Ecology of Emerald Ash Borer Spread in Maritime Canada

by

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Abstract

Only a small fraction of introduced species become established and invasive in new habitats, necessitating an increased understanding of the ecology of species establishment. The Allee effect is an ecological phenomenon characterized by a positive correlation between population density and per-capita population growth rate in a population and is important in the establishment success of invasive species. My thesis examines the establishment dynamics of emerald ash borer (*Agrilus planipennis* Fairmaire) by analyzing establishment characteristics in models using sensitivity analyses and empirically measuring Allee effects early during establishment. We found that the Allee effect threshold, the number of introductions required for establishment, provided the greatest variation in establishment models and that empirical measures of mating success revealed no evidence for strong mate-finding Allee effects. These findings highlight important characteristics in establishment models of invasive species and underscore the importance of understanding emerald ash borer Allee effects to increase risk model accuracy.

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Chapter 1: General introduction

Biological invasions are a severe ecological problem and a major driver of biodiversity loss worldwide (Pimentel et al. 2005; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) 2019). Invasive forest insects are causing shifts to animal and plant species distribution, community structure, and ecological functioning in North American forests due in large part to large-scale tree mortality (Eschtruth et al. 2006; Liebhold et al. 2017; Klooster et al. 2018), resulting in cascading effects to forest plant and animal communities (Stadler et al. 2005; Gandhi and Herms 2010). Large-scale mortality of an entire tree species or genus can cause declines in biodiversity, including but not limited to bird, amphibian, and mammal assemblages (Rabenold et al. 1998; Brooks 2001; Lishawa et al. 2007). Studies measuring the impact of large-scale tree mortality from invasive forest insects on other groups of organisms, such as detritivores and the ecosystem, remain underexplored, and its impact is likely much farther reaching than currently reported (Kenis et al. 2009).

Invasive forest insects are also causing ecological problems in urban forest ecosystems. Urban forests provide ecosystem services that include carbon sequestration, air purification, and climate regulation (Escobedo et al. 2011). In urban environments, this large-scale mortality is often due to the homogeneity of planted trees in urban forests (Nowak 1994; Aronson et al. 2017), leading to large-scale decimation of entire urban forests. This could cause large changes in the community composition resulting in entire neighbourhoods becoming treeless (Nowak et al. 2016). In North America, several invasive species including the Dutch elm disease (a fungus spread by bark beetles), the Asian longhorn beetle (*Anoplophora glabripennis* Motschulsky), and the current outbreak

of the emerald ash borer (*Agrilus planipennis* Fairmaire, Coleoptera: Buprestidae) hereafter referred to as EAB, (Hubbes 1999; Cappaert et al. 2005; Meng et al. 2015) have caused such widespread urban forest destruction. Interestingly, in urban environments, ash trees (*Fraxinus* spp.), which are now being extirpated in many regions by EAB, were often planted as a replacement for the American elm trees (*Ulmus americana*) that were killed by the Dutch Elm Disease outbreak that occurred across North America in the mid-20th century (Kovacs et al. 2010).

Models estimate that invasive species cost over 25 billion dollars USD annually in North America with invasive forest insects being one of the more impactful (Bradshaw et al. 2016). Invasive forest insects have major economic impacts on forestry practices, urban amenities, and horticulture (Holmes et al. 2009). Invasive species can also decrease the value of harvested wood products and cause large losses in timber value (Leroy et al. 2021). Homeowners can also suffer due to tree damage from invasive species on their property. The cost to treat and remove dead ash trees due to EAB was estimated to reach up to 12.7 billion dollars in the USA over ten years (Kovacs et al. 2010).

Integrated pest management (IPM) techniques developed from scientific studies can help alleviate the economic and environmental impacts of biological invasions (Hanley and Roberts 2019). Essential IPM strategies include properly forecasting arrival and establishment of species by identifying vulnerable pathways, monitoring for the early detection, eradicating if possible, and containing the spread of established populations (Larson et al. 2011). Invasive species risk models can help managers prioritize efforts by determining high-risk areas as well as cost-effectiveness of evaluating risk. Modelling has been used effectively in assisting the development of IPM strategies for a number of

important invasive species. For example, for zebra mussel invasions it is more successful to eradicate newly introduced populations than attempting to manage established populations (Leung et al. 2002); and for EAB, treating asymptomatic trees with injected insecticides at the earliest stages of infestation is more effective than tree removal or foregoing treatment (Bushaj et al. 2020).

Determining which species to concentrate modeling efforts prior to invasion can pose a challenging task. This is because only about 1% of species introduced to new habitats establish successfully and become invasive enough to cause ecological and economic damage (Williamson 1996). It would therefore be beneficial to model establishment rather than introduction. However, the establishment stage of invasions is complex to model due to the inherent difficulties of sampling and the chaotic dynamics of low population densities (Dennis et al. 1997; Fauvergue 2013). Establishment is primarily influenced by the population dynamics, changes in populations over time and space, of newly introduced species (Simberloff 2009). New introduced species are often subject to density-dependent mechanisms, such as Allee effects, that cause populations to decline when below a critical population size (Stephens et al. 1999).

Allee effects are mechanisms that decrease population fitness leading to negative population growth rates when below a critical population density threshold (Allee 1938). Allee effects can result from the inability to find mates (Régnière et al. 2013), inbreeding depression (Wittmann et al. 2018), high predation (Courchamp and Macdonald 2001), or difficulty acquiring food (Teixeira Alves and Hilker 2017). The mate-finding Allee effects is the most common mechanism affecting small population densities in arthropods (Kramer et al. 2009). Mate finding Allee effects occur when densities are so low that

locating mates become difficult. Mate-finding Allee effects have been empirically measured in two invasive forest insects: the spongy moth (*Lymantria dispar* Linnaeus, Lepidoptera: Lymantriidae) (Sharov et al. 1995; Johnson et al. 2006; Contarini et al. 2009; Tobin et al. 2013), and the brown spruce longhorn beetle (*Tetropium fuscum* Fabricius) (Rhainds et al. 2015). Despite their importance in the establishment of invasive species, mate-finding Allee effects are seldom studied due to the difficulties of generating biologically meaningful conclusions when measuring small populations (Fauvergue 2013).

The mate-finding Allee effects in EAB have not been empirically measured, despite its success at expanding their range in North America and eastern Europe (Kovacs et al. 2010; McKenney et al. 2012; Valenta et al. 2017). EAB has spread from the epicentre of introduction in Michigan and Southern Ontario to a distance of over 2000 km in approximately 20 years (Emeraldashborer.info 2022; United States Department of Agriculture 2023), far outpacing their natural dispersal rate of approximately 20 km a year (Prasad et al. 2010). This discrepancy can be attributed to long-distance dispersal events to new regions, primarily through the human-assisted movement of unprocessed ash wood products, firewood and nursery stock (Cappaert et al. 2005). Each new population of EAB transported by long-distance dispersal would be subject to Allee effects that would require population densities large enough to surpass the Allee threshold (McDermott and Finnoff 2016). EAB present an opportunity to study mate-finding Allee effects of an invasive species that has vastly expanded its range through long-distance movement.

The second chapter discusses the impact of population dynamics on invasive species establishment models, using EAB as a model organism. We use a model to simulate the movement of firewood into campgrounds in the Maritime provinces to compare characteristics such as timing of EAB emergence, camper distance travel trends, and propagule pressure threshold that affect EAB introduction and establishment. We implement two sensitivity analyses to determine which of these characteristics most influence establishment probability. We found that propagule pressure greatly influences overall establishment outcome. Such information could be useful in generation future models for new invasive species.

In the third chapter, we empirically measured mate-finding Allee effects in an area recently invaded by EAB. To accomplish this, we collected EAB in Halifax, Nova Scotia, to investigate the relationship between mating success and male population density along a population density gradient. We found that EAB did not exhibit a strong Allee effect. This finding indicates that models estimating EAB introduction may be an accurate method of predicting invasion risk.

The results from the two main chapters provide useful tools and knowledge that can potentially assist in the application of IPM for forest invasive species and EAB. Establishment characteristics such as mate-finding Allee effects should be included in risk models for species experiencing strong Allee effects. EAB management techniques like trapping and tree injections should be prioritized early in the invasion for the best chances of successful control and eradication. Despite Allee effects being important in invasive establishment models, EAB does not experience strong Allee effects.

Publication plans and author contributions

The second chapter of this thesis was authored by myself, with Dr. James Watmough, Dr. Stephen B. Heard, and Dr. Deepa Pureswaran as coauthors. I was responsible for the bulk of this research including the conception of the study, the data collection, the analysis and the interpretation of the results, manuscript writing, and manuscript editing. Dr. James Watmough provided expertise and guidance in the creation of the model. Drs. Stephen B. Heard and Deepa S. Pureswaran provided supervisory roles by guiding the research projects using their expertise. We will be submitting this chapter to Biological Invasions.

The third chapter of this thesis, that empirically measures EAB Allee effects, was authored by myself, with Dr. Stephen B. Heard, and Dr. Deepa Pureswaran as coauthors. I was responsible for the bulk of this research including the conception of the study, the data collection, the analysis and the interpretation of the results, manuscript writing, and manuscript editing. Drs. Stephen B. Heard and Deepa S. Pureswaran provided supervisory roles by guiding the research projects using their expertise. We will be submitting this chapter to NeoBiota.

Bibliography

Allee WC (1938) The social life of animals. W.W. Norton & Company, inc., New York,

Aronson MF, Lepczyk CA, Evans KL, et al (2017) Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment 15:189–196. https://doi.org/10.1002/fee.1480

Bradshaw CJA, Leroy B, Bellard C, et al (2016) Massive yet grossly underestimated global costs of invasive insects. Nature Communications 7:1–8. https://doi.org/10.1038/ncomms12986

Brooks RT (2001) Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. Forest Ecology and Management 149:197–204. https://doi.org/10.1016/S0378-1127(00)00553-3

Bushaj S, Büyüktahtakın IE, Yemshanov D, Haight RG (2020) Optimizing surveillance and management of emerald ash borer in urban environments. Natural Resource Modeling 34:1–36. https://doi.org/10.1111/nrm.12267

Cappaert D, Mccullough DG, Poland TM, Siegert NW (2005) Emerald ash borer in North America: a research and regulatory challenge. American Entomologist 51:152–165. https://doi.org/10.1093/ae/51.3.152.

Contarini M, Onufrieva KS, Thorpe KW, et al (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. Entomologia Experimentalis et Applicata 133:307–314. https://doi.org/10.1111/j.1570-7458.2009.00930.x

Courchamp F, Macdonald DW (2001) Crucial importance of pack size in the African wild dog *Lycaon pictus*. Animal Conservation 4:169–174. https://doi.org/10.1017/S1367943001001196

Dennis B, Desharnais RA, Cushing JM, Costantino RF (1997) Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. The Journal of Animal Ecology 66:704. https://doi.org/10.2307/5923

Emerald Ash Borer Network (2022) Emerald ash borer state detection table. emeraldashborer.info. Accessed 14 Aug 2023

Eschtruth AK, Cleavitt NL, Battles JJ, et al (2006) Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 36:1435–1450. https://doi.org/10.1139/x06-050

Escobedo FJ, Kroeger T, Wagner JE (2011) Urban forests and pollution mitigation: analyzing ecosystem services and disservices. Environmental Pollution 159:2078–2087. https://doi.org/10.1016/j.envpol.2011.01.010

Fauvergue X (2013) A review of mate-finding Allee effects in insects: from individual behavior to population management. Entomologia Experimentalis et Applicata 146:79–92. https://doi.org/10.1111/eea.12021

Gandhi KJK, Herms DA (2010) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biological Invasions 12:389–405. https://doi.org/10.1007/s10530-009-9627-9

Hanley N, Roberts M (2019) The economic benefits of invasive species management. People and Nature 1:124–137. https://doi.org/10.1002/pan3.31

Holmes TP, Aukema JE, Von Holle B, et al (2009) Economic impacts of invasive species in forests: past, present, and future. Annals of the New York Academy of Sciences 1162:18–38. https://doi.org/10.1111/j.1749-6632.2009.04446.x

Hubbes M (1999) The American elm and dutch elm disease. The Forestry Chronicle 75:265–273. https://doi.org/10.5558/tfc75265-2

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (2019) Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Version 1. IPBES secretariat, Bonn, Germany. URL https://zenodo.org/record/6417333

Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON (2006) Allee effects and pulsed invasion by the gypsy moth. Nature Letters 444:361–363

Kenis M, Auger-Rozenberg MA, Roques A, et al (2009) Ecological effects of invasive alien insects. Biological Invasions 11:21–45. https://doi.org/10.1007/978-1-4020-9680-8_3

Klooster W, Gandhi K, Long L, et al (2018) Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in North America. Forests 9:1–14. https://doi.org/10.3390/f9050250

Kovacs KF, Haight RG, McCullough DG, et al (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009-2019. Ecological Economics 69:569–578. https://doi.org/10.1016/j.ecolecon.2009.09.004

Kramer AM, Dennis B, Liebhold AM, Drake JM (2009) The evidence for Allee effects. Population Ecology 51:341–354. https://doi.org/10.1007/s10144-009-0152-6

Larson DL, Phillips-Mao L, Quiram G, et al (2011) A framework for sustainable invasive species management: environmental, social, and economic objectives. Journal of

Environmental Management 92:14–22. https://doi.org/10.1016/j.jenvman.2010.08.025

Leroy BML, Lemme H, Braumiller P, et al (2021) Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems: an experimental approach. Ecological Solutions and Evidence 2:1–16. https://doi.org/10.1002/2688-8319.12045

Leung B, Lodge DM, Finnoff D, et al (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London Series B: Biological Sciences 269:2407–2413. https://doi.org/10.1098/rspb.2002.2179

Liebhold AM, Brockerhoff EG, Kalisz S, et al (2017) Biological invasions in forest ecosystems. Biol Invasions 19:3437–3458. https://doi.org/10.1007/s10530-017-1458-5

Lishawa SC, Bergdahl DR, Costa SD (2007) Winter conditions in eastern hemlock and mixed-hardwood deer wintering areas of Vermont. Canadian Journal of Forest Research 37:697–703. https://doi.org/10.1139/X06-256

McDermott SM, Finnoff DC (2016) Impact of repeated human introductions and the Allee effect on invasive species spread. Ecological Modelling 329:100–111. https://doi.org/10.1016/j.ecolmodel.2016.03.001

McKenney DW, Pedlar JH, Yemshanov D, et al (2012) Estimates of the potential cost of emerald ash borer (*Agrilus planipennis* Fairmaire) in Canadian municipalities. Arboriculture and Urban Forestry 38:81–91

Meng PS, Hoover K, Keena MA (2015) Asian longhorned beetle (Coleoptera: Cerambycidae), an introduced pest of maple and other hardwood trees in North America and Europe. Journal of Integrated Pest Management 6:1–14. https://doi.org/10.1093/jipm/pmv003

Nowak DJ (1994) Understanding the structure of urban forests. Journal of Forestry October:42–46

Nowak DJ, Hoehn RE, Bodine AR, et al (2016) Urban forest structure, ecosystem services and change in Syracuse, NY. Urban Ecosystems 19:1455–1477. https://doi.org/10.1007/s11252-013-0326-z

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Prasad AM, Iverson LR, Peters MP, et al (2010) Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecology 25:353–369. https://doi.org/10.1007/s10980-009-9434-9

Rabenold KN, Fauth PT, Goodner BW, et al (1998) Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the Southern Appalachians. Conservation Biology 12:177–189

Régnière J, Delisle J, Pureswaran DS, Trudel R (2013) Mate-finding Allee effect in spruce budworm population dynamics. Entomologia Experimentalis et Applicata 146:112–122. https://doi.org/10.1111/eea.12019

Rhainds M, Heard SB, Hughes C, et al (2015) Evidence for mate-encounter Allee effects in an invasive longhorn beetle (Coleoptera: Cerambycidae). Ecological Entomology 40:829–832. https://doi.org/10.1111/een.12255

Sharov AA, Liebhold AM, Ravlin FW (1995) Prediction of gypsy moth (Lepidoptera: Lymantriidae) mating success from pheromone trap counts. Environmental Entomology 24:1239–1244. https://doi.org/10.1093/ee/24.5.1239

Simberloff D (2009) The Role of Propagule Pressure in Biological Invasions. Annual Review of Ecology, Evolution, and Systematics 40:81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Stadler B, Müller T, Orwig D, Cobb R (2005) Hemlock woolly adelgid in New England forests: canopy impacts transforming ecosystem processes and landscapes. Ecosystems 8:233–247. https://doi.org/10.1007/s10021-003-0092-5

Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? Oikos 87:185–190

Teixeira Alves M, Hilker FM (2017) Hunting cooperation and Allee effects in predators. Journal of Theoretical Biology 419:13–22. https://doi.org/10.1016/j.jtbi.2017.02.002

Tobin PC, Onufrieva KS, Thorpe KW (2013) The relationship between male moth density and female mating success in invading populations of *Lymantria dispar*. Entomol Exp Appl 146:103–111. https://doi.org/10.1111/j.1570-7458.2012.01299.x

United States Department of Agriculture (2023) Emerald ash borer beetle known infested counties.

Valenta V, Moser D, Kapeller S, Essl F (2017) A new forest pest in Europe: a review of emerald ash borer (*Agrilus planipennis*) invasion. Journal of Applied Entomology 141:507–526. https://doi.org/10.1111/jen.12369

Williamson M (1996) Biological Invasions, 1st edn. Springer Netherlands

Wittmann MJ, Stuis H, Metzler D (2018) Genetic Allee effects and their interaction with ecological Allee effects. Journal of Animal Ecology 87:11–23. https://doi.org/10.1111/1365-2656.12598

Chapter 2: Gaps in population data could limit predictive potential of invasive species establishment models: The case of the emerald ash borer

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Abstract

Invasive species that are capable of travelling long-distances through human mediated dispersal can pose significant ecological and economic threats as they surpass their natural dispersal abilities. Risk analysis models measuring invasive species dispersal typically do not consider establishment probability, despite establishment being an important step in biological invasions. Here, we explored forest insect establishment characteristics, Allee effects and the timing of firewood arrival, that are not commonly accounted for in risk models but are known to be theoretically and empirically influential in establishment. We develop a risk assessment model to simulate emerald ash borer transportation in firewood by campers in the maritime provinces of Canada. Then using this data, we perform a local and global sensitivity analysis to measure the importance of introduction and establishment characteristics in our risk analysis model. Our global sensitivity analysis revealed that Allee effect threshold was the most important factor in determining the establishment of emerald ash borer in the model. This research highlights the importance of measuring Allee effects in invasive forest insects as this could increase the accuracy of risk assessment models.

Introduction

Invasive species travel long distances through transportation by human activities that may exceed their physiological dispersal ability (Hulme 2009). Since the early 2000s trade and transportation by humans have increased significantly (Hulme 2009). Consequently, invasive species dispersed by these methods tend to move in jump-dispersal events along transportation networks to new regions not easily reached by natural dispersal (Lewis 1997).

Introduced populations of invasive species are susceptible to survival and establishment pressures associated with the timing of arrival in their new habitat and Allee effects (Crooks and Soulé 1999; Leung et al. 2004; Taylor and Hastings 2005; Duncan 2016). The timing of arrival is important in the survival of an introduced population because, depending on the time of year, introduction may occur either before or after the mobile stages of the species are present, thus reducing their dispersal ability and hence their spread (Teulon and Stufkens 2002; Peacock and Worner 2008). Allee effects can influence the establishment of an introduced population because population density needs to surpass a critical threshold to alleviate difficulties in finding mates and avoiding predators to result in positive population growth (Johnson *et al.*, 2006). As a result, multiple introductions can be required to overcome Allee effects and increase population density (Zalewski et al. 2010; Novo et al. 2015).

Despite substantial barriers to establishment, some species can establish, spread in their new range, and cause widespread ecological damage. Consequently, predicting when and how likely establishment may occur is essential to manage invasive species. Since species moved along transportation networks can be difficult to monitor, they may require specialized means of estimating movement compared to animals that disperse naturally. Risk assessment models are useful tools that can include any number of steps involved in the dispersal and distribution of invasive species including introduction, establishment, spread, and impact (Lodge et al. 2016). Such models can be used to predict probability for dispersal and distribution of invasive species moved by humans along transportation networks (Koch et al. 2012; Büyüktahtakın and Haight 2018). However, for many forest insects, assessing establishment risk has been challenging

(Nathan et al. 2003), probably due to the difficulty in detecting them when they are at low densities, early in the invasion period (Mehta et al. 2007). Risk assessment modelling can therefore provide information that can better inform policy and management efforts for invasive species and effectively reduce economic and ecological damage caused by the invasive species (Lodge et al. 2016; Jane Elith 2017).

The emerald ash borer (hereafter referred to as EAB; *Agrilus plannipennis* Fairmaire Coleoptera: Buprestidae), is an invasive wood-borer introduced from Eastern Asia to North America and Eastern Europe that has caused large scale mortality of North American ash (*Fraxinus* spp., Oleaceae) (Kovacs et al. 2010; McKenney et al. 2012; Valenta et al. 2017). EAB remains difficult to detect as it is cryptic and asymptomatic until tree mortality begins (Herms and McCullough 2013). The beetle travels through jump dispersal events to new areas (Herms and McCullough 2013), commonly via the movement of firewood by campers to campgrounds (Poland and McCullough 2006). Although several models exist to predict the probability of EAB introduction to new areas in North America through firewood movement (Muirhead et al. 2006; Prasad et al. 2010), prediction of establishment risk remains limited, particularly for the Maritime provinces of Canada where the establishment of this insect is relatively recent (Canadian Food Inspection Agency 2018a, b). This presents a rare opportunity to explore EAB dispersal in area region that has yet to be heavily invaded.

Here, we explored forest insect establishment characteristics, Allee effects and the timing of firewood arrival, that are not commonly accounted for in risk models but are known to be theoretically and empirically influential in establishment. To do this, we developed a risk assessment model along firewood transportation networks that simulates

EAB dispersal and establishment from firewood movement by campers in the Maritime provinces. We used this model to better understand the influence of two factors on the expected establishment and spread: 1) timing of firewood arrival on insect survival and 2) overcoming local mate-encounter Allee effects. We conducted a two-way ANOVA to examine the differences in the expected establishment probability under low and high Allee effect thresholds, requiring few monthly introductions or many monthly introductions, and the timing of arrival. We predicted that timing of arrival during peak EAB emergence and a high Allee effect threshold would decrease the overall EAB establishment probability. Subsequently, we conducted a global sensitivity analysis to evaluate assumptions of EAB ecology and camper travel trends that could most influence the establishment probability of the EAB in our model. We found that overcoming the Allee effect was our model's most important factor in determining EAB establishment.

Methods

Study Species

EAB is a small green metallic buprestid beetle that infests ash trees (*Fraxinus spp*.) (Haack et al. 2015). EAB typically has a one-year life cycle but can also follow a two-year life cycle (Siegert et al. 2010). Adult emergence in eastern Canada usually starts by mid-June, peaks in July, and finishes around late August, coinciding with the movement of firewood during the camping season. EAB lives for 3-6 weeks as adults, during which they feed on ash leaves, locate conspecifics, and mate (Herms and McCullough 2013). Following mating, gravid females oviposit into bark crevices and other protected areas on the trunks of ash trees. Following egg hatch, larvae enter the tree via the ventral surface

of the egg (Bauer et al. 2003). Here, they feed on the inner bark and sapwood, with most larvae overwintering as 4th instar prepupal larvae (Bauer et al. 2003).

Theoretical Framework

We modelled the dispersal and distribution of EAB using the movement of infested firewood conceptualized as a sequence of steps. These were arrival, introduction, and establishment (Fig. 2.1), each having a step-specific transition probability. Arrival probability is the probability that a piece of EAB-infested firewood (~40 cm long) is transported to an uninfested location. For simplicity we do not model the number of larvae in a piece of infested wood; conceptually, the distribution of number of larvae can be thought of as implicit in the probability of an infested piece. Introduction probability is the probability that EAB emerges from firewood at a phenologically appropriate time when food is available for beetles to successfully complete development, mate, and oviposit. Establishment probability is the probability that sufficient introduction events occur for EAB to overcome a minimal Allee effect threshold. Allee effect threshold refers to specific densities below which population density cannot increase due low mating opportunities and high predation rates resulting from low population densities (Courchamp et al. 1999; Liebhold and Tobin 2008).

Our model used road networks from established population centres to regional campgrounds. This was to simulate EAB-infested firewood movement throughout the region over a twenty-year period. The model was simulated using Python 3.9 (Van Rossum, G. and Drake, F.L. 2009) and the Pandas 1.4 (Pandas development team 2020), SciPy 1.9 (Virtanen et al. 2020), and NetworkX 2.8 (Hagberg et al. 2008) packages.

Model Overview

Our model simulated the movement of infested firewood from 28 origin population centres (indexed by *i*, see Fig. 2.2) to 314 destination campgrounds (indexed by *j*, see Fig. 2.2). The simulation began with the five Maritime population centres with known established populations of EAB as of 2021: Edmundston, Fredericton, Moncton, Oromocto, and Halifax, spreading EAB infested firewood. Every year a new city would become infested based on their distance from another infested city and travel between the two locations. Transportation of EAB-infested firewood was simulated by modelling the distribution of firewood leaving population centres for campgrounds, using campground size and distance from infested population centres as metrics of attraction between both locations. Firewood arriving at a campground was distributed on a per-monthly basis using the mean monthly campsite reservation rate from the New Brunswick Provincial Park campground reservation records of 2015 to 2019 (Fig. 2.3). We used a sensitivity analysis to vary the values of the timing of firewood arrival and Allee effect threshold to estimate their influence on the establishment model. The timing of firewood arrival was simulated based on the probability that EABs emerge from pieces of unburnt EAB-infested firewood. Lastly, establishment was simulated based on the probability that sufficient beetles from infested firewood emerged to surpass the Allee effect threshold for establishment to occur.

Establishment of new populations of EAB to population centres were also included as a factor in the model. The model assigned one new population centre that becomes infested with EAB each year based on population size and tourist travel between counties

as recorded in the Travel Survey of Residents of Canada. Simulations were iterated for 20 years, with 1000 replications of the entire time series.

Following these steps, the model then estimated the probability of new infestations of EAB in areas based on the introduction and establishment of EAB to campgrounds following arrival. The Maritimes were divided into hexagonally shaped areas with varying campgrounds found within each hexagon. We estimated the probability that an area becomes infested based on the establishment of one population of EAB into a campground.

We varied the two establishment characteristics, timing of firewood arrival, which measures the probability emerald ash borer emerge from firewood based on the month of firewood arrival and the Allee effect threshold, the probability that emerald ash borer establishes based on the number of introductions of EAB infested firewood. We used a local sensitivity analysis to determine their impact on establishment probability under four scenarios using a two-way ANOVA. We then conducted a global sensitivity analysis to understand how introduction and establishment characteristics influence the establishment probability of EAB in the maritime provinces (see supplementary Table 1 for a list of the parameters we measured).

Model Development

Per Capita Campground Reservation Rate

We used residents' postal codes attached to campground reservations made to Parks New Brunswick to model the relationship of the number of reservations that a given population centre would make to a campground. Camper reservation data was provided by Parks New Brunswick and included reservations made to provincial park

campgrounds in New Brunswick from 2015 to 2019. We found that the population size of a population centre was a good predictor of the number of reservations made to campgrounds (r^2= 0.71, p=0.001). We assumed the per capita reservation rate, r_i, of $1.67e^{-3}$ from a linear regression of the population centres population. We compiled all the reservation-related data using ArcGIS (version 10.4). We collected the location of campgrounds and population centres using Google Earth Pro (version 7.3.4.86, Google LLC, California, USA). We gathered the population centre size from the Maritime provinces with at least 5,000 residents (Statistics Canada 2017).

Dispersal from Population Centres to Campgrounds

The number of pieces of EAB-infested ash firewood O_i (Table 1: eq. 1a) leaving a population centre *i* to campsites *j*, is assumed proportional to: 1) the number of camping reservations/year made from each population centre, r_i; 2) the probability that the camper brings firewood from outside the campground, *s*; and 3) the probability that the firewood is ash and contains live larvae or pupae, *b*. The probability that firewood is transported to campgrounds was estimated from Jacobi et al. (2011). The probability that firewood contained live EAB was estimated from Haack et al. (2010). These estimated values may not be representative of values found within the Maritime provinces; however, we used a global sensitivity analysis to measure these parameters' importance on the model's results. We use *O* to denote the vector of these quantities (Table 1: eq. 1b) representing the number of pieces of EAB-infested ash firewood leaving each population centre with an established population of EABs.

Within the model, infested firewood was distributed to campgrounds based on a modified gravity equation that measures the attractiveness between locations. The

attractiveness A_{ij} (Table 1: eq. 2a), of population centre *i* and campground *j* is proportional to the number of campsites in a campground and the exponential decay curve equation of the distance between the population centre and campground. The gravity equation measures the degree of interaction between two locations and has frequently been used to estimate the human transportation of invasive species (Schneider et al. 1998; Muirhead et al. 2006).

The number of campsites at a campground was estimated as C_j because the number of campsites has been shown to be directly related to the amount of firewood brought by campers (Muirhead et al. 2006). For public campgrounds, we generated a list of national and provincial campgrounds from government websites. We also generated a list of private and municipal campgrounds from campground owner groups. Private campground information was sourced from associations of campground owners for the Maritimes (Campground Owners Association of Nova Scotia; Canadian Camping and RV Council; New Brunswick Campground Owners Association; The Association of Atlantic RV Parks & Campground; Tourism PEI). For public campgrounds, we collected data from the national parks' reservation websites, provincial park reservation websites, and the uscampgrounds.info website.

The number of people travelling from population centre *i* to campground *j* is assumed as a decreased factor of 2 for every 100 km of travel ($2^{d_{ij}/100}$) (Eagles et al. 2015). This equation used the shortest road distance travelled, d_{ij}, between the population centre and the campground. We also imported road and ferry segments from the National Road Network of the three Maritime provinces from the government of Canada to estimate the shortest road distance between locations (Statistics Canada 2015). Road

distances were estimated using ArcGIS and the Network Analyst extension (ArcGIS Desktop 10.8.1).

Dispersal Among Population Centres

We modelled the dispersal of EAB from origin population centre *i* to destination population centre *j* to better represent the establishment of new urban (source) populations over time. The attractiveness B_{ij} (Table 1: eq. 3a), of population centre *i* to population centre *j* is assumed as proportional to the population, P_i, of population centre *i* and the number of people, M_{ij}, travelling from counties of population centre *i* to population centre *j*. M_{ij} is estimated using data from the Travel Survey of Residents of Canada (Statistics Canada 2018); a major data source in measuring tourism between Canadian counties. Using data from 2006 to 2017 (without 2012 because there was no survey done that year), we calculated the mean number of visits between the origin and destination counties for each population centre in our model. We based these measurements on the population and county-level travel using the Travel Survey of Residents of Canada as an indicator of inter-city travel. Larger population centres (P_i >50 000) were all found in separate counties making it easier to distinguish population centre travel based on population in their counties. We denoted the total attraction to population centre *j* by TB_j and assumed this is the sum of attraction from each population centre (Table 1: eq. 3b).

Timing of Firewood Arrival

We modelled the effect of timing of firewood arrival on EAB establishment in campgrounds. We used data from Tobin et al. (2021) to predict EAB emergence using degree days, and the accumulated daily mean temperature over 10 degrees. We then

calculated the number of pieces of firewood from which beetles had not yet emerged, using the degree days from Fredericton, New Brunswick in 2021 (dashed line in Fig. 2.4). The probability that firewood is burnt before all EAB had emerged was assumed to be a negative linear relationship, starting at the beginning of the camping season, and ending at the end of EAB emergence (dotted line, Fig.2.4). We estimated the probability that EAB successfully emerged from firewood based on the arrival date (solid line, Fig. 2.4), by calculating the product of the probability of EAB emergence, and the probability of firewood being burnt. We then calculated the EAB emergence probability based on the month of arrival (bars, Fig. 2.4). Finally, we grouped emergence probability by month based on camping reservation data.

We grouped campgrounds into spatially explicit areas given the high likelihood of dispersion to adjoining campgrounds following emergence. In ArcGIS, we grouped areas into a clustered 4.5 million square kilometre grid of hexagons encompassing all the Maritime provinces (Fig. 2.2). Hexagons were removed from the analysis if they did not contain a campground.

Forest Composition

To better understand the risk that EAB poses in the Maritimes, we collected data on the distribution of ash in Maritime forests (Beaudoin et al. 2014). From this, we extracted stand-level abundance as a percentage of total forest cover at a 250 m^2 resolution for green ash (*Fraxinus pennsylvanica* Marsh.), white ash (*Fraxinus americana* L.), and black ash (*Fraxinus nigra* Marsh.). We imported the files into ArcMap and calculated the total abundance of the three species. To better view the abundance of forest plots, we resampled the abundance of ash to 1km^2 and then overlayed the ash composition over the

introduction probability of EAB. We visually compared the probability of EAB transportation and the distribution of ash stands to understand high-density ash stands that are most at risk to EAB.

Sensitivity Analysis

We used a local sensitivity analysis to estimate the influence of the two establishment parameters, timing of firewood arrival and Allee effect threshold. A local sensitivity analysis will vary parameter values to see how they affect the output. The analysis measured the proportion of hexagons that experienced EAB establishment using the simulation for 1000 replications (Table 2). We used a two-way ANOVA to determine the impact of establishment characteristics on the probability of overall EAB establishment in the Maritimes.

We used a global sensitivity analysis to identify uncertainties that impacted EAB establishment variability the most. We used Sobol indices to identify how much variance could be attributed to each parameter in the model (Sobol 2001). We tested the variance that nine parameters and their interactions had on the probability of EAB establishment (see Supplementary Table 1) using the SAlib package in Python (Herman and Usher 2017) and generated 60,000 samples to test variation in model parameters. We represented the parameters' influence on the model using 95% confidence intervals.

Results

Our model determined that Central Nova Scotia, central Prince Edward Island, and southeastern New Brunswick have the highest expected probability of EAB introduction (>25 EAB-infested pieces per year; Fig. 2.2). Specifically, this included the areas near

Halifax, Moncton, and Charlottetown. Generally, the areas at the highest risk of introduction are adjacent to the largest population centres of each province. Southwestern Nova Scotia and southern New Brunswick have the most high-risk locations where significant wild ash populations are present (Fig. 2.2). The risk of transportation to Prince Edward Island is moderate to high (>10 EAB-infested pieces per year).

The distribution of the three ash species in the Maritimes is generally sparse (less than 1% per km^2). In the Wolastoq (Saint John) River Valley and in the Northern Kespukwitk (Annapolis Valley) region in Nova Scotia, values may range from 1-5% per km^2, peaking at 19% in a $1km^2$ area. Ash distribution is generally low throughout northeastern Nova Scotia, eastern New Brunswick, and Prince Edward Island.

In the local sensitivity analysis, we found a significant decrease in the probability of EAB establishment due to timing of firewood arrival (Fig. 2.5), Allee effect threshold parameters, and their interaction (Table 3). A higher Allee effect threshold, requiring more introductions to reach establishment was significant and decreased EAB establishment probability by 33% (Fig. 2.6). Late arrival (August, September, October) of infested firewood during the camping season decreased the probability of EAB establishment by 7%. The interaction between a high Allee effect threshold and late arrival of firewood caused the largest decrease in the EAB establishment probability, decreasing EAB establishment probability by 74%. With this interaction, the only areas that remain with a high establishment probability are those adjacent to large population centres with a close to zero EAB establishment probability outside of those areas (Fig. 2.6).

The global sensitivity analysis corroborated our results related to the effect of Allee effects and timing of firewood arrival on establishment success. Uncertainty in the Allee effect threshold had a significantly higher impact on the spread of EAB (95% CI [0.53,0.90]), while the timing of firewood arrival alone had little impact (Fig 2.7). The interaction of model parameters did not influence the global sensitivity analysis on the overall probability of EAB establishment.

Discussion

Incomplete data often compromise efforts to forecast the spread of invasive species. Identifying data useful for predicting spread and establishment is essential and should be prioritized in a world of limited scientific resources. Our findings suggest that modelling the future spread of EAB will strongly depend on population parameters at low densities, including the Allee effect threshold. We found that the Allee effect threshold had the greatest impact on the establishment of EAB in both the local and global sensitivity analysis. This reveals the importance of considering population dynamics when forecasting invasive forest insect dispersal and distribution in risk assessment models. We additionally found that the interaction between the Allee effect threshold and the timing of firewood arrival drove large changes in the establishment probability in the local sensitivity analysis.

Two factors could explain differences in the local and global sensitivity analysis. All but the establishment parameters are fixed in the former, while the timing of firewood arrival and Allee effect threshold are fixed variables in the latter. This may lead to changes in how the timing of firewood arrival affects the model and changes the impacts

of the probability of EAB establishment. Future studies should measure and include the Allee effect threshold for invasive forest insects in establishment models.

In our model, we chose to use an exponential decay curve to represent the relationship between campground reservations and distance. However, some studies have shown that exponential decay curves overestimate camper reservations at short distances (Koch et al. 2012). We used the exponential decay curve because short-distance dispersal was less important in our model due to grouping locations into larger areas.

We did not anticipate that using Fredericton, New Brunswick to approximate degree days across the Maritimes would impact the results of EAB survival in firewood because values are ultimately binned into monthly emergence probability; therefore variation in degree days between locations would remain unchanged when measured at a monthly rate.

Since firewood transport can be higher near large population centres, travelling distance is likely an important predictor in EAB establishment. This follows the general trend that EAB individuals will experience many short-distance and comparatively fewer long-distance jump dispersal events (Muirhead et al. 2006). These few long-distance jump dispersal events are, however, (Ward et al. 2020) the most important means by which new regional foci of expansion are established. Some locations are at moderate to high risk of EAB-infested firewood transportation far from large population centres, such as eastern New Brunswick and the northern Kespukwitk region in Nova Scotia. This is likely due to the existence of many large campgrounds in these areas. Our results highlight priority areas for the surveillance of new populations of the EAB in the Maritimes.

Educational campaigns, such as providing flyers or writing emails to campground users, can potentially decrease long distance dispersal (Solano et al. 2022). Modelling of firewood transport from Ontario, Quebec and Manitoba has shown that unless the rate of spread is slow and intervention strategies are well-funded, transportation of infested firewood is unlikely to decrease (Jentsch et al. 2020). We believe that EAB spread may be slower in the Maritimes because of a much lower human population density than in other regions of introduction. However, a significant investment into education and enforcement will still be required to slow the spread of the beetle. Our results suggest that particular areas in which that investment could be prioritized could include northeastern New Brunswick and central Prince Edward Island.

Our model does not include the influence of ash abundance on the probability of EAB establishment. Rather, we only visually compared the impact that EAB would have on ash forests if the insect is introduced into those regions. The lack of ash abundance data could result in potential overestimates in the probability of EAB establishment in areas with low ash abundance, such as the northern tip of Prince Edward Island, and may underestimate probabilities in areas of high ash abundance, such as the Wolastoq River Valley. Future research should incorporate the distribution of ash trees near campgrounds into models to represent the probability that EAB will find a suitable host for mating and egg laying. This could be achieved using the forest composition data such as that of Beaudoin et al. (2014) to represent the probability that EAB finds a suitable host based on the ash distribution around campgrounds.

Our study shows that one area that is at lower risk of ash borer transportation and establishment is the northwestern Wolastoq River Valley. Compared to other regions, this

area contained fewer campgrounds and is far away from major population centres. This is an area with a high proportion of ash trees and may be a potential refugium for ash populations for the next 20 years. This refugium could be very important for black ash, a species commonly found in wet soils near rivers and an important source of wood fibre for Indigenous communities in the Maritime provinces for basket weaving, snowshoe frames, and canoe ribs (COSEWIC 2018). It is also important for conservation of three Maritime ash species found in the northeastern edge of their distribution in North America, which may make these populations better adapted to extreme climatic events (Rehm et al. 2015). These refugia may still be at risk of EAB dispersal from already established populations in the north near Edmundston to the southeast around Fredericton. These areas should be monitored and protected as they are important for cultural and ecological conservation.

Experimental studies have also highlighted the importance of individual survival and population dynamics in determining invasive species establishment success (Britton and Gozlan 2013; Duncan 2016). For invasive forest insects, information on population characteristics that lead to establishment is lacking. Studying populations at early phases in their invasion could decrease the uncertainty in predicting establishment characteristics of forest insects, such as using genetic markers to estimate the number of introductions and mating success of populations early in their establishment phase (Contarini et al. 2009; Zalewski et al. 2010). Including establishment characteristics into predictive models could improve estimates of time scales over which spread will occur, leading to better early detection and eradication opportunities.

Due to limited surveys on camper firewood trends, ash firewood prevalence and insect prevalence in firewood from the Maritime provinces, we used data from other studies. We made assumptions based on the applicability of these studies to the Maritimes. We found that the Allee effect threshold significantly impacted model variability in the global sensitivity analysis compared to all the other assumptions in our model, which had little impact on the variability of overall EAB establishment probability.

Wood movement for home heating may also be a vector of forest insect dispersal (Solano et al. 2021), as firewood accounts for approximately a quarter of fuels used for heating homes in the Maritimes (Statistics Canada 2011). While our model considers firewood transportation for recreation, it does not consider heating. However, we predict that wood transported for home heating would not significantly change the establishment probability of the EAB. This is because firewood for home heating is moved less frequently and is transported at shorter distances than recreational firewood (United States Department of Agriculture Animal and Plant Health Inspection Service 2010) which would not affect long-distance dispersal parameters estimated in our model.

Accurately modelling insect movement may be difficult when long-distance chance dispersal events are common (Lewis 1997). However, by developing a model that considers transportation, survival, and population dynamics, we can create better risk assessment models that may predict the dispersal and distribution of invasive forest insects. Understanding population dynamics would also increase knowledge of insect ecology and provide insights into future risk assessments. More accurate risk assessment

models would decrease economic costs associated with detecting, managing, and eradicating invasive forest insects.

Bibliography

Bauer LS, Haack RA, Miller DL, et al (2003) Emerald ash borer life cycle: a reassessment. Research and Technology Development meeting 1–2

Beaudoin A, Bernier PY, Guindon L, et al (2014) Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Canadian Journal of Forest Research 44:521–532. https://doi.org/10.1139/cjfr-2013-0401

Britton JR, Gozlan RE (2013) How many founders for a biological invasion? Predicting introduction outcomes from propagule pressure. Ecology 94:2558–2566. https://doi.org/10.1890/13-0527.1

Büyüktahtakın IE, Haight RG (2018) A review of operations research models in invasive species management: state of the art, challenges, and future directions. Annals of Operations Research 271:357–403. https://doi.org/10.1007/s10479-017-2670-5

Campground Owners Association of Nova Scotia Find a Campground. https://campingnovascotia.com/campground-nova-scotia/. Accessed 27 Jun 2023

Canadian Camping and RV Council Find a Campground. https://ccrvc.ca/campgrounds-canada/. Accessed 27 Jun 2021

Canadian Food Inspection Agency (2018a) Emerald ash borer confirmed in Edmunston. Government of Canada

Canadian Food Inspection Agency (2018b) Emerald ash borer confirmed in Bedford, Nova Scotia. Government of Canada

Contarini M, Onufrieva KS, Thorpe KW, et al (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. Entomologia Experimentalis et Applicata 133:307–314. https://doi.org/10.1111/j.1570-7458.2009.00930.x

COSEWIC (2018) COSEWIC assessment and Status Report on the Black Ash (Fraxinus nigra) in Canada. Ottawa

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405–410. https://doi.org/10.1016/S0169-5347(99)01683-3

Crooks JA, Soulé ME (1999) Lag times in population explosions of invasive species: causes and implications. In: Invasive Species and Biodiversity Management. Springer Netherlands, pp 103–125

Duncan RP (2016) How propagule size and environmental suitability jointly determine establishment success: a test using dung beetle introductions. Biological Invasions 18:985–996. https://doi.org/10.1007/s10530-016-1083-8

Eagles PFJ, Johnson PA, Potwarka LR, Parent C (2015) Travel distance classes for tourism destinations: a proposal from Ontario provincial park camping. Journal of Ecotourism 14:64–84. https://doi.org/10.1080/14724049.2015.1071829

Haack RA, Baranchikov Y, Bauer LS, Poland TM (2015) Emerald ash borer biology and invasion history. In: Driesche RGV, Reardon RC (eds) Biology and control of emerald ash borer. United States Department of Agriculture, Morgantown, WV, pp 1–13

Haack RA, Petrice TR, Wiedenhoeft AC (2010) Incidence of bark- and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. Journal of Economic Entomology 103:1682–1692. https://doi.org/10.1603/EC10041

Hagberg AA, Schult DA, Swart PJ (2008) Exploring network structure, dynamics, and function using NetworkX. In: Proceedings of the 7th Python in Science Conference. Pasadena, CA USA, pp 11–15

Herman J, Usher W (2017) SALib: an open-source Python library for sensitivity analysis. The Journal of Open Source Software 2:97–97. https://doi.org/10.21105/joss.00097

Herms DA, McCullough DG (2013) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annual Review of Entomology 59:13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Hulme PE (2009) Trade , transport and trouble : managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46:10–18

Jacobi WR, Goodrich BA, Cleaver CM (2011) Firewood transport by national and state park campers: a risk for native or exotic tree pest movement. Arboriculture and Urban Forestry 37:126–138

Jane Elith (2017) Predicting distributions of invasive species. In: Robinson AP, Walshe T, Burgman MA, Nunn M (eds) Invasive species: Risk assessment and management, 1st edn. Cambridge University Press, Cambridge, pp 93–129

Jentsch PC, Bauch CT, Yemshanov D, Anand M (2020) Go big or go home: a model-based assessment of general strategies to slow the spread of forest pests via infested firewood. PLoS ONE 15:1–18. https://doi.org/10.1371/journal.pone.0238979

Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON (2006) Allee effects and pulsed invasion by the gypsy moth. Nature Letters 444:361–363

Koch FH, Yemshanov D, Magarey RD, Smith WD (2012) Dispersal of invasive forest insects via recreational firewood: a quantitative analysis. Journal of Economic Entomology 105:438–450. https://doi.org/10.1603/EC11270

Kovacs KF, Haight RG, McCullough DG, et al (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009-2019. Ecological Economics 69:569–578. https://doi.org/10.1016/j.ecolecon.2009.09.004

Leung B, Drake JM, Lodge DM (2004) Predicting invasions: propagule pressure and the gravity of Allee effects. Ecology 85:1651–1660. https://doi.org/10.1890/02-0571

Lewis M (1997) Variability, patchiness, and jump dispersal in the spread of an invading population. In: Tilman D, Kareiva P (eds) Spatial Ecology the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, pp 46–69

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annual Review of Entomology 53:387–408. https://doi.org/10.1146/annurev.ento.52.110405.091401

Lodge DM, Simonin PW, Burgiel SW, et al (2016) Risk analysis and bioeconomics of invasive species to inform policy and management. Annual Review of Environment and Resources 41:453–488. https://doi.org/10.1146/annurev-environ-110615-085532

McKenney DW, Pedlar JH, Yemshanov D, et al (2012) Estimates of the potential cost of emerald ash borer (*Agrilus planipennis* Fairmaire) in Canadian municipalities. Arboriculture and Urban Forestry 38:81–91

Mehta SV, Haight RG, Homans FR, et al (2007) Optimal detection and control strategies for invasive species management. Ecological Economics 61:237–245. https://doi.org/10.1016/j.ecolecon.2006.10.024

Muirhead JR, Leung B, Van Overdijk C, et al (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Diversity and Distributions 12:71–79. https://doi.org/10.1111/j.1366-9516.2006.00218.x

Nathan R, Perry G, Cronin JT, et al (2003) Methods for estimating long-distance dispersal. Oikos 103:261–273. https://doi.org/10.1034/j.1600-0706.2003.12146.x

New Brunswick Campground Owners Association Campgrounds. In: NBCOA. https://nbcampgrounds.com/campgrounds/. Accessed 27 Jun 2021

Novo M, Cunha L, Maceda-Veiga A, et al (2015) Multiple introductions and environmental factors affecting the establishment of invasive species on a volcanic island. Soil Biology and Biochemistry 85:89–100. https://doi.org/10.1016/j.soilbio.2015.02.031

Pandas development team (2020) Pandas version 1.4. https://doi.org/10.5281/zenodo.3509134

Peacock L, Worner SP (2008) Biological and ecological traits that assist the establishment of alien invasive insects. From Biosecurity to BioControl 7:1–7

Poland TM, McCullough DG (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. Journal of Forestry 104:118–124. https://doi.org/10.1093/jof/104.3.118

Prasad AM, Iverson LR, Peters MP, et al (2010) Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecology 25:353–369. https://doi.org/10.1007/s10980-009-9434-9

Rehm EM, Olivas P, Stroud J, Feeley KJ (2015) Losing your edge: climate change and the conservation value of range-edge populations. Ecology and Evolution 5:4315–4326. https://doi.org/10.1002/ece3.1645

Schneider DW, Ellis CD, Cummings KS (1998) A transportation model assessment of the risk to native mussel communities from zebra mussel spread. Conservation Biology 12:788–800. https://doi.org/10.1111/j.1523-1739.1998.97042.x

Siegert NW, McCullough DG, Williams DW, et al (2010) Dispersal of *agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. Environmental Entomology 39:253–265. https://doi.org/10.1603/EN09029

Sobol IM (2001) Global sensitivity indices for nonlinear mathematical models and their Monte Carlo estimates. Mathematics and Computers in Simulation 55:271–280. https://doi.org/10.1016/S0378-4754(00)00270-6

Solano A, Rodriguez SL, Greenwood L, et al (2022) Achieving effective outreach for invasive species: firewood case studies from 2005 to 2016. Biological Invasions 24:3321–3339. https://doi.org/10.1007/s10530-022-02848-w

Solano A, Rodriguez SL, Greenwood L, et al (2021) Firewood transport as a vector of forest pest dispersal in North America: A scoping review. Journal of Economic Entomology 114:14–23. https://doi.org/10.1093/jee/toaa278

Statistics Canada (2017) Population and Dwelling Count Highlight Tables. 2016 Census. 2016 Census

Statistics Canada (2015) National Road Network

Statistics Canada (2018) Travel Survey of Residents of Canada. 2006-2017

Statistics Canada (2011) Households and the Environment: Energy Use

Taylor CM, Hastings A (2005) Allee effects in biological invasions. Ecology Letters 8:895–908. https://doi.org/10.1111/j.1461-0248.2005.00787.x

Teulon DAJ, Stufkens MAW (2002) Biosecurity and aphids in New Zealand. New Zealand Plant Protection 55:12–17. https://doi.org/10.30843/nzpp.2002.55.3906

The Association of Atlantic RV Parks & Campground Find a Campground. https://atlanticrvparksandcampgrounds.ca/campground-atlantic/. Accessed 27 Jun 2021

Tobin PC, Strom BL, Francese JA, et al (2021) Evaluation of trapping schemes to detect emerald ash borer (Coleoptera: Buprestidae). Journal of Economic Entomology 114:1201–1210. https://doi.org/10.1093/jee/toab065

Tourism PEI Where to Stay in Prince Edward Island. https://www.tourismpei.com/where-to-stay. Accessed 27 Jun 2021

United States Department of Agriculture Animal and Plant Health Inspection Service (2010) Risk Assessment of the Movement of Firewood within the United States

Valenta V, Moser D, Kapeller S, Essl F (2017) A new forest pest in Europe: a review of emerald ash borer (*Agrilus planipennis*) invasion. Journal of Applied Entomology 141:507–526. https://doi.org/10.1111/jen.12369

Van Rossum, G., Drake, F.L. (2009) Python 3 Reference Manual. CreateSpace, Scotts Valley, CA

Virtanen P, Gommers R, Oliphant TE, et al (2020) SciPy 1.0: fundamental algorithms for scientific computing in Python. Nature Methods 17:261–272. https://doi.org/10.1038/s41592-019-0686-2

Ward SF, Fei S, Liebhold AM (2020) Temporal dynamics and drivers of landscape-level spread by emerald ash borer. Journal of Applied Ecology 57:1020–1030. https://doi.org/10.1111/1365-2664.13613

Zalewski A, Michalska-Parda A, Bartoszewicz M, et al (2010) Multiple introductions determine the genetic structure of an invasive species population: american mink *Neovison vison* in Poland. Biological Conservation 143:1355–1363. https://doi.org/10.1016/j.biocon.2010.03.009

Figures and Tables

Table 2.1 Equations used in the model development with equation numbers referenced in the text.

Equation Reference	Equation
1a	$O_i = r_i \cdot s \cdot b$
1b	$O = \begin{bmatrix} o_1 \\ o_2 \\ \vdots \\ o_n \end{bmatrix}$
2	$A_{ij} = C_j \cdot 2^{d_{ij}/100})$
3a	$B_{ij} = P_j \cdot M_{ij}$
3b	$TB_j = B_{1j} + B_{2j} + \cdots + B_{nj}$

Table 2.2. Establishment characteristics of the emerald ash borer for four scenarios of risk assessment models

Scenario	Timing of firewood arrival	Allee effect threshold
1	Off	Low (2 firewood pieces)
2	On	Low (2 firewood pieces)
3	Off	High (6 firewood pieces)
4	On	High (6 firewood pieces)

Table 2.3. ANOVA table measuring the impact for two establishment characteristics, timing of firewood arrival and Allee effect threshold

	Sum of squares	Degrees of freedom	F-statistic	P-value
Timing of firewood arrival	57.1	1	75697.5	<0.001
Propagule pressure threshold	250.7	1	332624.2	<0.001
Timing of firewood arrival : Propagule pressure threshold	28.4	1	37702.9	<0.001
Residual	3.0	3996		

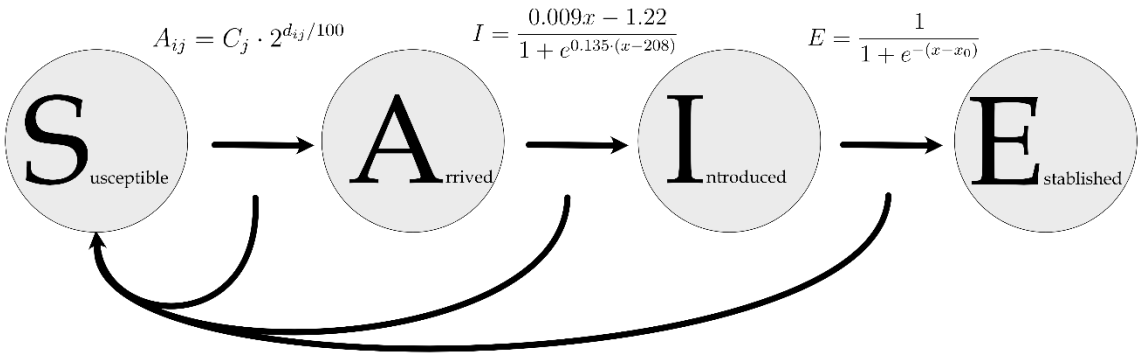

Figure 2.1. Emerald ash borer establishment into a new location in steps. “Arrived” is the probability that a piece of ash-infested firewood is transported from a city to a campground. “Introduced” is the probability that emerald ash borer can survive in the firewood based on the firewood timing of arrival. “Established” is the probability that there are enough for introductions to surpass the Allee effect threshold and establish.

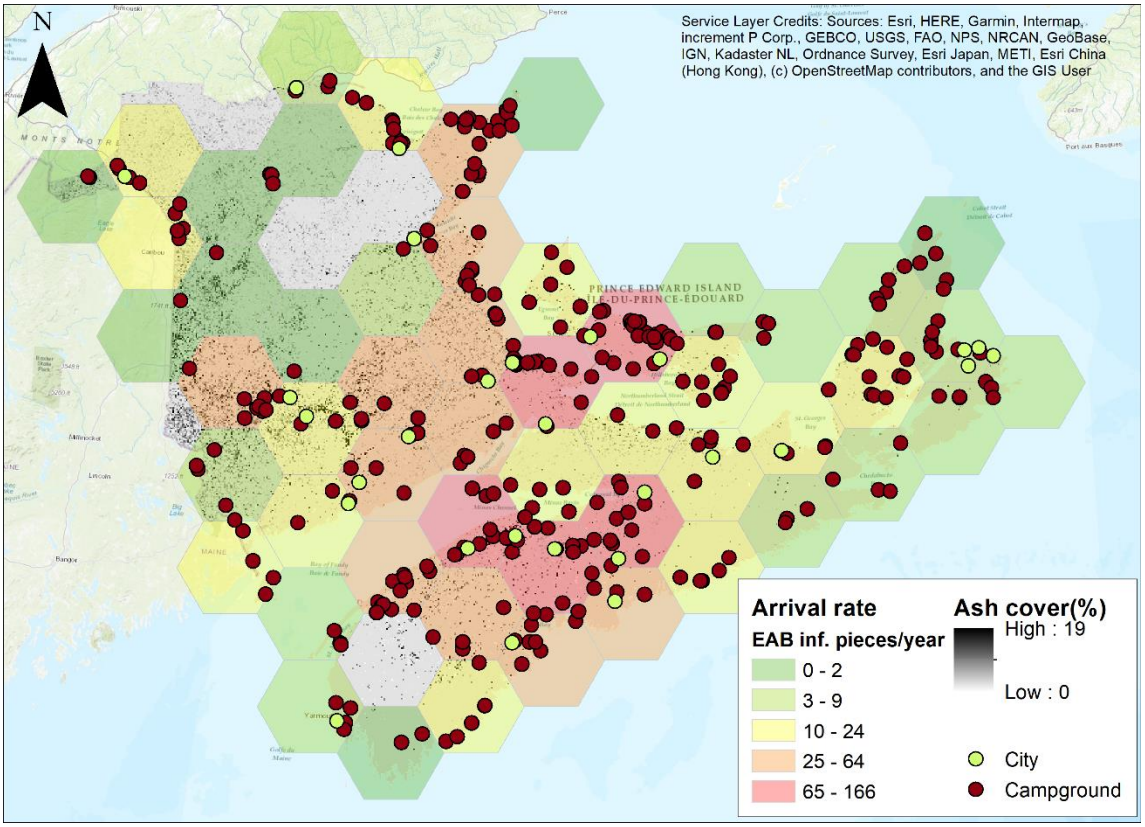

Figure 2.2. Introduction probability of emerald ash borer into the Maritime provinces of New Brunswick, Prince Edward Island, and Nova Scotia. Green dots represent cities with a population larger than 5,000. Red dots represent campgrounds. The coloured hexagons represent the mean arrival rate of emerald ash borer infested firewood pieces each year. Percent of ash forest cover is represented as a greyscale of square grid cells measuring $1km^2$

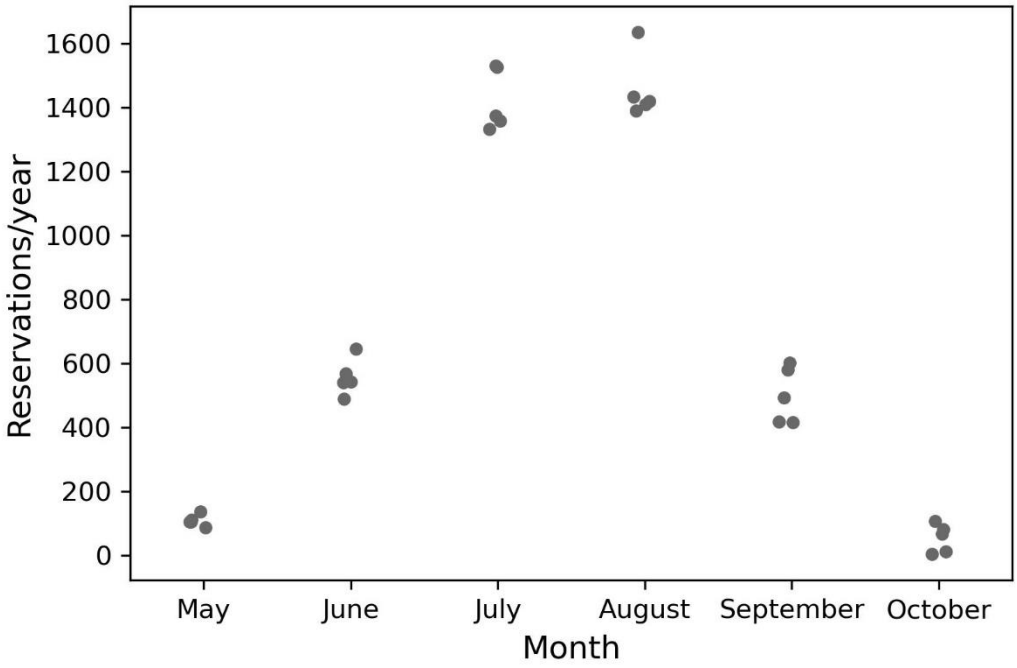

Figure 2.3 Monthly camping reservations made by campers from New Brunswick provincial parks from the years of 2015-2020. Each dot represents the monthly reservations made per year.

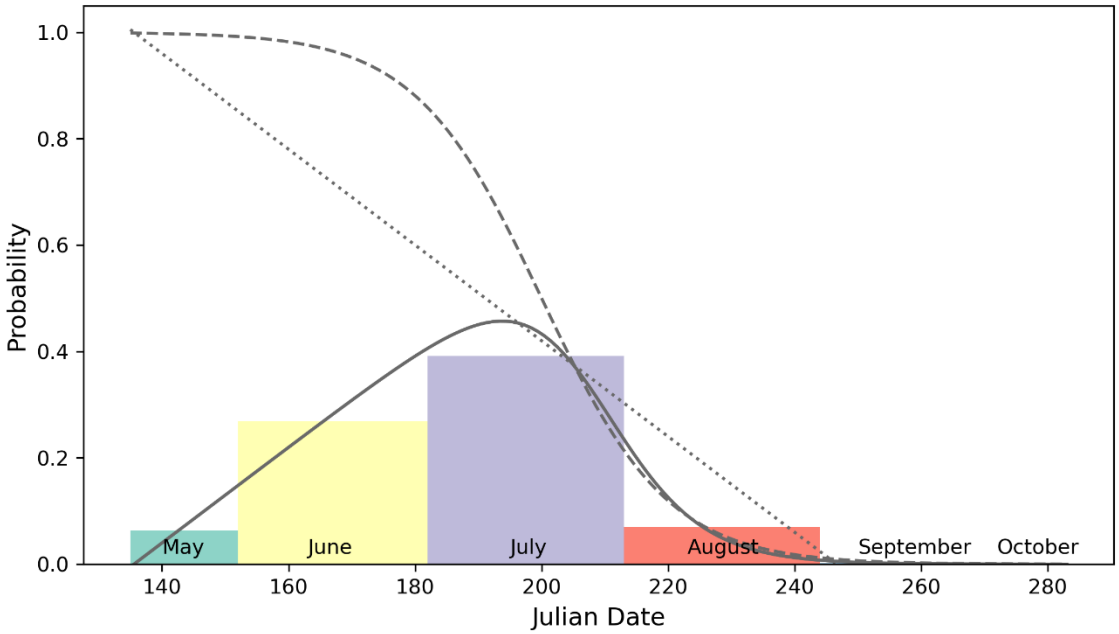

Figure 2.4. Temporal patterns of introduction probability of emerald ash borer from firewood. Lines represent the product of the proportion of emerald ash borer left to emerge (dashed line) and probability that firewood is burnt before the end of emerald ash borer emergence (dotted line). These are combined to calculate the probability that emerald ash borer emerges from unburnt firewood (solid line) at a given arrival date. Bars represent the mean monthly probability of emerald ash borer emergence from unburnt firewood.

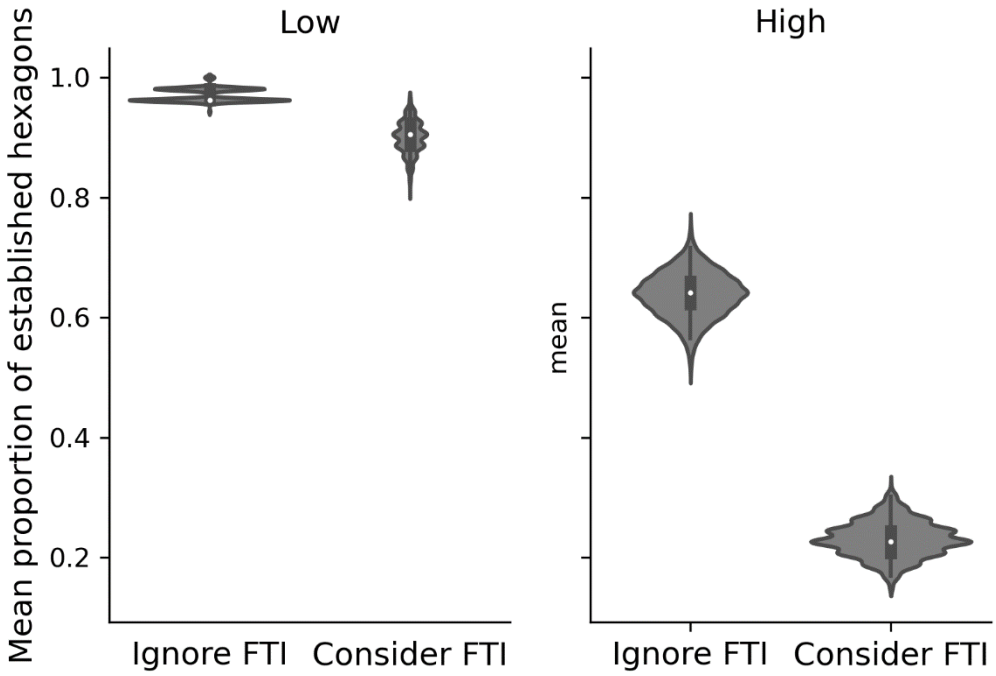

Figure 2.5. Mean proportion of established hexagons under four scenarios of firewood timing of arrival and Allee effect threshold. Low and high represent values the strength of the Allee effect threshold. FTI represents the firewood timing of arrival.

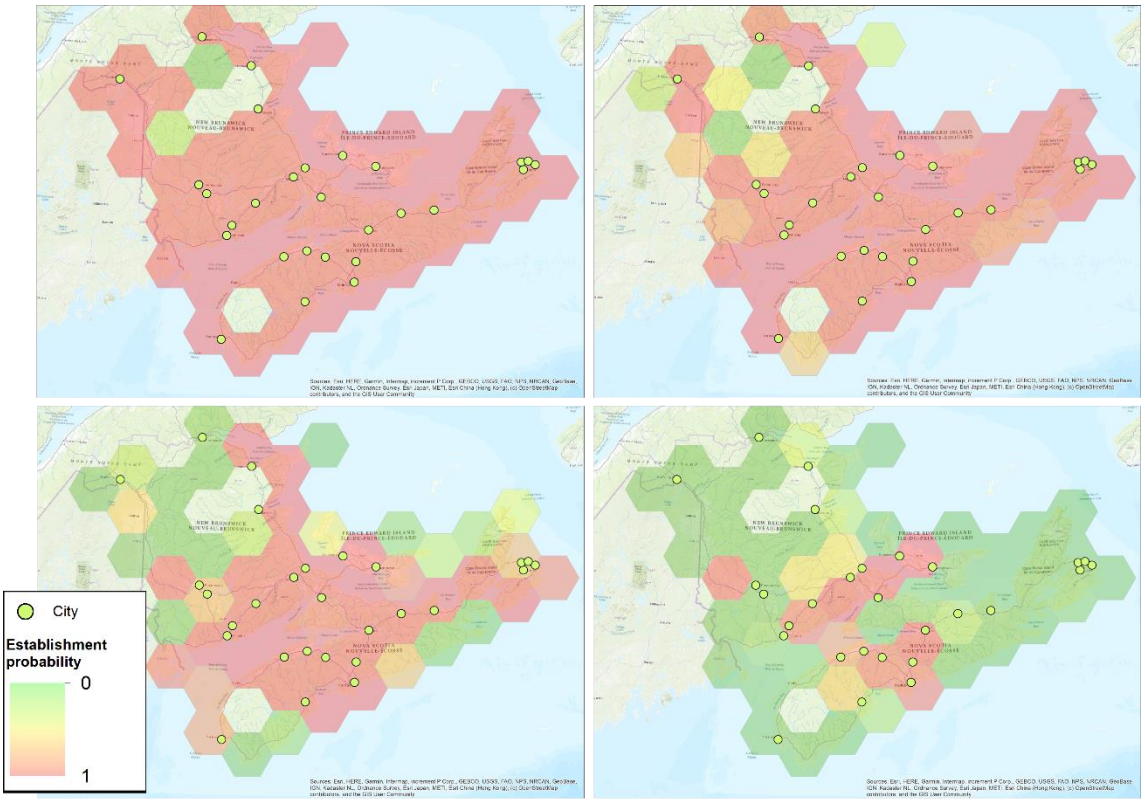

Figure 2.6. Four scenarios of timing of firewood arrival and Allee effect threshold on the establishment for the emerald ash borer. a) Low Allee effect threshold, ignore firewood timing b) low Allee effect threshold, consider timing of firewood arrival c) High Allee effect threshold, ignore timing of firewood arrival d) High Allee effect threshold, consider timing of firewood arrival

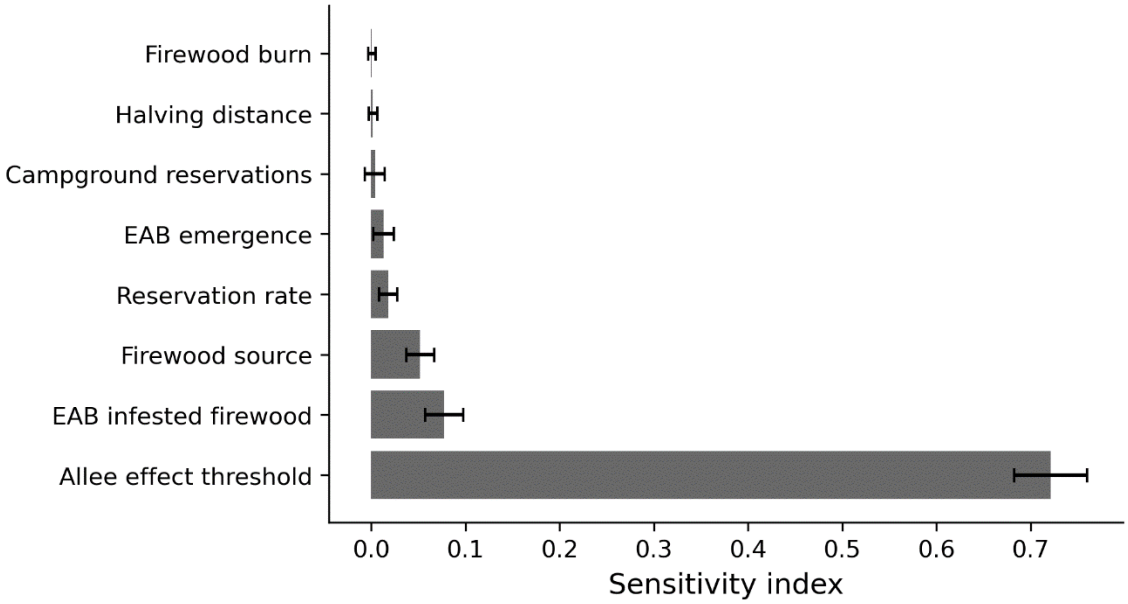

Figure 2.7. Sensitivity index of model parameters from the global sensitivity analysis run for 20 000 replications. Error bars represent 95% confidence intervals.

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Supplementary Materials

Supplementary table 1. Explanation of parameter variable choices for the global sensitivity analysis

Parameter	Low Value	High Value	Description of parameter	Literature and data
Halving Distance	50km	400km	The distance at which the number of camping reservations is halved.	Eagles et al. 2015, Koch et al 2012, New Brunswick provincial park reservation data (2015-2020)
Incidence of live borers	0.005 probability/year	0.08 probability /year	The probability that firewood contains live wood borers inside it and that the firewood is within the *Fraxinus* genus.	Haack et al. 2010
Firewood source	0.1 probability/year	0.7 probability/year	The probability that the firewood is transported from outside of the campground.	Jacobi et al. 2011
Per capita reservations	0.001 reservations/person	0.0035 reservations/person	The number of camping reservations made to a single campground based on the population	New Brunswick provincial park reservation data(2015-2020)
Allee effect threshold	1 introduced pieces of infested firewood	15 introduced pieces of infested firewood	The number of introductions occurring in a month where there is a greater than 50% probability of establishment.	Korsu & Huusko 2009, Britton and Gozlan 2013

Campground reservation evenness	(1) 2 (2) 1	(1) 18 (2) 3.2	Campground reservations dispersal across all months of the camping season	New Brunswick provincial park reservation data (2015-2020)
Probability of firewood burn	0 probability firewood is burnt/day	1 probability firewood is burnt/day	This measures the probability that firewood is burnt before emerald ash borer emerges from the firewood.	
Timing of emerald ash borer emergence	-45 days before peak emergence	45 days before peak emergence	This measures the movement of the timing of emerald ash borer emergence.	Herms et al. 2014, Forrest et al. 2016

Supplementary note 1. Rationale for the selection of parameters in the global sensitivity analysis.

Halving distance: Literature has shown that campers travel more than 100km to a campground and that halving distance of reservations is somewhere between 50-400 km. An analysis of NB provincial park reservations from maritime campers has shown that distance travelled where number of reservations is halved is approximately ~350 km.

Incidence of live borers: A study measuring firewood surrender from Michigan has shown that approximately 0.1455 of firewood surrendered was ash (*Fraxinus spp.)* and approximately 0.31 of that firewood contains live borers. The probability of ash firewood that contains live borers is 0.045.

Fraxinus is likely more abundant in Michigan than the Maritimes and is at a different stage in the invasion. Therefore, we chose wide margins for the incidence of live borers. We limited probability to between 0.005 and 0.08. We limited our values to 0.005 because we found that values below reduced firewood movement to effectively reach zero and 0.08 because firewood is less abundant in Michigan and the invasion is much less advanced.

Firewood source: A study surveying camper firewood sources found that approximately 56% of campers were firewood coming from outside of parks. However, this may be largely variable based on camper behaviour in the regions and firewood limitations from campgrounds. Therefore, we chose wide margins to encompass uncertainty. We limited our values to 0.1 because we believe that campers are still likely to transport firewood despite firewood movement moratoriums.

Per capita reservations: This measures the slope of the relationship between reservations made to campgrounds based on the city population size. This value varies the slope to reach the limits of reservations to campgrounds based on city size. We conducted an analysis on the number of camper reservations made to New Brunswick campgrounds from New Brunswick cities. We extrapolated the number of reservations made to a single campground and then multiplied this to by the total number of campgrounds that we measured in the model. Due to potential variations in camper reservations we chose to lower and upper bounds based on confidence intervals from the measure of campground reservations.

Allee effect threshold: Empirical evidence on the number of individuals and introductions that favor establishment is lacking. A study on fish establishment shows that multiple individuals are required to reach a high probability of the establishment. We vary the required propagule pressure for successful establishment because many introductions may be required for there to be a high probability of establishment. We cautiously estimated that more than 15 introduction events would not be required for a new region to see establishment.

Campground reservation evenness: These values vary the monthly reservations distribution to campgrounds to change the relationship between a normal distribution peaking in July and August to a uniform distribution of equal number of reservations across all months.

Probability of firewood burn: The probability that firewood is burnt emerald ash borer is capable of emerging. We vary this value to represent that firewood sees no influence from firewood to a 100% probability that firewood will be burnt before emergence occurs.

Timing of emerald ash borer emergence: The timing of emerald ash borer emergence could vary based on yearly variation of temperatures that could affect when firewood could move. Emergence timing could shift by weeks or even potentially a month. To cover possible variation, we include a month and a half.

Chapter 3: No evidence for strong mate-finding Allee effects in the emerald ash borer (*Agrilus planipennis* Fairmaire)

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Keywords: Emerald ash borer, Allee effects, Invasion biology, Population ecology, Invasion dynamics, Mating success

Abstract

Allee effects are density-dependent barriers that can impact species establishment and population growth. The emerald ash borer, *Agrilus planipennis* Fairmaire, has been extremely successful at expanding its North American range rapidly. The impact of Allee effects early in the invasion period of the emerald ash borer remains unknown. We measured the role of mating success in females as a function of population density in a region where the emerald ash borer was recently discovered. We placed clusters of prism traps along an invasion gradient of emerald ash borer population density and collected beetles for measurement of mating success. We dissected female reproductive tracts to measure mating success. We fit a linear regression to the mating success of beetles based on male population density. We found that emerald ash borer did not present a strong mate-finding Allee effect, and there was no significant positive relationship between mating success and male population density. This finding may provide insights into why the emerald ash borer has effectively spread far and quickly in North America and help management decisions in treating new detections of emerald ash borer.

Introduction

Introduced species must overcome several ecological barriers before establishment and population growth occur. One such barrier can be the Allee effect, a density-dependent mechanism that prevents low-density populations from increasing (Allee 1938; Taylor and Hastings 2005; Liebhold and Tobin 2006; Gertzen et al. 2011). Allee effects often occur in introduced species because populations are small, leading to difficulty finding mates, inbreeding depression, high predation, or difficulty acquiring food (Courchamp et al. 1999, 2008; Kramer et al. 2009).

An introduced species that has caused widespread ecological and economic damage throughout North America in a relatively short period is the emerald ash borer (hereafter referred to as EAB), *Agrilus plannipennis* Fairmare (Coleoptera: Buprestidae). It was introduced from eastern Asia to North America and eastern Europe (Cappaert et al. 2005; Valenta et al. 2017). First discovered in Detroit, MI, in 2002 (Haack et al. 2002), EAB has spread rapidly throughout the eastern USA and Canada.

The incredible expansion of EAB in its North American range can be attributed to the movement of ash materials such as seedlings, wood chips, and untreated firewood (Cappaert et al. 2005). Human-mediated dispersal of these products has led to the introduction of many satellite populations across both planted and natural ash ranges in North America (Muirhead et al. 2006). Each long-distance movement would subject the insect to the ecological pressures of building up a new population in a new habitat to spread. Consequently, the EAB has infested over 1400 counties in Canada and the United States (Emeraldashborer.info 2022; United States Department of Agriculture 2023) and threatens to extirpate ash from the North American continent (Herms and McCullough 2013). Population modelling has shown that EAB could be managed if invading populations were under a strong Allee effect (McDermott and Finnoff 2016). However, incipient EAB populations are difficult to monitor accurately, affecting their ability to manage their populations properly (Siegert et al. 2014; Ryall 2015). Consequently, the importance of Allee effects during the invasion period of EAB is largely unknown. Specifically, empirical studies on density dependence concerning mate-finding in the EAB remain limited (McDermott and Finnoff 2016). Mating success has been commonly used as an indicator for Allee effects because it is a proxy for encounters between beetles

(Fauvergue 2013). Mating success has been measured in the brown spruce long-horn beetle, *Tetropium fuscum* Fabricius (Rhainds et al. 2015), the spongy moth, *Lymantria dispar* Linnaeus (Sharov et al. 1995; Contarini et al. 2009) and is represented as a positive relationship between mating success and population density. A strong Allee effect can be represented as a threshold population density where mating success leads to a negative population growth rate (Fauvergue 2013).

We examined the mating success of EAB as a function of population density in a recently invaded region in Atlantic Canada. We compared mating success and distance from the epicentre of introduction to see if EAB population density decreased with distance. We empirically measured female mating success as a function of male density along a population density gradient. We hypothesized that if strong Allee effects were present, female mating success would be low at low population densities and and would see a significant growth in mating success with increased population densities. We did not find evidence for a strong mate-finding Allee effect in EAB but could not rule out a weak mate-finding Allee effect nor Allee effects due to other density-dependent factors such as predation.

Methods

Study System

EAB (Siegert et al. 2014) can be distinguished from native North American ash borers (Coleoptera: Buprestidae) by its metallic green colouration along the body exterior and metallic red on the dorsal portion of the abdomen (Wei et al. 2004; Volkovitsh et al. 2019). The EAB is univoltine. Adults lay eggs in the bark of ash trees in the summer. Larvae emerge and feed on the phloem tissue beneath the bark, causing significant

damage to the conductive tissues of the tree (Cappaert et al. 2005). EAB overwinter as late larvae or pupae and emerge from the bark the following summer (Bauer et al. 2004; Poland et al. 2011). Peak adult emergence occurs at 450-500 degree days Celsius, a accumulation of degrees where temperature is above 10 degrees, and sharply ends at 833 degree days (Bauer et al. 2004; Tobin et al. 2021). Adult EAB will typically live for three to six weeks, when they feed on ash foliage, search for mates, and oviposit on ash trees, *Fraxinus spp.* (Bauer et al. 2004; Cappaert et al. 2005). Females can mate multiple times with several males (Rutledge and Keena 2012). When mating, sperm is transferred as a spermatophore to the female. When the spermatophore dissolves, the sperm, bundled in a hyaline sheath, are transported into the spermatheca bulb (Rutledge and Keena 2019) and can be observed by dissection and microscopic examination. The presence or absence of these sheaths is useful in confirming the mating status of a given female.

Site and Sampling Design

We conducted the study in 2022 using urban street trees and parks in the Halifax regional municipality, Nova Scotia, Canada (44° 40’ N, 63° 36’ W). The Bedford Basin, a large, enclosed bay, bisects the Halifax regional municipality. EAB was first detected at Harry DeWolf Park municipal park, located at the tip of this basin. Halifax is a mid-sized city with a population of approximately 440 000 people and an area of 5 500 km^2. Halifax manages approximately 49 000 public trees (City of Halifax 2020). The most common species in the Halifax urban forest are Norway maple (*Acer platanoides* Linnaeus), American elm (*Ulmus americana* Linnaeus), and red maple (*A. rubrum* Linnaeus), accounting for about 32% of all publicly surveyed trees (City of Halifax 2020). Ash trees (*Fraxinus spp.)* account for approximately 2.5% of all publicly surveyed

trees in Halifax (City of Halifax 2020). Green ash (*F. pennsylvanica* Marshall) is the most common ash species surveyed, accounting for approximately 65% of all ash trees in Halifax. While EAB may have a preference for green ash, the preference does not appear to be strong (Anulewicz et al. 2008; Pureswaran and Poland 2009a). Since its discovery, the provincial government has monitored EAB populations using green prism traps. Street trees were not treated with insecticides, enabling EAB to infest trees unhindered by additional barriers. In 2021, parasitoid wasp releases began but their range was limited to a few hundred meters from the release site, outside of our sampling locations (Cory Hughes, Natural Resources Canada, Pers. comm., 2022).

To measure EAB populations, we arranged green (Andermatt Canada Inc., Fredericton, New Brunswick) and purple (WestGreen Global Technologies Inc., Langley, British Columbia) prism traps in clusters of at least four ash trees (Fig. 3.1). Each cluster had traps placed on four trees, with one green and one purple trap per tree. Green traps were baited with EAB adult pheromones (Silk et al. 2011) (3Z-lactone, 3mg load rate, 50 µg/day release rate, Andermatt Canada Inc., Fredericton, New Brunswick) and host kairomones (3Z-hexenol, 5ml load rate, 50mg/day release rate Andermatt Canada Inc., Fredericton, New Brunswick) to increase trap catch. The attraction radius of traps baited with these pheromones remains relatively constant, effective at approximately 28 m and up to 70m (Wittman et al. 2021).

We chose cluster locations based on the availability of public ash trees following a gradient of EAB population density from the point of first detection to the furthest detections of the current population. Clusters were at least 350 meters apart to minimize trap interference (Wittman et al. 2021). Trees within the clusters were at most 150 meters

apart, with one green and one purple trap per tree. Traps were placed on the south side of the tree to increase trap catch (Lyons et al. 2009). We placed a green prism trap near the upper crown and a purple prism trap near the mid crown. We placed two dead female EAB as decoys in the upper left corner and near the center of each side of our traps to increase trap catch (Domingue et al. 2015). Purple prism traps are reported to attract females as they might mimic oviposition sites (Francese et al. 2010). Each decoy was marked in white on the abdomen and head to ensure they were not accidentally collected. Decoys were replaced as needed during weekly checks.

We measured degree days above 10°C (DD_{10}) from a weather station monitored by the Government of Canada in Halifax to know when to deploy and finish trap collection. Traps were deployed at the beginning of the EAB flight on June 3rd, 2022, at approximately 260 degree days, and were collected on August 15th, at approximately 745 degree days, when the flight neared its end. We checked traps weekly, collected all the buprestid beetles into a cooler, and immediately transferred and stored in a -18°C freezer until dissection.

Identification and Dissection of the Female Reproduction System

We cleaned glue residue from collected beetles by brushing the residue off using limonene. Beetles were then identified using field guides and keys (Bright, 1987; Paiero et al., 2012). EAB can be separated from other North American buprestids by their larger size and the colour on the dorsal side of the abdomen. The sex of beetles can be determined using general body morphology, where females typically have an enlarged 1st abdominal segment and a lack of dense setae on the prosternum (Wang et al. 2010). For beetles that did not evidently express these characteristics, we examined the last

abdominal section for an ovipositor. We measured female beetles at the widest point of the pronotum and from the top to the end of the elytra using digital callipers (Absolute Digimatic, Mitutoyo, Japan). We dissected female reproductive systems by pulling the ovipositor with forceps, removing the reproductive tract, and mounting it onto a slide. We cut the bulb of the spermatheca and gently squeezed the spermatheca to push out any sperm. We stained the slide with Giemsa stain (G. Giemsa 1904) to make sperm more visible. We assessed the slides for sperm and scored beetles for the presence or absence of sperm. A female was considered successfully mated if we identified sperm in the reproductive tract (Rhainds 2010).

Statistical Analysis

We measured the Euclidean distance of clusters from the epicentre of the EAB invasion using ArcGIS (version 10.4). We fit a linear regression model to evaluate the relationship between population density and distance from the invasion epicentre.

We also fit a linear regression model and calculated the 95% confidence intervals to evaluate the relationship between the proportion of mated females as a function of male density determined by trap catches. Estimating absolute abundance for EAB in an urban area with non-random ash tree distribution makes choosing the appropriate sampling unit like area or number of ash trees, difficult. We chose instead to work with relative density estimates (trap catches) because traps baited with (3Z)-lactone and 3Z-hexenol have shown to have comparatively similar attractance radii (Wittman et al. 2021). For the remainder of the text, we use "density" to refer to this relative density estimate of beetles collected from clusters. We measure the relative density of male beetles based on the number of beetles caught per cluster. Proportion of mated females was measured as the

proportion of the number of mated females divided by the total number of females collected in a cluster. We only used sites where we collected at least eight females from a tree cluster for the linear regression analysis.

We also analyzed whether mated females were larger than unmated ones. To do this, we performed a two-sample t-test to test the differences in the mating success of females based on their body width and length. We visually inspected the frequency distribution and performed a Shapiro-Wilkes test to check if assumptions of normality were met. If assumptions were not met, we checked to see if sample sizes were large enough to forgo the normality assumptions.

We used the Scipy (V.1.9.3) and Scikit Learn (V.1.0.2) packages in Python (V.3.9.16) to conduct the statistical analyses performed. We performed data visualization using the Matplotlib (V.3.6.2) and Seaborn (V.0.12.2) packages.

Results

We collected 1673 adult EAB (1329 males and 356 females) over the course of the study. Of the 356 females, 174 were mated. More than half (983 individuals) of the beetles were collected from a site nearest the invasion epicentre. We found that while population density decreased with distance from the epicentre, distance from the epicentre did not quite predict population density (r^2=0.19, p= 0.061, Fig. 3.2). However, when the cluster with the greatest catch rate (total catch= 983) is removed, distance is not a good predictor of distance (r^2=0.035, p= 0.46). The number of females collected was correlated with the number of males collected within clusters (r^2=0.98, p=$2.5e^{-14}$). We collected eight or more female beetles from six of the eighteen clusters during the collection period. Female mating success was not positively correlated with male

population density (r^2=0.13, p=0.48, 95% CI slope = [-6.4e-04, 3.6e-04], Fig. 3.3). The confidence interval includes a slope of zero, and some weakly positive slopes, therefore we cannot rule out the possibility of a weak mate-finding Allee effect, although we can rule out a strong one.

The mean female width was 3.1 mm, height was 11 mm, and body area was 28 mm^2. The Shapiro-Wilkes test was statistically significant (p=0.0002); due to the large sample size (n=353) and the distribution of the data appearing normal, we chose to proceed with one sample t-test (Supplementary Figure 1). Mated females were significantly wider (p= 0.0004, Fig. 3.4) but not longer (p=0.39, Fig. 3.4) than unmated females.

Discussion

Allee effects are important factors that can influence the establishment success of non-native species that become invasive in their introduced range. These can contribute strongly to demographic factors determining whether populations continue to grow in the invaded habitat. Allee effects have been shown to influence population dynamics and suppress populations between outbreaks of both native forest insects such as the spruce budworm (*Malacosoma disstria* Hübner) (Régnière et al. 2013) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Raffa and Berryman 1983) as well as non-native insects such as the spongy moth (*Lymantria dispar* Linnaeus) (Liebhold and Bascompte 2003). Contrary to our expectation that male density would decrease with increasing distance from the epicentre of introduction, we found that such a correlation was minimal (Fig. 3.2). However, this was likely because low population densities yield higher variability (Fauvergue 2013). An increasing number of clusters collected would likely

show a significant relationship between male population density and distance, similar to other invasive species (Rhainds et al. 2015).

Long-distance dispersal in EAB is facilitated to a large extent by human movement of firewood (Cappaert et al. 2005). Therefore, areas outside Halifax could receive high beetle loads sooner if they were transported there by motorists, compared to their natural dispersal. This has been seen through rapid EAB movement to numerous invasion centres in the USA. Following EAB discovery in 2002, new beetle reports increased rapidly in the first three years, with ash mortality directly proportional to proximity to the epicentre (Muirhead et al. 2006). However, 35% of new populations could neither be accounted for by models of diffusive spread, nor by logistic regression models as a function of distance from the epicentre and human population size (Muirhead et al. 2006), suggesting that long-distance movement could obscure the predictability of new infestation sites.

Contrary to our prediction, we did not find evidence for strong mate-finding Allee effects in EAB (Fig. 3.3). Female beetles were successfully mated even at sites with low male densities, suggesting that mate-finding failure may not occur in incipient populations of EAB. If an Allee threshold exists, the threshold would be found at lower population densities than those measured in this study, and thus would be rather easy for a new population to surpass. Mate-finding Allee effects have been demonstrated in very few forest insect systems because it is typically difficult to determine mating status when observing individuals at low densities (Kramer et al. 2009; Rhainds 2010). Experimental manipulation of population densities could yield more conclusive results on the successful mating of female EAB. In systems where mate-finding is mediated by visual or olfactory cues, insects can be attracted to pheromone-baited traps to determine if they

are mated (Régnière et al. 2013; Parker et al. 2020). EAB uses multimodal cues to identify host trees and find mates. Both males and females are attracted to volatiles of ash trees, particularly 3Z-hexenol, a component of ash foliage (De Groot et al. 2008). In addition, they are visually attracted to wavelengths in the green range (530-540 nm) (Crook et al. 2009; Francese et al. 2010) as they spend a two-week maturation period feeding on foliage before mating. They are also attracted to purple traps, which resembles the wavelengths of tree bark onto which they oviposit (Lelito et al. 2007; Rodriguez-Saona et al. 2007; Crook et al. 2009; Francese et al. 2010). For mate location, females produce a pheromone (3Z)-lactone, which is attractive to males (Silk et al. 2011, 2015, Ryall et al. 2013). Mate-finding Allee effects in low-density populations generally exist when organisms are sparsely distributed in space and encounters among individuals are low. The multimodal nature of host and mate-finding behaviours in EAB appears to allow them to aggregate on trees and potentially overcome mate-finding Allee effects, at least at the densities measured in our study.

Our results demonstrate that the EAB may not be subject to a strong mate-finding Allee effect as reported in other introduced species, such as the brown spruce longhorn beetle. The brown spruce longhorn beetle, *Tetropium fuscum* Fabricius, invasion appears to stall at the range edge, possibly due to mating failure (Rhainds et al. 2015). Conversely, we found no such evidence for mating failure at the range edge of the EAB establishment. Additionally, we found that approximately half of EAB females were mated at low population densities. This is contrary to other studies that found close to no mating success in females at low population densities (Johnson et al. 2006; Rhainds et al. 2015).

We found that distance from epicenter nearly predicted population density, however when we removed our cluster with the highest population density the linear regression the p-value drops to a value that is not nearing significance. This negative relationship between distance and density has been shown in the brown spruce longhorn beetle. We do not believe this extreme value is an outlier, rather it represents a single site where population is high. Adding more sites that have a higher population densities could reveal the negative population density.

Mated EAB females were significantly wider than unmated females (Fig. 3.4). This was similar to findings in the invasive Japanese beetle (*Popillia japonica* Newman), in which there was strong selection for a wider and rounder body by males (Kelly 2020). Typically, male beetles select larger females because they sire more offspring, increasing male fitness (Bonduriansky 2001). High fecundity in females is also important for invasive species that exhibit long-distance dispersal because it can lead to rapid population growth, alleviating mate-finding Allee effects as they colonize a new area (Fahrner and Aukema 2018).

Invasive species experiencing strong Allee effects may be better managed at low densities (Tobin et al. 2011). For EAB, a lack of strong Allee effects may explain the difficulties encountered in population management following detection. Understanding the strength of Allee effects on invasive species remains important, as it can impact how management strategies are implemented. For example, if Allee effects are strong, detection early during the introduction may be less necessary. In contrast, detection is a high priority for EAB early in new introductions because eradication may only be possible at the start of the introduction.

Conclusion

Risk modelling the long-distance dispersal of an invasive species, the emerald ash borer has shown that Allee effects are an important characteristic in the establishment of invasive species (Caouette 2023). However, the findings of this study show that EAB is not affected by a strong mate-finding Allee effect at detectable levels. A lack of such effect, in combination with other factors such as the widespread planting of clonal ash cultivars and lack of natural enemies, may contribute to the rapid spread of EAB in North America and elsewhere. Allee effects remain an important and seldomly studied aspect of biological invasions. By studying population dynamics, we can increase our knowledge of population growth to help determine the best methods and timing for managing species.

Bibliography

Allee WC (1938) The social life of animals. W.W. Norton & Company, inc., New York,

Anulewicz AC, McCullough DG, Cappaert DL, Poland TM (2008) Host range of the emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) in North America: results of multiple-choice field experiments. Environmental Entomology 37:230–241. https://doi.org/10.1603/0046-225X(2008)37[230:HROTEA]2.0.CO;2

Bauer LS, Haack RA, Miller DL, et al (2004) Emerald ash borer life cycle. In: Proceedings of the Emerald Ash Borer Research and Technology Development Meeting. USDA Forest Service, Morgantown, West Virginia

Bonduriansky R (2001) The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biol Rev 76:305–339. https://doi.org/10.1017/S1464793101005693

Cappaert D, Mccullough DG, Poland TM, Siegert NW (2005) Emerald ash borer in North America: a research and regulatory challenge. American Entomologist 51:152–165. https://doi.org/10.1093/ae/51.3.152.

City of Halifax (2020) Public Trees [shapefile]

Contarini M, Onufrieva KS, Thorpe KW, et al (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. Entomologia Experimentalis et Applicata 133:307–314. https://doi.org/10.1111/j.1570-7458.2009.00930.x

Courchamp F, Berec L, Gascoigne J (2008) Allee Effects in Ecology and Conservation. Oxford University Press, Oxford, UK

Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405–410. https://doi.org/10.1016/S0169-5347(99)01683-3

Crook DJ, Francese JA, Zylstra KE, et al (2009) Laboratory and field response of the emerald ash borer (Coleoptera: Buprestidae), to selected regions of the electromagnetic spectrum. Journal of Economic Entomology 102:2160–2169. https://doi.org/10.1603/029.102.0620

De Groot P, Grant GG, Poland TM, et al (2008) Electrophysiological response and attraction of emerald ash borer to green leaf volatiles (GLVs) emitted by host foliage. J Chem Ecol 34:1170–1179. https://doi.org/10.1007/s10886-008-9514-3

Domingue MJ, Pulsifer DP, Lakhtakia A, et al (2015) Detecting emerald ash borers (*Agrilus planipennis*) using branch traps baited with 3D-printed beetle decoys. Journal of Pest Science 88:267–279. https://doi.org/10.1007/s10340-014-0598-y

Emerald Ash Borer Network (2022) Emerald ash borer state detection table. emeraldashborer.info. Accessed 14 Aug 2023

Fahrner S, Aukema BH (2018) Correlates of spread rates for introduced insects. Global Ecology and Biogeography 27:734–743. https://doi.org/10.1111/geb.12737

Fauvergue X (2013) A review of mate-finding Allee effects in insects: from individual behavior to population management. Entomologia Experimentalis et Applicata 146:79–92. https://doi.org/10.1111/eea.12021

Francese JA, Fraser I, Rietz ML, et al (2010) Relation of color, size, and canopy placement of prism traps in determining capture of emerald ash borer (Coleoptera: Buprestidae). Canadian Entomologist 142:596–600. https://doi.org/10.4039/n10-041

G. Giemsa (1904) Eine vereinfachung und vervollkommnung meiner Methylenblau-Eosin-Färbemethode zur erzielung der Romanowsky-Nocht'schen chromatinfärbung. Centralblatt für Bakteriologie 32:307–313

Gertzen EL, Leung B, Yan ND (2011) Propagule pressure, allee effects and the probability of establishment of an invasive species (*Bythotrephes longimanus*). Ecosphere 2:1–17. https://doi.org/10.1890/ES10-00170.1

Haack RA, Jendek E, Liu H, et al (2002) The emerald ash borer: a new exotic pest in North America. Newsletter of the Michigan Entomological Society 47:1–5. https://doi.org/10.1017/CBO9781107415324.004

Herms DA, McCullough DG (2013) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annual Review of Entomology 59:13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON (2006) Allee effects and pulsed invasion by the gypsy moth. Nature Letters 444:361–363

Kelly CD (2020) Sexual selection on size and shape in japanese beetles (*Popillia japonica*). Behavioral Ecology 31:1073–1083. https://doi.org/10.1093/BEHECO/ARAA054

Kramer AM, Dennis B, Liebhold AM, Drake JM (2009) The evidence for Allee effects. Population Ecology 51:341–354. https://doi.org/10.1007/s10144-009-0152-6

Lelito JP, Fraser I, Mastro VC, et al (2007) Visually mediated "paratrooper copulations" in the mating behavior of *Agrilus planipennis* (Coleoptera: Buprestidae), a highly destructive invasive pest of North American ash trees. Journal of Insect Behavior 20:537–552. https://doi.org/10.1007/s10905-007-9097-9

Liebhold A, Bascompte J (2003) The Allee effect, stochastic dynamics and the eradication of alien species. Ecology Letters 6:133–140. https://doi.org/10.1046/j.1461-0248.2003.00405.x

Liebhold AM, Tobin PC (2006) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. Population Ecology 48:253–262. https://doi.org/10.1007/s10144-006-0014-4

Lyons DB, De Groot P, Jones GC, Scharbach R (2009) Host selection by *Agrilus planipennis* (Coleoptera: Buprestidae): inferences from sticky-band trapping. Can Entomol 141:40–52. https://doi.org/10.4039/n08-045

McDermott SM, Finnoff DC (2016) Impact of repeated human introductions and the Allee effect on invasive species spread. Ecological Modelling 329:100–111. https://doi.org/10.1016/j.ecolmodel.2016.03.001

Muirhead JR, Leung B, Van Overdijk C, et al (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Diversity and Distributions 12:71–79. https://doi.org/10.1111/j.1366-9516.2006.00218.x

Parker K, Ryall K, Aukema BH, Silk P (2020) Early detection of *Agrilus planipennis*: investigations into the attractive range of the sex pheromone (3Z)-lactone. Entomologia Experimentalis et Applicata 168:166–173. https://doi.org/10.1111/eea.12872

Poland TM, McCullough DG, Anulewicz AC (2011) Evaluation of double-decker traps for emerald ash borer (Coleoptera: Buprestidae). jnl econ entom 104:517–531. https://doi.org/10.1603/EC10254

Pureswaran DS, Poland TM (2009) Host selection and feeding preference of *Agrilus planipennis* (Coleoptera: Buprestidae) on ash (*Fraxinus spp.*). Environmental Entomology 38:757–765. https://doi.org/10.1603/022.038.0328

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs 53:27–49. https://doi.org/10.2307/1942586

Régnière J, Delisle J, Pureswaran DS, Trudel R (2013) Mate-finding Allee effect in spruce budworm population dynamics. Entomologia Experimentalis et Applicata 146:112–122. https://doi.org/10.1111/eea.12019

Rhainds M (2010) Female mating failures in insects. Entomologia Experimentalis et Applicata 136:211–226. https://doi.org/10.1111/j.1570-7458.2010.01032.x

Rhainds M, Heard SB, Hughes C, et al (2015) Evidence for mate-encounter Allee effects in an invasive longhorn beetle (Coleoptera: Cerambycidae). Ecological Entomology 40:829–832. https://doi.org/10.1111/een.12255

Rodriguez-Saona CR, Miller JR, Poland TM, et al (2007) Behaviors of adult *Agrilus planipennis* (Coleoptera: Buprestidae). Great Lakes Entomologist 40:1–16

Rutledge CE, Keena MA (2012) Mating frequency and fecundity in the emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae). Annals of the Entomological Society of America 105:66–72. https://doi.org/10.1603/AN11037

Rutledge CE, Keena MA (2019) Mating behavior and reproductive biology of emerald ash borer (Coleoptera: Buprestidae) and two of its native congeners, the twolined chestnut borer and the bronze birch borer. Journal of Economic Entomology 112:2620–2631. https://doi.org/10.1093/jee/toz182

Ryall K (2015) Detection and sampling of emerald ash borer (Coleoptera: Buprestidae) infestations. Canadian Entomologist 147:290–299. https://doi.org/10.4039/tce.2015.7

Sharov AA, Liebhold AM, Ravlin FW (1995) Prediction of gypsy moth (Lepidoptera: Lymantriidae) mating success from pheromone trap counts. Environmental Entomology 24:1239–1244. https://doi.org/10.1093/ee/24.5.1239

Siegert NW, Mccullough DG, Liebhold AM, Telewski FW (2014) Dendrochronological reconstruction of the epicentre and early spread of emerald ash borer in North America. Diversity and Distributions 20:847–858. https://doi.org/10.1111/ddi.12212

Silk PJ, Ryall K, Mayo P, et al (2011) Evidence for a volatile pheromone in *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) that increases attraction to a host foliar volatile. Environmental Entomology 40:904–916. https://doi.org/10.1603/EN11029

Taylor CM, Hastings A (2005) Allee effects in biological invasions. Ecology Letters 8:895–908. https://doi.org/10.1111/j.1461-0248.2005.00787.x

Tobin PC, Berec L, Liebhold AM (2011) Exploiting Allee effects for managing biological invasions. Ecology Letters 14:615–624. https://doi.org/10.1111/j.1461-0248.2011.01614.x

Tobin PC, Strom BL, Francese JA, et al (2021) Evaluation of trapping schemes to detect emerald ash borer (Coleoptera: Buprestidae). Journal of Economic Entomology 114:1201–1210. https://doi.org/10.1093/jee/toab065

United States Department of Agriculture (2023) Emerald ash borer beetle known infested counties.

Valenta V, Moser D, Kapeller S, Essl F (2017) A new forest pest in Europe: a review of emerald ash borer (*Agrilus planipennis*) invasion. Journal of Applied Entomology 141:507–526. https://doi.org/10.1111/jen.12369

Volkovitsh MG, Orlova-Bienkowskaja MJ, Kovalev AV, Bieńkowski AO (2019) An illustrated guide to distinguish emerald ash borer (*Agrilus planipennis*) from its congeners in Europe. Forestry 316–325. https://doi.org/10.1093/forestry/cpz024

Wang XY, Yang ZQ, Gould JR, et al (2010) The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. Journal of Insect Science 10:1–23. https://doi.org/10.1673/031.010.12801

Wei X, Reardon D, Wu Y, Sun J-H (2004) Emerald ash borer, *Agrilus Planipennis* Fairmaire (Coleoptera: Buprestidae), in China: a review and distribution survey. Acta Entomologica Sinica 47:679–685

Wittman JT, Silk P, Parker K, Aukema BH (2021) Optimizing early detection strategies: defining the effective attraction radius of attractants for emerald ash borer *Agrilus planipennis* Fairmaire. Agr Forest Entomol 23:527–535. https://doi.org/10.1111/afe.12457

Figures and Tables

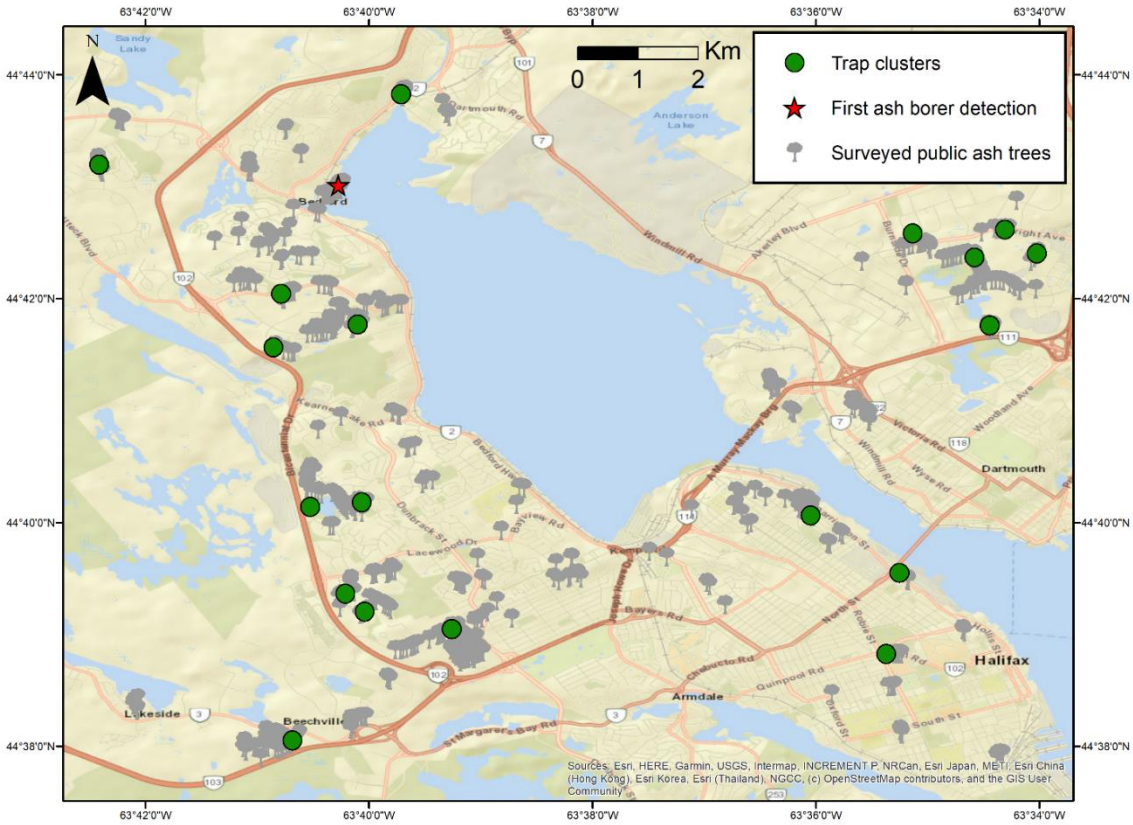

Figure 3.1. Emerald ash borer collection in the Halifax Regional Municipality, Nova Scotia. Green circles represent sampled clusters of ash trees. Red star represents the location of the first ash borer detection in the Halifax Regional Municipality. Grey tree icons represent ash trees identified during street tree surveys.

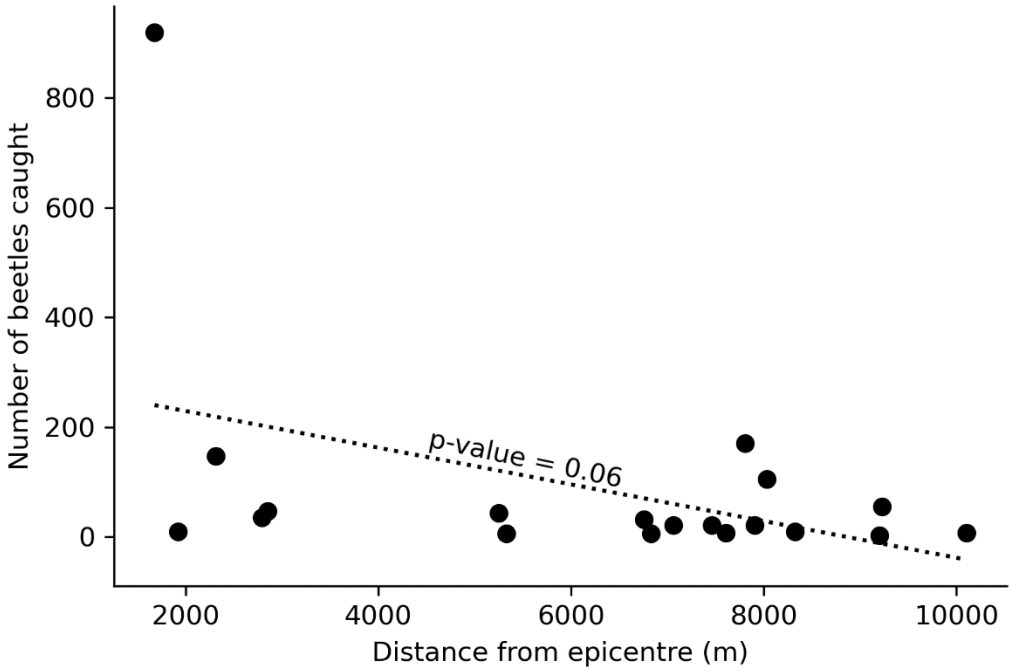

Figure 3.2. Number of beetles caught in a cluster based on the distance from the invasion epicentre. Each point represents a cluster of green and purple prism traps in ash trees. Distances were measured from the center of the location, Harry Dewolfe Park, of the first detection of EAB in the Halifax regional municipality, Nova Scotia, Canada. The dotted line represents the slope of the linear regression (not significant).

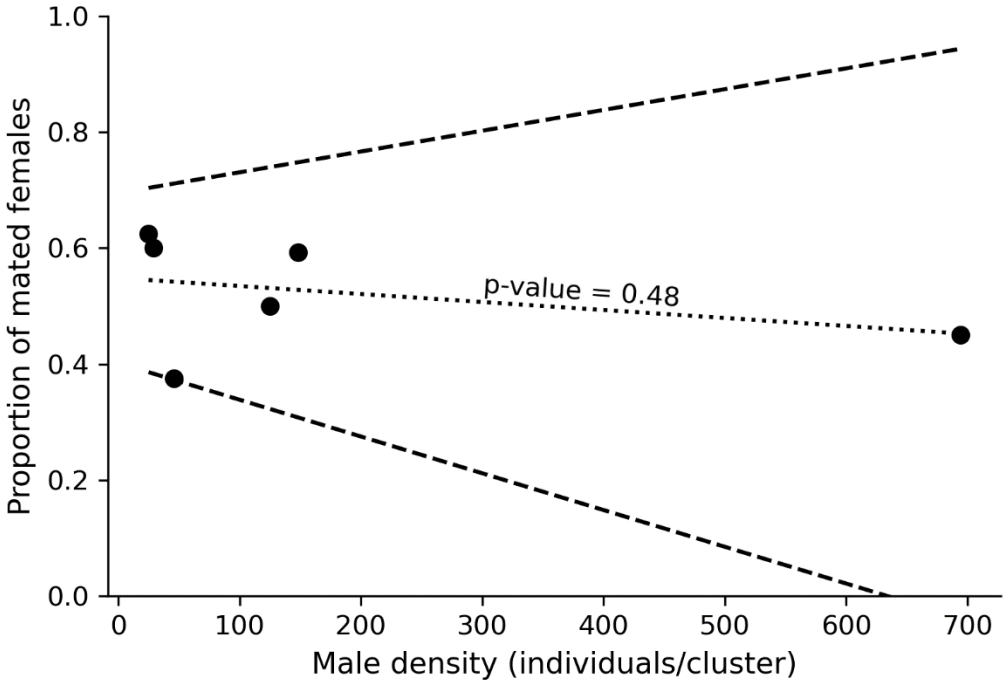

Figure 3.3.Female mating success as a function of male population density. Collected from prism traps in Halifax, Nova Scotia, Canada, in 2022. Dots represent clusters of trees where beetles were trapped. Clusters were plotted if least eight females were collected during the study period. The dotted line represents the slope of the linear regression (not significant). Dashed lines represent 95% confidence intervals.

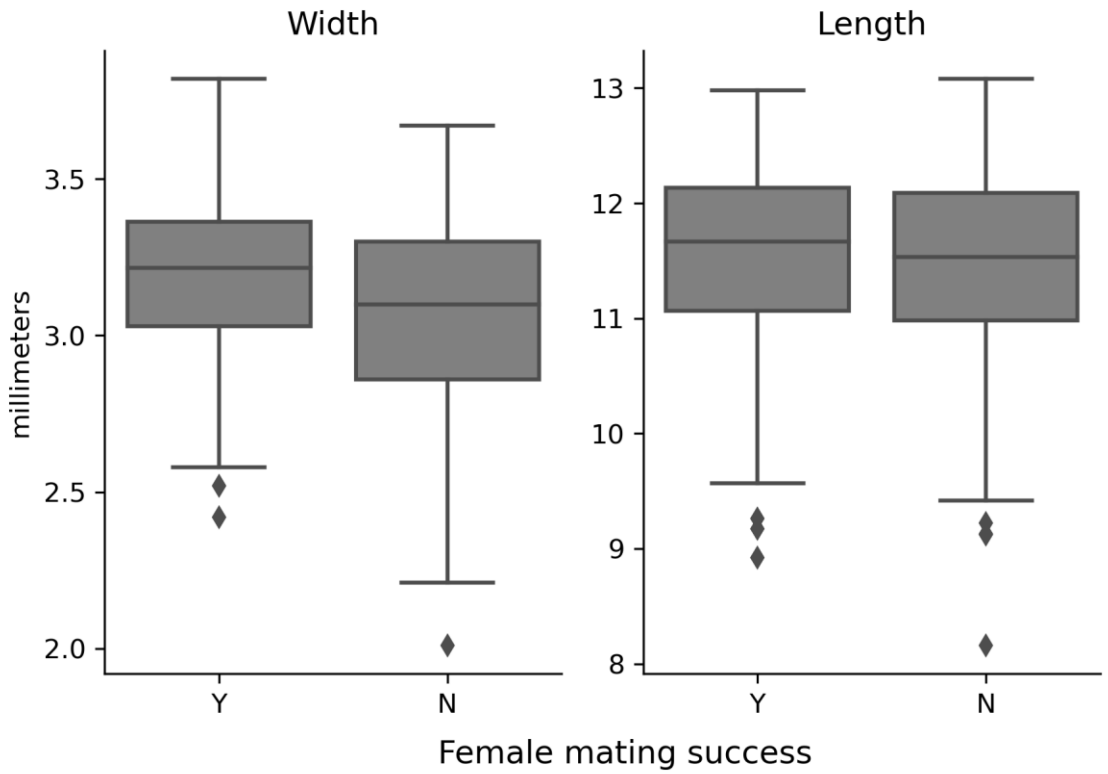

Figure 3.4. Female EAB mating success is a function of the width and length of the body. The width was measured from the widest point on the dorsal side of the abdomen. The length was measured from the dorsal edge of the pronotum to the end of the abdomen. Y represents the females that were mated. N represents females that were not mated. The box extends from the lower to the upper quartiles, with the line representing the median. The whiskers extend from the box to show one and a half times the interquartile range of the data. Points represent outliers in the data.

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Supervision: Stephen B. Heard, Deepa S. Pureswaran

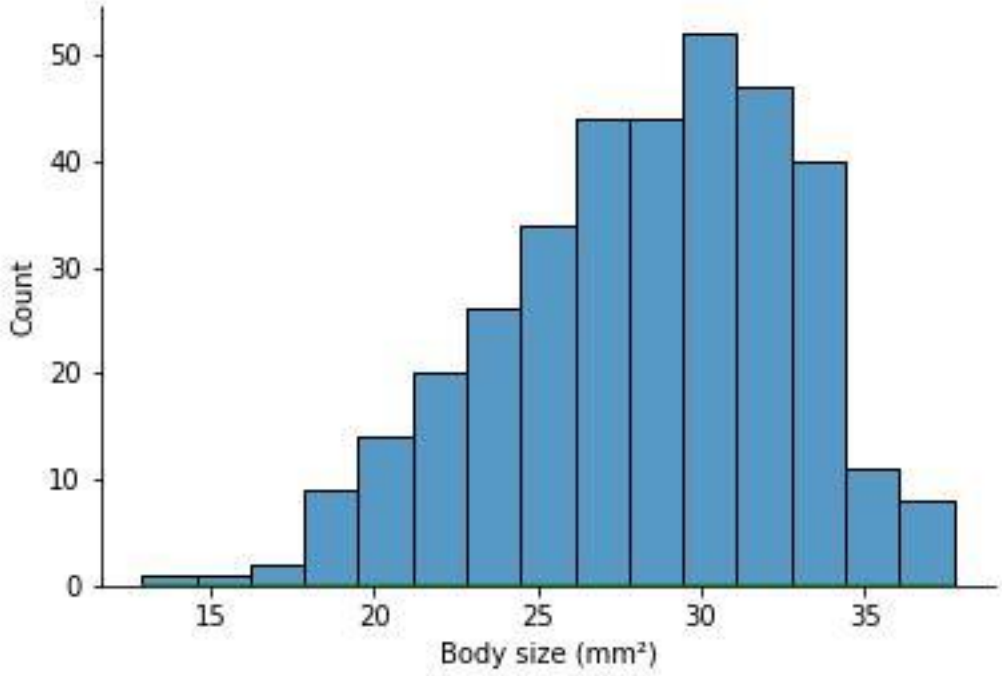
Validation: Alexandre P. Caouette

Visualization : Alexandre P. Caouette

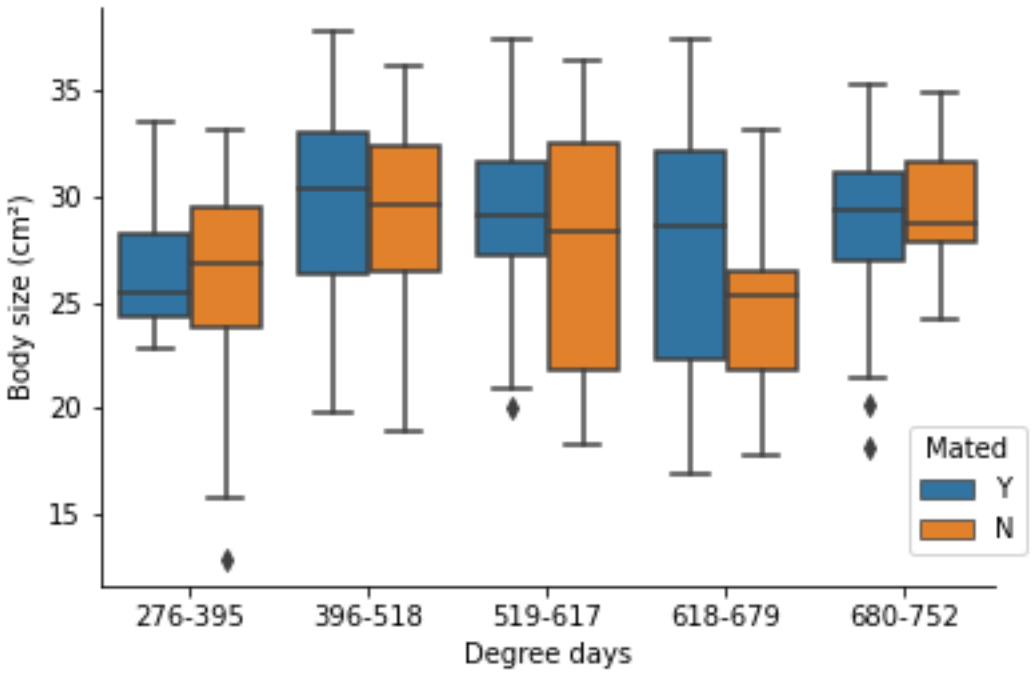
Writing – Original Draft Preparation: Alexandre P. Caouette

Writing – Review & Editing: Alexandre P. Caouette, Stephen B. Heard, Deepa S. Pureswaran

Supplementary Materials



Supplementary figure 1. Distribution of body size in mm^2 of the emerald ash borer collected from prism traps in the Halifax regional municipality, Nova Scotia, Canada in 2022



Supplementary figure 2. Mating success of female emerald ash borer beetles based on the body size in millimetres separated by degree days of collection. Collected from prism traps in Halifax, Nova Scotia, Canada in 2022

Chapter 4: General discussion

In this thesis, we combined modelling and empirical approaches to understand the invasion ecology of a highly destructive forest pest. Our results revealed two major findings: 1) that Allee effects can impact the outcome of invasive species in establishment models; and 2) the emerald ash borer (*Agrilus plannipenis* Fairmaire) (Coleoptera: Buprestidae), hereafter referred to as EAB, does not experience strong demographic Allee effects. Propagule pressure threshold appears to drive the establishment probability of EAB in our long-distance forecasting model (Chapter 2). Our results suggest that the number of introductions required for EAB to surpass the establishment threshold greatly influences establishment probability (Chapter 2). This finding lends support to the idea that including the Allee effect threshold, the number of introductions required before establishment, in models can increase the reliability of forecasting establishment risk (Drake and Lodge 2006). Models that measure introduction potential based on invasive species dispersal could overestimate their actual invasion range because many of the population introductions will fail to establish (Veit and Lewis 1996). Incorporating species-specific Allee effect parameters into models can influence predictive models and reduce the probability of predicted invasive pressure in new locations (Wang and Kot 2001). However, introduction models that estimate long-distance dispersal may be more suitable for EAB because we did not find evidence for a strong Allee effect at low population densities (Chapter 3). For species that experience Allee effects, density-dependent population growth parameters are important to increasing the reliability of spread rates in establishment risk models. This highlights the need to collect empirical data on Allee effects for invasive species to better understand

their importance species movement modelling. Empirical observations of the population ecology in incipient populations of invasive forest insects are limited; impacts of Allee effects have only been reported for the spongy moth (*Lymantria dispar* Linnaeus) (Johnson et al. 2006; Contarini et al. 2009) and the brown spruce longhorn beetle (*Tetropium fuscum* Fabricius) (Rhainds et al. 2015). Information on population dynamics at low population densities could be beneficial for many species that are currently undergoing large scale dispersal such as the spotted lanternfly (*Lycorma delicatula* White), the Asian long-horned beetle (*Anoplophora glabripennis* Motschulsky), the larch sawfly (*Pristiphora erichsonii* Hartig), and the hemlock woolly adelgid (*Adelges tsugae* Annand). New information on population ecology for impactful species like those above could decrease their economic impacts by helping managers with early detection. Establishment studies should include hymenopteran parasitoids because they are frequently used as biological control agents for invasive species and can experience Allee effects themselves before they successfully establish to control populations of their host insect (Fauvergue et al. 2012). Currently, four species of non-native hymenopteran parasitoids are being released to help control EAB populations in North America (Duan et al. 2022).

Studies on native pest and invasive forest insects report moderate to strong Allee effects (Raffa and Berryman 1983; Johnson et al. 2006; Contarini et al. 2009; Régnière et al. 2013; Rhainds et al. 2015), and evidence for weak or non-existent Allee effects generally goes unreported (Gregory et al. 2011). Our study presents a unique instance where a forest insect may be experiencing little or no Allee effect. One or many adaptations may help alleviate mate finding Allee effects in EAB (at the densities

measured in this study)(Liebhold and Bascompte 2003). We demonstrated that female size is an important factor in male selection, which may increase reproductive rates population fitness (Kajita and Evans 2010). EAB can locate mates through visual or olfactory cues, which will help with finding mates at low population densities (Gascoigne et al. 2009; Pureswaran and Poland 2009b). EAB has escaped from native predators and parasites that help regulate population growth (Wang et al. 2010; Duan et al. 2022).

A weak or non-existent Allee effect in EAB population dynamics could be a prominent factor the rapid spread of this species in North America and Europe (Wang and Kot 2001). This would mean that a lower propagule pressure would be required for establishment. Other species like the brown spruce longhorn beetle, that was discovered at a similar time, did not expand their range at rates comparable to EAB in their introduced range. The brown spruce longhorn beetle has only expanded its range a few hundred kilometres since its establishment (CFIA 2017). A factor that could have led to their slow expansion is the presence of a strong mate-finding Allee effect (Rhainds et al. 2015). This is not surprising because it has been frequently demonstrated that a strong Allee effect can significantly slow spread rates of invasive species (Hurford et al. 2006; Tobin et al. 2007; Smith et al. 2014).

Weak or non-existent Allee effects can have implications for the control of new populations of EAB. Management at first detection would be required to manage EAB in order to eradicate arriving and newly-established populations (McDermott and Finnoff 2016). EAB is difficult to detect, and often, following detection, populations are difficult to eliminate (Herms and McCullough 2013). Public education and early detection should be considered in locations moderate to high probability of establishment (Mccullough

and Poland 2017; Solano et al. 2022). Public education can help decrease the movement of firewood by informing campers about the impacts of firewood movement (Barlow et al. 2014; Solano et al. 2022). And providing free, locally collected dry firewood can provide incentives for campers to leave firewood at home (Jacobi et al. 2011; Barlow et al. 2014; Solano et al. 2022). Deploying green sticky prism traps baited with female mating pheromone (3Z-lactone) and host kairomone (3Z-hexenol) as well as branch sampling are effective tools for detecting and monitoring low-density EAB populations. (Ryall et al. 2011; Mccullough and Poland 2017). Following detection, various integrated pest management tactics can be applied; for example, using classical biological control using parasitic wasps. These parasitic wasps are introduced into North America, from their native range in Asia, and can be effective at lowering populations and potentially protecting some ash (*Fraxinus spp.*) populations (Butler et al. 2022; Duan et al. 2022). These wasps have limited negative impacts on native wood borers, and populations can potentially be self-sustaining once established (Yang et al. 2008; Duan et al. 2015, 2022). In urban and the surrounding areas, directly injecting trees with neonicotinoid pesticides, such as Imidacloprid and Emamectin Benzoate, can help protect high-value trees (Sadof et al. 2023).

Our camper firewood dispersal model predicted that locations at the highest risk of EAB introductions to campgrounds in the Maritimes were near large cities (Chapter 2, Figure 2). This is consistent with the historical trends of EAB dispersal North America (Ward et al. 2020) and with models that have estimated EAB movement (Muirhead et al. 2006; Prasad et al. 2010). We found that the Wolastoq (Saint John) river valley and the northern Kespukwitk (Annapolis Valley) region in Nova Scotia have large populations of

ash trees and a moderate to high risk of EAB introduction and would benefit from integrated pest management strategies to limit introduction and impact. The northwestern section of the Wolastoq River Valley in New Brunswick has a low probability of EAB introduction and could be a potential refugium for black ash (*Fraxinus nigra* Marsh) populations, an important resource for First Nation communities like the Wabanaki for basket making and for native teachings and healing (Costanza et al. 2017).

Managing invasive forest insects is important to keep forests healthy because disturbed forests are less resilient to change (Johnstone et al. 2016). Invasive species can cause shifts in the distribution of forests, allowing for other invasive species to establish (Eschtruth et al. 2006), and in combination with climate change, can cause "megadisturbances" resulting in large-scale transformations of forests (Millar and Stephenson 2015). By understanding the role of population dynamics in the success of invasive species establishment management and modelling, we can more reliably predict and respond to future movement and spread of invasive species.

Bibliography

Barlow LA, Cecile J, Bauch CT, Anand M (2014) Modelling interactions between forest pest invasions and human decisions regarding firewood transport restrictions. PLoS ONE 9:1–12. https://doi.org/10.1371/journal.pone.0090511

Butler S, Dedes J, Jones G, et al (2022) Introduction and establishment of biological control agents for control of emerald ash borer (*Agrilus planipennis*) in Canada. The Canadian Entomologist 154:1–20. https://doi.org/10.4039/tce.2022.32

CFIA (2017) Questions and answers: prohibition of movement zone in Memramcook, New Brunswick. https://inspection.canada.ca/plant-health/invasive-species/insects/brown-spruce-longhorn-beetle/q-amp-a-memramcook-nb-/eng/1491939495541/1491939573528. Accessed 13 Oct 2023

Contarini M, Onufrieva KS, Thorpe KW, et al (2009) Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. Entomologia Experimentalis et Applicata 133:307–314. https://doi.org/10.1111/j.1570-7458.2009.00930.x

Costanza KKL, Livingston WH, Kashian DM, et al (2017) The precarious state of a cultural keystone species: tribal and biological assessments of the role and future of black ash. Journal of Forestry 115:435–446. https://doi.org/10.5849/jof.2016-034R1

Drake JM, Lodge DM (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biological Invasions 8:365–375. https://doi.org/10.1007/s10530-004-8122-6

Duan JJ, Gould JR, Fuester RW (2015) Evaluation of the host specificity of *Spathius galinae* (Hymenoptera: Braconidae), a larval parasitoid of the emerald ash borer (Coleoptera: Buprestidae) in Northeast Asia. Biological Control 89:91–97. https://doi.org/10.1016/j.biocontrol.2015.06.005

Duan JJ, Van Driesche RG, Schmude J, et al (2022) Significant suppression of invasive emerald ash borer by introduced parasitoids: potential for North American ash recovery. Journal of Pest Science 95:1081–1090. https://doi.org/10.1007/s10340-021-01441-9

Eschtruth AK, Cleavitt NL, Battles JJ, et al (2006) Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 36:1435–1450. https://doi.org/10.1139/x06-050

Fauvergue X, Vercken E, Malausa T, Hufbauer RA (2012) The biology of small, introduced populations, with special reference to biological control. Evolutionary Applications 5:424–443. https://doi.org/10.1111/j.1752-4571.2012.00272.x

Gascoigne J, Berec L, Gregory S, Courchamp F (2009) Dangerously few liaisons: a review of mate-finding Allee effects. Population Ecology 51:355–372. https://doi.org/10.1007/s10144-009-0146-4

Gregory SD, Bradshaw CJA, Brook BW, Courchamp F (2011) Limited evidence for the demographic Allee effect from numerous species across taxa. Ecology 91:2151–2161

Herms DA, McCullough DG (2013) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annual Review of Entomology 59:13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Hurford A, Hebblewhite M, Lewis MA (2006) A spatially explicit model for an Allee effect: why wolves recolonize so slowly in Greater Yellowstone. Theoretical Population Biology 70:244–254. https://doi.org/10.1016/j.tpb.2006.06.009

Jacobi WR, Goodrich BA, Cleaver CM (2011) Firewood transport by national and state park campers: a risk for native or exotic tree pest movement. Arboriculture and Urban Forestry 37:126–138

Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON (2006) Allee effects and pulsed invasion by the gypsy moth. Nature Letters 444:361–363

Johnstone JF, Allen CD, Franklin JF, et al (2016) Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378. https://doi.org/10.1002/fee.1311

Kajita Y, Evans EW (2010) Relationships of body size, fecundity, and invasion success among predatory lady beetles (Coleoptera: Coccinellidae) inhabiting alfalfa fields. Annals of the Entomological Society of America 103:750–756. https://doi.org/10.1603/AN10071

Liebhold A, Bascompte J (2003) The Allee effect, stochastic dynamics and the eradication of alien species. Ecology Letters 6:133–140. https://doi.org/10.1046/j.1461-0248.2003.00405.x

Mccullough DG, Poland TM (2017) Building double-decker traps for early detection of emerald ash borer. Journal of Visualized Experiments 128:1–7. https://doi.org/10.3791/55252

McDermott SM, Finnoff DC (2016) Impact of repeated human introductions and the Allee effect on invasive species spread. Ecological Modelling 329:100–111. https://doi.org/10.1016/j.ecolmodel.2016.03.001

Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. Science 349:823–826. https://doi.org/10.1126/science.aaa9933

Muirhead JR, Leung B, Van Overdijk C, et al (2006) Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Diversity and Distributions 12:71–79. https://doi.org/10.1111/j.1366-9516.2006.00218.x

Prasad AM, Iverson LR, Peters MP, et al (2010) Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Landscape Ecology 25:353–369. https://doi.org/10.1007/s10980-009-9434-9

Pureswaran DS, Poland TM (2009) The role of olfactory cues in short-range mate finding by the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). Journal of Insect Behavior 22:205–216. https://doi.org/10.1007/s10905-008-9166-8

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs 53:27–49. https://doi.org/10.2307/1942586

Régnière J, Delisle J, Pureswaran DS, Trudel R (2013) Mate-finding Allee effect in spruce budworm population dynamics. Entomologia Experimentalis et Applicata 146:112–122. https://doi.org/10.1111/eea.12019

Rhainds M, Heard SB, Hughes C, et al (2015) Evidence for mate-encounter Allee effects in an invasive longhorn beetle (Coleoptera: Cerambycidae). Ecological Entomology 40:829–832. https://doi.org/10.1111/een.12255

Ryall KL, Fidgen JG, Turgeon JJ (2011) Detection of emerald ash borer in urban environments using branch sampling. Canadian Forest Service 74–76. https://doi.org/10.1603/0022-0493(2008)101[1643:POACTA]2.0.CO;2

Sadof CS, McCullough DG, Ginzel MD (2023) Urban ash management and emerald ash borer (Coleoptera: Buprestidae): facts, myths, and an operational synthesis. Journal of Integrated Pest Management 14:1–13. https://doi.org/10.1093/jipm/pmad012

Smith R, Tan C, Srimani JK, et al (2014) Programmed Allee effect in bacteria causes a tradeoff between population spread and survival. Proceedings of the National Academy of Sciences 111:1969–1974. https://doi.org/10.1073/pnas.1315954111

Solano A, Rodriguez SL, Greenwood L, et al (2022) Achieving effective outreach for invasive species: firewood case studies from 2005 to 2016. Biological Invasions 24:3321–3339. https://doi.org/10.1007/s10530-022-02848-w

Tobin PC, Whitmire SL, Johnson DM, et al (2007) Invasion speed is affected by geographical variation in the strength of Allee effects. Ecology Letters 10:36–43. https://doi.org/10.1111/j.1461-0248.2006.00991.x

Veit RR, Lewis MA (1996) Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. The American Naturalist 148:255–274. https://doi.org/10.1086/285924

Wang M-H, Kot M (2001) Speeds of invasion in a model with strong or weak Allee effects. Mathematical Biosciences 171:83–97

Wang XY, Yang ZQ, Gould JR, et al (2010) The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. Journal of Insect Science 10:1–23. https://doi.org/10.1673/031.010.12801

Ward SF, Fei S, Liebhold AM (2020) Temporal dynamics and drivers of landscape-level spread by emerald ash borer. Journal of Applied Ecology 57:1020–1030. https://doi.org/10.1111/1365-2664.13613

Yang Z-Q, Wang X-Y, Gould JR, Wu H (2008) Host specificity of *Spathius agrili* Yang (Hymenoptera: Braconidae), an important parasitoid of the emerald ash borer. Biological Control 47:216–221. https://doi.org/10.1016/j.biocontrol.2008.08.001

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