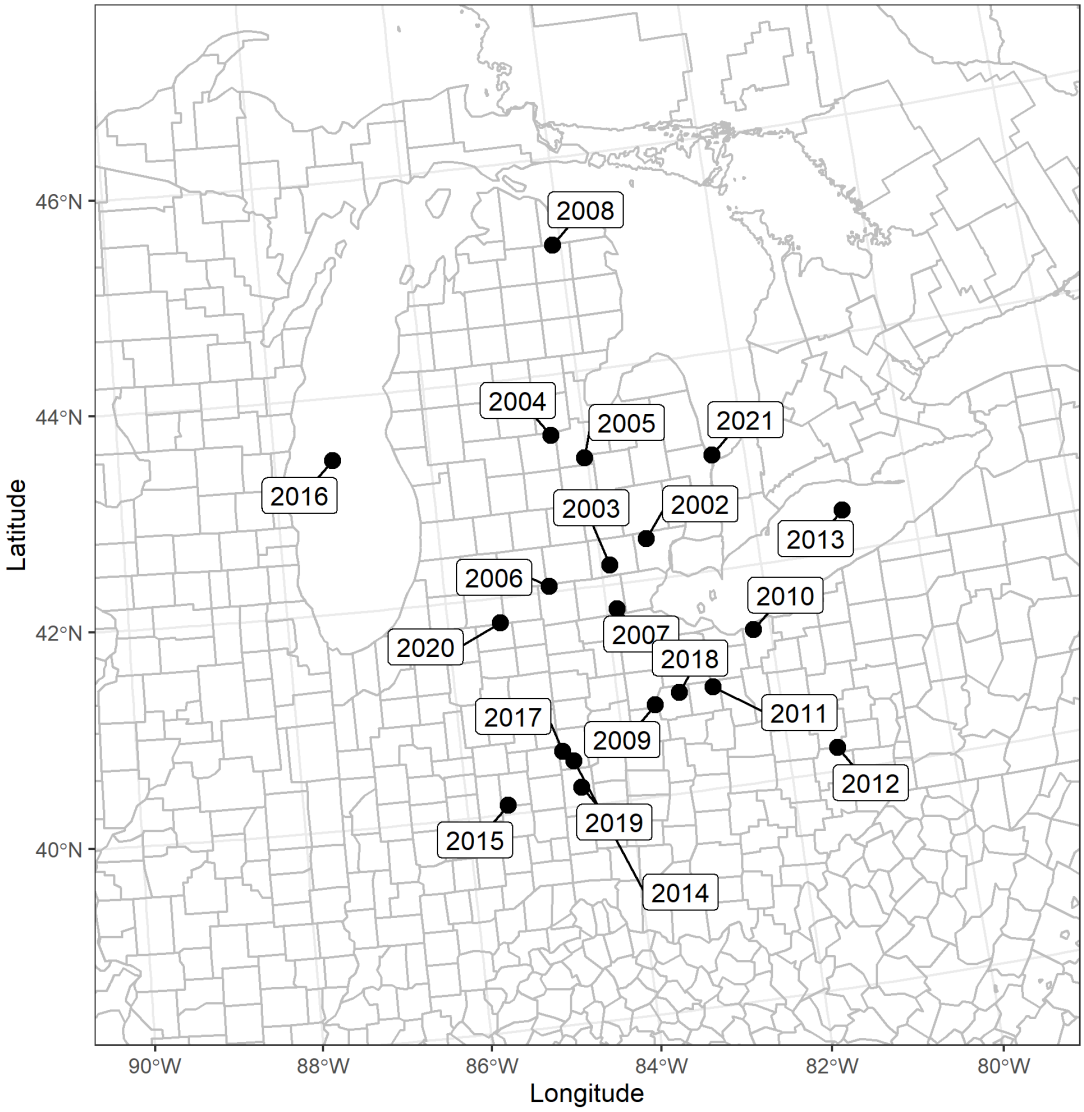

Figure 3.3: Changes in the location of the centroid of the area invaded by emerald ash borer through time. Changes in the position of the centroid allow a visualization of potential anisotropy in spread. The centroid appears to shift mainly to the south and southeast from the initial detection near Detroit, MI, USA.

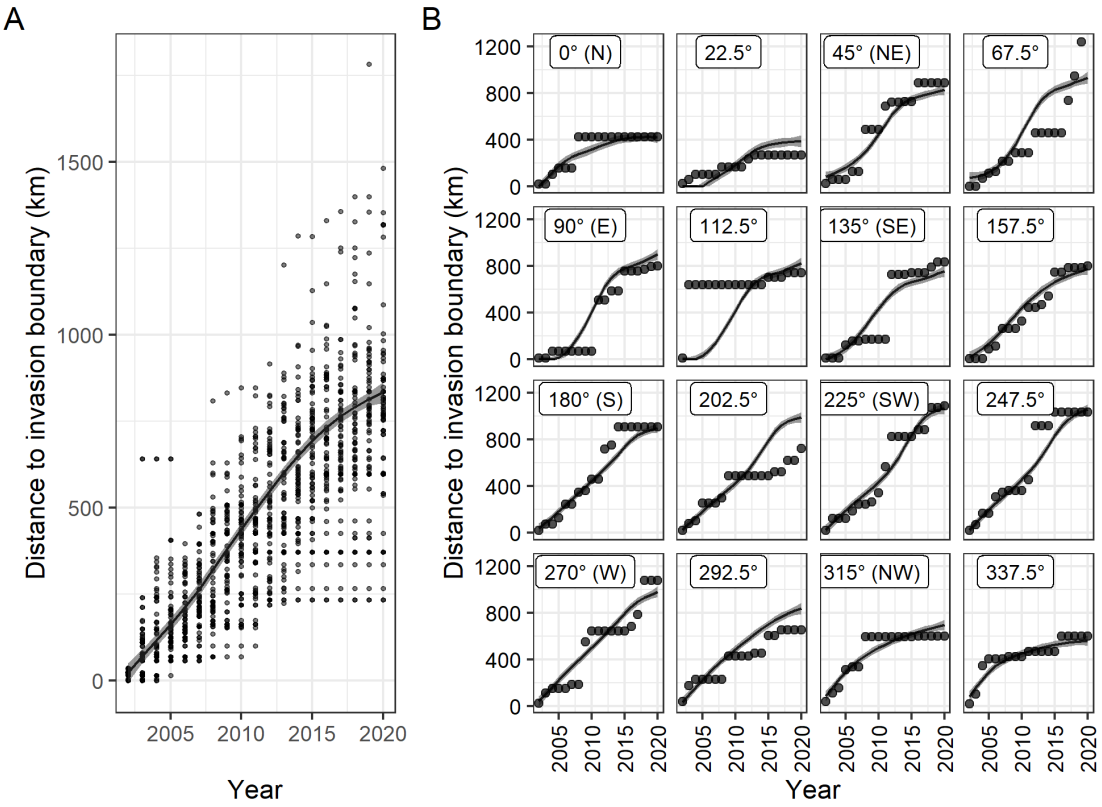

Figure 3.4: Growth of the boundary of the area invaded by emerald ash borer across the entire invaded range (A) and in various directions (B). Lines are fitted values of the boundary distance from generalized additive models (GAM) and the grey ribbon represents the 95% confidence interval for these fitted values. The points in A have been shrunk to facilitate viewing of the fitted line.

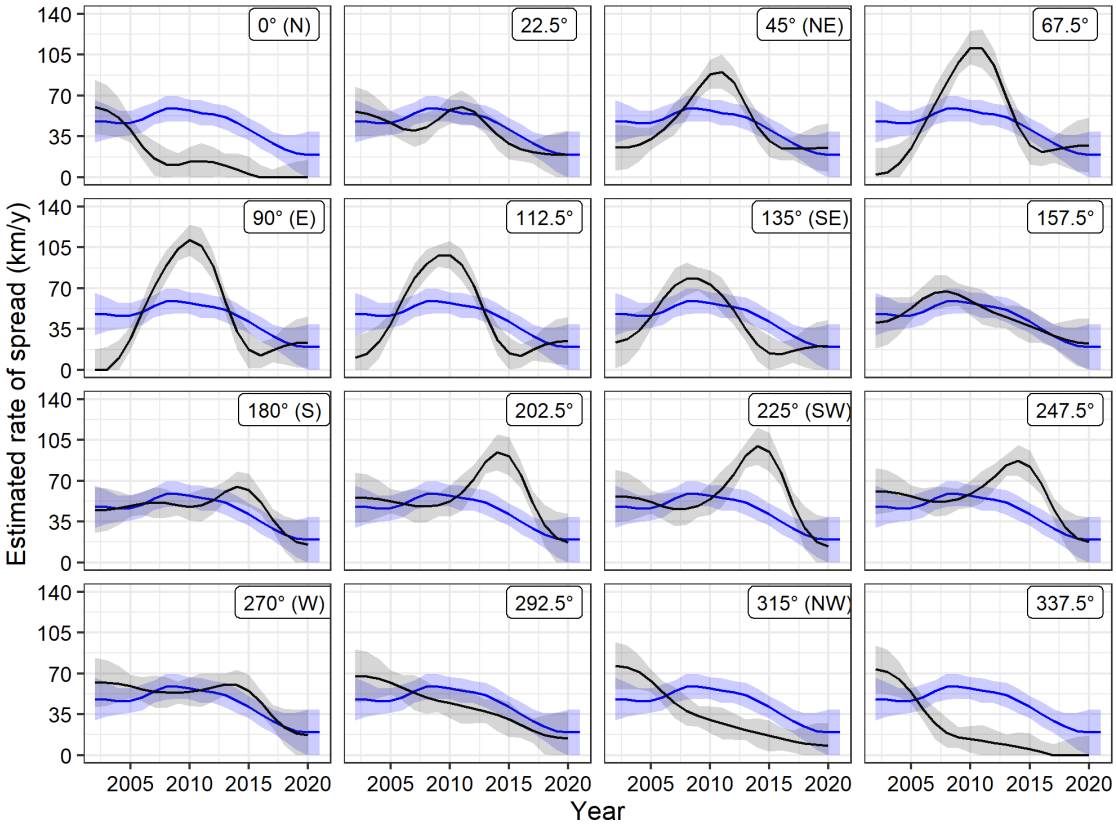

Figure 3.5: Estimated rate of spread of emerald ash borer in different directions (in grey) across its invaded range in North America. The blue line is the estimated spread rate for the overall growth of the invasion boundary. Ribbons represent the 95% simultaneous confidence interval for the smooth. These estimates come from the derivative of the models shown in Fig. 3.4.

Dissertation Conclusions

Chapter 1

1) *Spathius galinae* appear to be cold tolerant enough to survive most winters up to USDA Plant Hardiness Zone 4b (-25°C). *Spathius galinae* suffered extensive mortality below -25°C in our field studies, but laboratory assays revealed that some larvae may also be able to survive temperatures as low as -32°C. Several larvae survived temperatures as low as -29°C in the field studies and successfully completed development after being placed in an incubator in the spring.

2) *Spathius galinae* may exhibit a mixed cold tolerance strategy. The majority of insects used in this study died after freezing (i.e., were freeze intolerant), but seven insects chilled in the laboratory exhibited exotherms and continued to complete development afterwards. These latter patterns are indicative of freeze tolerance.

3) *Spathius galinae* may not be as cold tolerant as emerald ash borer. The point at which 90% of the insects chilled in the laboratory froze was -26.7°C. Recent research has shown that emerald ash borer exposed to sufficiently cold winter conditions may have supercooling points as low as -50°C. This differential in supercooling point may make *Spathius galinae* less effective at the northern most range of ash in North America.

Chapter 2

1) Green prism traps baited with the host volatile (3*Z*)-hexenol and the emerald ash borer sex pheromone (3*Z*)-lactone have an effective radius of attraction between

16 - 73 meters. This knowledge can be used to place traps efficiently, maximizing the area monitored by these traps and minimizing costs.

2) Placing pairs of traps with increasing distances between them appears to be a useful method for estimating the range of attraction of a semiochemical bait. The results of our study were consistent with previous work done evaluating the range of attraction of semiochemicals used in traps for emerald ash borer.

3) Quantification of the full distribution of the range of attraction in a Bayesian analysis captures the natural variation present in the dispersal of semiochemicals. This analysis offers advantages reflecting biological properties within the experimental design.

Chapter 3

1) Emerald ash borer has spread anisotropically across North America, spreading fastest to the south and east of its introduction near Detroit, Michigan, USA. The fastest observed rates of spread were approximately 105 km/year. Spread slowed most quickly to the north, northwest, and northeast, likely due to the geographic barrier presented by the Great Lakes. The beetle appears to be entering the saturation phase of its invasion in the eastern range of ash in North America.

2) Environmental factors that are known to affect the demography of insects were associated with varying rates of spread. Minimum winter temperatures had the largest effect of the factors examined, slowing spread by approximately 1 km/year for every decrease in the average minimum winter temperature. This work provides further empirical evidence that environmental heterogeneity can

contribute to variable rates of spread, as suggested by theoretical models of spread.

Synthesis

Goals for management programs may include temporary and/or permanent suppression, detection and eradication, and preventing and predicting further spread of pest populations. Often multiple management tools are chosen based on the biology of the pest, area over which management efforts will be targeted, and the cost:benefit ratio of proposed management techniques. Due to the difficulty in detecting emerald ash borer in new locations, its human-aided dispersal via the movement of infested wood, and the ubiquity of ash across much of eastern North America, eradication of this insect is difficult. Management efforts have thus focused on the suppression of beetle populations to slow ash mortality and reduce the rate of spread. Reducing the growth and spread of beetle populations provides managers in affected areas the ability to spread out management activities, and thus costs, over longer time periods.

The importation biological control program supports efforts to reduce the population growth and spread of emerald ash borer. This program is particularly valuable in forested areas, where other management options may be infeasible due to time or costs associated with their application. The rearing and release of biological control agents is costly, and so releases should occur in areas where the likelihood of establishment is high to reduce the cost:benefit ratio. Our forecasts of overwintering survival for *S. galinae* provide managers with information to ensure that releases occur in areas where populations of this parasitoid are likely to survive overwintering conditions. Our models may also be helpful in identifying areas that may need supplemental releases of

parasitoids after the occurrence of extreme cold weather events to help any remaining parasitoids rebound. Managers may also wish to release parasitoids in locations where it is likely emerald ash borer will be spreading more quickly, such as areas with warmer winters or experiencing droughts.

Detecting emerald ash borer as it spreads to new areas is also key to suppressing population growth and spread. When emerald ash borer is detected in a new area, ash trees can be injected with systemic insecticide and then girdled to produce highly lethal trap trees. This practice reduces the population growth of emerald ash borer in the area. Managers can use the information provided in this dissertation to obtain estimates of how quickly emerald ash borer may be expected to spread in their management region. Our estimates of the effective range of attraction of baited green prism traps can then be used to design a cost-efficient trap deployment plan that spaces traps appropriately according to the area of spatial coverage desired. These traps can be placed in locations that may be high risk due to proximity to current infestations or the presence of likely introduction pathways, such as campgrounds where infested firewood may be brought. The effective range of attraction values we estimated are currently being used by managers in the United Kingdom to deploy traps efficiently in high risk introduction locations.

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Appendix A

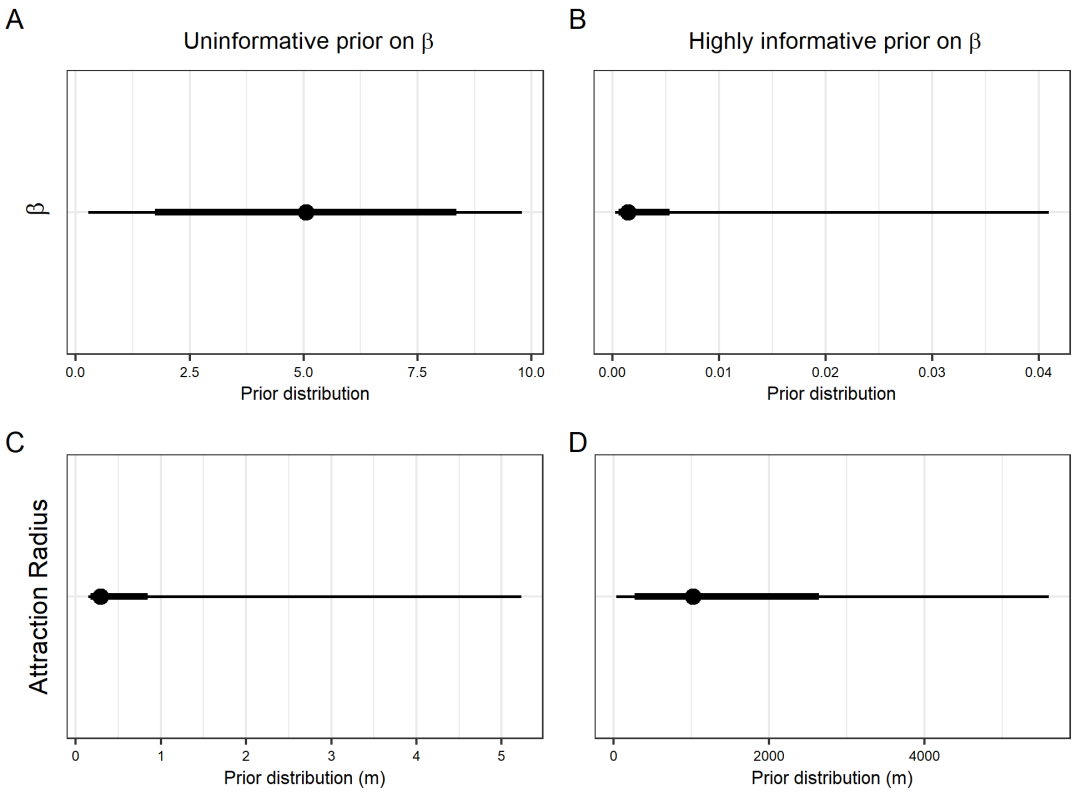

Figure A.1: Examples of how two different prior distributions on β (A and B) translate to a corresponding prior distributions on the attraction radius (C and D). In the logistic equation with two parameters, the attraction radius is equal to $\frac{1.4722}{\beta}$. An uninformative Uniform(0, 10) prior distribution on β (A) then is equivalent to a prior distribution on the attraction radius where 95% of the prior probability density is concentrated between 0 and 6m (B). A prior probability distribution on β that places 95% of the probability density between 0 and 0.0375 (C) is equivalent to a prior distribution on the attraction radius where 95% of the probability density lies between 0 and nearly 5000m (D). The point represents the median value of the prior distribution, the thick line represents the

50% probability density around the median, and the thin line is the 95% probability density around the median.

Appendix B

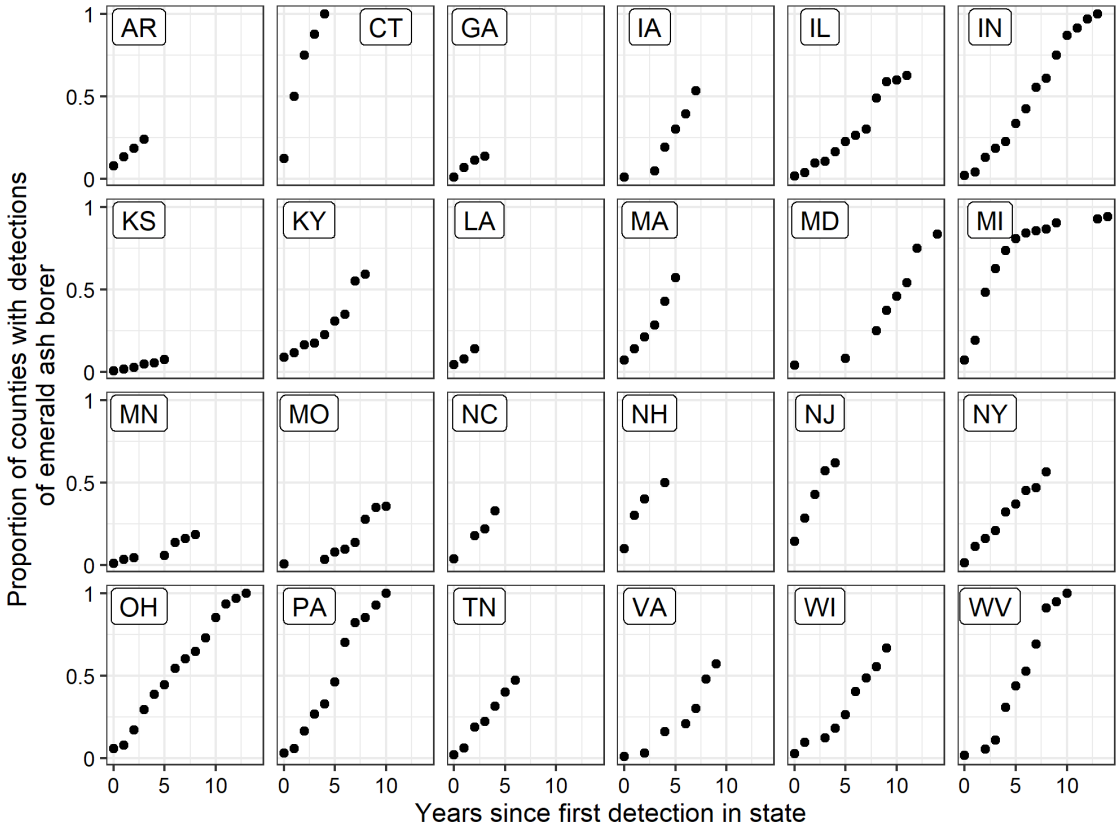

Figure B.1: The percent of counties in a state with positive detections of emerald ash borer over time since the first detection in that state. Two-letter abbreviations are used in each panel to denote the state.