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Gaps in population data could limit predictive potential of invasive species establishment models: The case of the emerald ash borer, *Agrilus planipennis* (Fairmaire)

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Abstract

Invasive species that travel long distances through human-mediated dispersal (such as transport of firewood) 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, the likelihood that an individual survives initial recruitment and persists at a site to which it is introduced, even though establishment is an important step in biological invasions. Here, we explore two aspects of establishment for forest insects: Allee effects and timing of firewood arrival - factors 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 model, we perform local and global sensitivity analyses to understand the importance of introduction and establishment characteristics in our risk analysis model. Our global sensitivity analysis revealed that the 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.

Key words: invasive species, establishment probability, firewood movement, Allee effects, data gaps

Introduction

Invasive species have a wide range of ecological and economic impacts including disrupting interactions within native communities, vectoring diseases and altering ecosystem services (Blackburn et al. 2014; Bacher et al. 2018). Understanding the spread and establishment of invasives outside their native range is therefore an important goal for invasion ecologists. Long distance spread of invasive species may exceed their physiological dispersal abilities through transportation by humans and other anthropogenic activities (Hulme 2009). Species dispersed by humans tend to move in jump-dispersal events along transportation networks to new regions not easily reached by natural dispersal (Lewis 1997). Establishment of introduced populations from jump-dispersal events will be constrained whenever per-capita population growth rates are negative below some critical threshold density, often referred to as "Allee effects" (Johnson et al. 2006). Such Allee effects are common and can arise from mate-finding difficulty (Rhainds et al. 2015), mate-choice errors (Anderson et al. 2022), failure of mass attack (Boone et al. 2011), or many other mechanisms. Additionally, timing of arrival is important in survival because, depending on the time of year, introduced individuals could be at stages in their life history that may not survive environmental conditions in the new region. Introduction of less mobile or immobile stages will reduce the species' ability to disperse, find suitable hosts, and mates (Teulon and Stufkens 2002; Peacock and Worner 2008). To overcome these challenges, multiple introductions at opportune times may be required for establishment and population growth (Zalewski et al. 2010; Novo et al. 2015).

Despite substantial ecological barriers to establishment, some species do successfully establish and spread in their new range, causing widespread damage to the environment and the economy. Therefore, predicting the timing and likelihood of establishment is essential for effective invasive species management. Risk assessment models are useful tools that can account for the dynamics and steps involved in dispersal and spread of invasive species, such as introduction, establishment, spread, and impact (Lodge et al. 2016). Such models can be used to predict the probability that a certain species might be moved by humans along transportation networks (Koch et al. 2012; Büyüktahtakın and Haight 2018), although specialized means of estimating human-assisted movement may be required. However, for many forest insects, assessing establishment risk has been challenging (Nathan et al. 2003), probably due to cryptic habits that make them difficult to detect at low densities, especially early in the invasion period (Mehta et al. 2007). This uncertainty highlights the need to better understand the factors that contribute to invasion success and how they are represented in risk assessment models. Examining these factors may improve predictive forecasting of risk assessment models and support effective policy and management efforts to reduce economic and ecological burdens from unexpected establishments into new regions of invasion (Lodge et al. 2016; Jane Elith 2017).

The emerald ash borer (hereafter referred to as EAB; *Agrilus plannipennis* Fairmaire; Coleoptera: Buprestidae) is a remarkable example of a highly destructive forest insect that has spread widely across North America since its introduction in the 1990s (Haack et al. 2002; Cappaert et al. 2005). Its extensive spread across the continent

81 is primarily by human-mediated transport of infested ash through firewood, nursery stock
82 and lumber, resulting in large-scale ash mortality in urban and natural forests (Kovacs et
83 al. 2010; Herms and McCullough 2014). The loss of ash has substantial ecological
84 impacts that have altered forest composition, ecosystem processes, and wildlife habitat,
85 incurring significant economic costs associated with tree removal, replacement, and
86 management (Kovacs et al. 2010). Because EAB often remains undetected until
87 infestations are well established, management efforts are most effective if potential areas
88 of establishment are identified before populations reach damaging levels (Herms and
89 McCullough 2014; Caouette et al. 2024). Understanding the factors that influence
90 establishment is therefore critical for prioritizing surveillance, directing management
91 resources, and implementing preventive measures to slow the spread of the insect.
92 Furthermore, regions such as Atlantic Canada, where EAB invasion is relatively recent,
93 provide a valuable opportunity to examine the drivers of establishment during the early
94 stages of invasion, when management interventions may still be effective, making EAB
95 an ideal study system to test species establishment modelling. Previous models of species
96 establishment and spread addressed either large-scale species distribution or local-scale
97 population spread, overlooking critical demographic and dispersal processes that drive
98 the establishment of invasive species (Lustig et al. 2017).

99 Here, we explore two ecological phenomena relevant to forest insect establishment
100 characteristics that are not commonly accounted for in risk models but are known to
101 theoretically and empirically influence establishment: post-dispersal survival (through the
102 timing of firewood arrival) and Allee effects during population establishment. We

developed a risk assessment model that simulates EAB dispersal based on assumed characteristics of firewood movement by campers in the Maritime provinces. We used this model to better understand the influence of timing of firewood arrival and its consequences for insect survival and the ability of newly introduced populations to overcome local mate-encounter Allee effects on establishment and spread. We examined differences in the predicted establishment probability under low and high Allee effect thresholds, and with respect to timing of arrival. We predicted that a low likelihood of EAB larvae emerging before firewood is burned and a high Allee effect threshold would decrease overall EAB establishment probability. Subsequently, we conducted a global sensitivity analysis to determine which factors of EAB ecology and camper travel trends most influenced establishment probability. Our model indicated that the ability to overcome the Allee effect threshold most significantly contributes to successful EAB establishment.

Methods

Study Species

Emerald ash borer 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 (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 adults live for 3-6 weeks, during which time they feed on ash leaves, locate conspecifics, and mate (Herms and McCullough 2014). Following mating, gravid females oviposit into bark crevices and other protected areas on the trunks of ash

125 trees. Larvae feed on the inner bark and sapwood, with most larvae overwintering as 4th
126 instar prepupae (Bauer et al. 2003).

127 **Model Overview**

128 We modelled the dispersal and distribution of EAB using movement of infested
129 firewood from Maritime (New Brunswick, Nova Scotia, and Prince Edward Island,
130 Canada) population centres to campgrounds, and between population centres. We
131 conceptualised movement as a sequence of steps. All uninfested population centres and
132 campground began at the susceptible step. Dispersal steps between population centres
133 and campgrounds were represented as arrival, introduction, and establishment (Fig. 1),
134 each step having a conditional probability of success. "Arrival" is the probability that a
135 single piece of EAB-infested firewood (~40 cm long) is transported to an uninfested
136 location. For simplicity we do not model the number of larvae in a piece of infested
137 wood; conceptually, the distribution of numbers of larvae can be thought of as implicit in
138 the probability of an infested piece of wood. "Introduction" is the probability that EAB
139 emerges from an infested piece of firewood at a phenologically appropriate time, i.e.,
140 when food and time are available for beetles to successfully complete development, mate,
141 and oviposit. Establishment is the probability that enough EAB emerge from infested
142 firewood and oviposit at a site to overcome the Allee effect threshold. The "Allee effect
143 threshold" is the population density below which population growth is limited due to low
144 mating opportunities and high predation rates (Courchamp et al. 1999; Liebhold and
145 Tobin 2008).

Our model simulated the movement of infested firewood from 28 origin population centres (indexed by *i,* see Fig. 2) to 314 destination campgrounds (indexed by *j*, see Fig. 2). The parameterization of the model began with five Maritime city population centres with known established populations of EAB as of 2021 (Edmundston, Fredericton, Moncton, and Oromocto, NB and Halifax, NS) from where EAB-infested firewood can spread. We modeled 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 to represent the likelihood that EAB survives. Lastly, we modeled establishment based on the probability that enough beetles from infested firewood emerged to surpass the Allee effect threshold for establishment to occur.

We also included establishment of new EAB populations to population centres in the model. The model assigned one new population centre to become infested with EAB each year based on population size and tourist travel between counties.

Model Parameterization

Per Capita Campground Reservation Rate

We begin by estimating the way campers travel from cities to campgrounds. We do so by estimating the combined number of camping reservations made to all campgrounds in the Maritimes, and in the next section we distribute these reservations to all campgrounds based on a gravity model. We used residents' postal codes from campground reservations made at provincial parks in New Brunswick to model the number of reservations that a given Maritime city population centre would contribute to

all campgrounds together as a linear function of that Maritime city population centre size. Camper reservation data was provided by Parks New Brunswick and included reservations made from 2015 to 2019. We compiled all the reservation-related data using ArcGIS (version 10.4). We collected the location of campgrounds and Maritime city population centres using Google Earth Pro (version 7.3.4.86, Google LLC, California, USA). We gathered the city population centre size from the Maritime provinces with at least 5,000 residents (Statistics Canada 2017). We found that the population size of a Maritime city population centre was a good predictor of the number of reservations made to campgrounds (r^2= 0.71, p=0.001) with an estimated per capita reservation rate "r" = 0.00167 yearly reservations per person.

Dispersal from Population Centres to Campgrounds

The number of pieces of EAB-infested ash firewood, O_i, leaving population centre i is assumed proportional to (1) the number of camping reservations/year, which is based on the population centre size P_i and the per capita reservation rate, r, (2) the probability that the camper brings firewood from outside the campground, s, which is assumed to be a constant s = 0.37, based on Jacobi et al. (2011) and (3) the probability that the firewood is ash and contains live larvae or pupae, b, which is assumed to be a constant b = 0.049, based on Haack et al. (2010) (Eq. 1a in table 1). Both constants, *s and b*, will be varied in the sensitivity analysis to help determine their influence on the output of the model. We use O to denote the vector of the number of pieces of EAB-infested ash firewood leaving all population centres with an established population of EAB (for all campsites in total) (Eq. 1b in table 1).

Once we had determined the flow of infested firewood from Maritime city population centres, it was distributed to individual campgrounds based on a modified gravity equation. Gravity equations measure the degree of interaction between two locations and have frequently been used to estimate human transportation of invasive species (Schneider et al. 1998; Muirhead et al. 2006). We represent the attractiveness, $A_{ij,}$ of campground j to population centre i, as proportional to the number of campsites, $C_{j,}$ in a campground and the exponential decay curve equation of the distance, D_{ij}, between the Maritime city population centre and campground (Eq. 2a in table 1). The number of people travelling from a Maritime city population centre i to campground j is assumed to decrease by a factor of 2 for every 100 km of travel (Eagles et al. 2015). Some studies have shown that exponential decay curves overestimate camper reservations at short distances (Koch et al. 2012). However, we used the exponential decay curve regardless because in our model we aggregated locations into relatively large spatial areas. That is, we focused on longer-range dispersal, not local dispersal around an introduction point. This equation used the shortest road distance, d_{ij}, between the Maritime city population centre and the campground. To calculate road distance we used road and ferry segments from the National Road Network of the three Maritime provinces from the Government of Canada (Statistics Canada 2015) estimated using the Network Analyst extension in ArcGIS (ArcGIS Desktop 10.8.1).

With attractiveness defined, we now apply the gravity model to simulate the distribution of infested firewood leaving from each population centre (Oi) to campgrounds j based on the attraction between both locations (Aij) stochastically with

212 expected transportations to campgrounds equalling I_{ij} (Eq. 2b in table 1). We can measure
213 the arrival rate (I_j) as the total number of pieces of firewood arriving to campground j
214 from all population centres (Eq. 2c in table 1).

215 We generated lists of both public and private campgrounds for our study area. For
216 national and provincial public campgrounds, we used lists from government websites
217 (national park reservation websites, provincial park reservation websites, and
218 uscampgrounds.info). For private and municipal campgrounds, we composed lists from
219 campground owner and similar groups (e.g. Campground Owners Association of Nova
220 Scotia; Canadian Camping and RV Council; New Brunswick Campground Owners
221 Association; The Association of Atlantic RV Parks & Campground; Tourism PEI). For
222 public campgrounds, we collected data from the national parks' reservation websites,
223 provincial park reservation websites, and the uscampgrounds.info website.

224 **Dispersal Among Population Centres**

225 We modelled the dispersal of EAB from origin population centre *i* to destination
226 population centre *j* to better represent the establishment of new urban (source)
227 populations over time. The attractiveness, B_{ik} (Eq. 3a in table 1), of a Maritime city
228 population centre *i* to another population centre *k* is assumed as proportional to the
229 population, P_i, of population centre *i* and travel rates, M_{ik}, between population centers.
230 The matrix *M* is estimated using data from the Travel Survey of Residents of Canada
231 (Statistics Canada 2018), a major data source in measuring tourism between Canadian
232 counties. Using data from 2006 to 2017 (without 2012 because there was no survey that
233 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. Although travel data only measures travel among counties, larger Maritime city population centres (P_i >50 000) were all found in separate counties, and we assumed that most travel goes to the most populous centre rather than simply travelling to a smaller town. We denoted the total attraction to population centre k by TB_k and assumed this is the sum of attraction from each population centre (Eq. 3b in table 1).

Timing of Firewood Arrival

We modelled the effect of timing of firewood arrival on EAB establishment in campgrounds. For EAB adults to be present, infested firewood must arrive early enough for beetles to still be present but must remain unburnt until they can emerge. We used data from Tobin et al. (2021) to predict EAB emergence using degree days, the accumulated daily mean temperature over 10 degrees. We then calculated the probability that EAB have not yet emerged from firewood, N, based on arrival date, a_d, in julian calendar days using degree day data from Fredericton, New Brunswick in 2021, where peak emergence date, a_p, is estimated at 208 degree days (dashed line in Fig. 3, Eq. 4a in table 1). We assumed that the probability that firewood remains unburnt before all EAB had emerged, F, declines linearly from the beginning of the camping season to the end of EAB emergence (dotted line in Fig. 3, Eq. 4b in table 1). We estimated the probability that EAB successfully emerged from firewood H based on the arrival date (solid line in Fig. 3, Eq. 4c in table 1), by calculating the product of the probability of EAB emergence from firewood, F, and the probability of that firewood remaining unburnt. Finally, we

grouped emergence probability by month based on camping reservation data (bars, Fig. 3). There are seven possibilities: emergence in one of the six camping months, or mortality. The highest probability of EAB emergence is in July and the lowest probability in October.

We randomly allocated firewood to campgrounds according to a generalized normal distribution (Eq. 4d in table 1), which closely approximated the monthly reservations made by campers between the years of 2015-2020 (See supplementary figure 1). The fitted distribution captures seasonal camping reservation trends, with peak reservations occuring between July and August. To assess the importance of firewood allocation to variations in seasonal reservations, we varied the scale (σ) and shape (β) parameters during our global sensitivity analysis. These parameters control the spread and shape of the distribution from a normal distribution to a more uniform distribution to test for changes in evenness of reservations and their influence on EAB establishment probability (see supplementary table 1 for explanation of global sensitivity analysis parameter variables).

Allee effects

We estimated the probability that EAB successfully establishes based on a demographic Allee effect. We calculate the product of the probability that EAB emerges from firewood H and the number of pieces of firewood arriving to campground j, I_j, to give us the number of pieces of firewood from which EAB emerges at that campground, W_j (Eq. 5a in table 1). We then use a logistic function to model the probability that emerald ash borer establishes, E, based on the number of pieces of introduced firewood

with emerged EAB, W_j, and an estimated propagule size to overcome the Allee effect, W_0 (Eq. 5b in table 1). Probability of establishment is near zero if the number of pieces of firewood, W_j , is much smaller than the threshold W_0; the probability is approximately 50% if W_j is equal to W_0, and the probability approaches 100% if Wj is much greater than W_0. W_0 is not a deterministic threshold, as in some Allee-effect models, but rather the propagule size for which establishment and failure are equally likely.

Analysis

We performed three analyses of our model. First, we interpreted the arrival risk of infested pieces of emerald ash borer firewood to areas in the Maritimes, by simulating the dispersal of firewood over a 20-year period using our arrival model. We simulated 1,000 replications of the model and reported on the mean yearly arrival rate of infested firewood, Ij, (Eq. 2c from table 1) from all the campgrounds to spatially explicit areas within the Maritime provinces. Second, we conducted a local sensitivity analysis to measure the importance of timing of firewood arrival and the Allee effect threshold on the overall establishment of EAB from infested firewood. Finally, we conducted a global sensitivity analysis to measure the influence of uncertainties in the parameter values chosen during the creation of the model. The model was implemented 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 (source code is available on our Dryad repository).

We grouped campgrounds into spatially explicit areas given the high likelihood of dispersion to adjoining campgrounds following emergence. In ArcGIS, we defined a

300 clustered 4.5 million square kilometre grid of hexagons encompassing all the Maritime
301 provinces (Fig. 2). Hexagons were removed from the analysis if they did not contain a
302 campground. We reported the mean risk that EAB infested firewood is transported into
303 these spatially explicit areas (hexagons) using the arrival rate, represented as the mean
304 yearly firewood being transported to all campgrounds in the area.

305 Our model did not incorporate the distribution of ash in Maritime forests as a
306 parameter for establishment. However, to better understand the risk EAB poses to ash
307 populations in the Maritime forests, we collected data on the distribution of ash in these
308 forests (Beaudoin et al. 2014). From this, we extracted stand-level abundance as a
309 percentage of total forest cover at a 250 m^2 resolution for green ash (*Fraxinus*
310 *pennsylvanica* Marsh.), white ash (*Fraxinus americana* L.), and black ash (*Fraxinus*
311 *nigra* Marsh.). We imported the files into ArcMap and calculated the total abundance of
312 the three species. To better view the abundance of forest plots, we resampled the
313 abundance of ash to 1 km^2 and then overlayed the ash composition over the introduction
314 probability of EAB. We visually compared the probability of EAB transportation with the
315 distribution of ash stands to understand high-density ash stands that are most at risk to
316 EAB.

317 We used a local sensitivity analysis to estimate the influence that timing of firewood
318 arrival and the Allee effect threshold have on the probability of EAB establishment in our
319 model. We analyzed this by including and excluding the timing-of-firewood-arrival
320 submodel *I* (Eq. 4c in table 1), which measures the probability that emerald ash borer
321 emerges from firewood based on the month of firewood arrival, and varying the Allee

effect threshold W_0 (Eq. 5b in table 1). We simulated four scenarios (Table 2), with low and high Allee thresholds and including and excluding timing of firewood arrival. We performed 1000 replications of the simulation for each scenario. We compared the mean proportion of established hexagons among scenarios using a two-way ANOVA.

We conducted a global sensitivity analysis to understand which parameters most influenced model outcomes. 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). We performed 60,000 replications of the simulation where input parameters are varied simultaneously. We represented the parameters' influence on the proportion of EAB establishment into our spatially explicit areas using 95% confidence intervals.

Results

Our model predicted that central Nova Scotia, central Prince Edward Island, and southeastern New Brunswick have the highest arrival rate of EAB-infested firewood, >25 EAB-infested pieces per year (Fig. 2). Because this simulates arrival, not establishment, it is best seen as a measure of introduction risk rather than infestation risk. Specifically, this included areas near Halifax, Moncton, and Charlottetown. Generally, areas at highest risk of introduction are adjacent to the largest population centres of each province. The risk of transportation to Prince Edward Island was highest in the central region of the island (>25 EAB-infested pieces per year) and slightly lower in the northwest and southeast regions of the island.

344 The distribution of the three ash species in the Maritimes is generally sparse (<1%).
345 In the Wolastoq (Saint John) River Valley and in the Northern Kespukwitk (Annapolis
346 Valley) region in Nova Scotia, values may range from 1-5%, peaking at 19% of forested
347 area. Ash distribution is also generally sparse throughout northeastern Nova Scotia,
348 eastern New Brunswick, and Prince Edward Island. Southwestern Nova Scotia and
349 southern New Brunswick have the most high-risk locations where the model predicts
350 high flows of infested firewood into areas where significant wild ash populations are
351 present (Fig. 2).

352 In the local sensitivity analysis, we found that the timing of firewood arrival (Fig. 4),
353 Allee effect threshold parameters, and their interaction all significantly affected the
354 probability of EAB establishment (Table 3). A higher Allee effect threshold decreased
355 EAB establishment probability by 33%. Including timing of firewood decreased the
356 probability of EAB establishment by 7%. Including both a high Allee effect threshold and
357 timing of firewood arrival caused the largest decrease in EAB establishment probability
358 (74%). With a high Allee effect threshold and timing of firewood arrival, the only areas
359 that retained high establishment probability were adjacent to large Maritime population
360 centres, with a very low establishment probability outside those areas (see Supplementary
361 figure 2).

362 Using the global sensitivity analysis, we found that the impact of the Allee effect
363 threshold on the probability of EAB establishment was 10-fold higher (95% CI
364 [0.68,0.76] than the incidence of live borers, which ranked second (95% CI
365 [0.057,0.098]), followed by firewood source (95% CI [0.037,0.067]) (Fig. 5). The

366 interaction between any two parameters did not significantly change overall EAB
367 establishment probability in our model.

368 **Discussion**

369 Long distance movement and establishment of new populations of EAB occurs
370 predominantly via transport of infested firewood and nursery stock (Muirhead et al. 2006;
371 Herms and McCullough 2014). The rapid spread of this insect across the eastern USA
372 and into Canada since its detection in Detroit, Michigan in 2002 (Cappaert et al. 2005;
373 Siegert et al. 2014; Ward et al. 2020; Sambaraju et al. 2025) led to several predictive
374 models to facilitate risk assessment and pest surveillance. Climate (DeSantis et al. 2012;
375 Cuddington et al. 2018), proximity to existing infestations (Muirhead et al. 2006;
376 Sambaraju et al. 2025), movement of infested firewood (Muirhead et al. 2006), human
377 population density (Sambaraju et al. 2025), and insect population management (Hudgins
378 et al. 2024) have been used as predictors of EAB spread. We incorporated factors that are
379 not commonly accounted for in risk models, including Allee effects and timing of
380 firewood arrival, to understand the importance of data relating to these factors for risk
381 assessment.

382 Our findings suggest that predicted spread of EAB will strongly depend on
383 population parameters at low densities, including the Allee effect threshold which had the
384 greatest impact on EAB establishment in both our local and global sensitivity analysis.
385 Allee effects refer to positive density-dependence between population density and
386 individual fitness (Allee 1938, 1949) and are recognized as important factors in the
387 establishment and spread of non-native species (Courchamp et al. 2008; Tobin et al.

388 2011). Our previous research found no evidence for a pronounced mate-finding Allee
389 effect in established EAB populations with low population densities (Caouette et al.
390 2024), suggesting that the Allee threshold for this insect is low – which may partially
391 explain its highly invasive spread in North America. Other factors for its invasion success
392 include naïveté of North American ash (Pureswaran and Poland 2009), low levels of
393 natural enemy control (Gould et al. 2015), continued movement of ash across
394 jurisdictions, and high costs and challenges of implementing regulatory measures to curb
395 wood movement (Cappaert et al. 2005; Hope et al. 2020). In general, Allee effects in
396 insects are difficult to measure, making it challenging to include them in establishment
397 models. This is particularly true of mate-finding failure, because sampling individuals to
398 determine mating status is challenging at low densities (Kramer et al. 2009). For EAB, a
399 pheromone emitted by females and perceived by males ((3Z)-dodecen-12-olide ((3Z)-
400 lactone) (Silk et al. 2019) could enable mate-finding at low densities (Pureswaran and
401 Poland 2009). Further, emerging brood can re-attack the natal tree for a few generations
402 (Liu et al. 2003), facilitating mating within small populations on infested trees,
403 potentially allowing a nascent population to overcome Allee effects.

404 Experimental studies have highlighted the importance of incorporating population
405 parameters such as propagule pressure, survival of individuals and population dynamics
406 to determine establishment success in invasive species (Britton and Gozlan 2013;
407 Brockerhoff et al. 2014; Duncan 2016; Chase et al. 2023). However, challenges of
408 studying populations for which Allee effects are measurable still prevail (Gascoigne et al.
409 2009; Kramer et al. 2009; Régnière et al. 2012). For invasive forest insects, empirical

410 data on demographic and component Allee effects as well as Allee thresholds that favor
411 establishment are lacking (Chase et al. 2023) and Allee effects are therefore not generally
412 incorporated into predictive models (Lewis and Kareiva 1993). Empirical data on
413 populations at early phases in their invasion could decrease uncertainties in models of
414 forest insect establishment (Contarini et al. 2009; Zalewski et al. 2010) and improve
415 temporal estimates of population spread for more reliable early detection and eradication
416 opportunities.

417 From a practical perspective, we found that the interaction between the Allee effect
418 threshold and the timing of firewood arrival drove large changes in EAB establishment
419 probability in the local sensitivity analysis. While it is not easy to regulate and monitor
420 movement of ash wood, there is potential for nuanced regulation to make a difference.
421 Our model, for instance, shows that arrival of infested wood to an uninfested area at a
422 phenologically unsuitable time would *not* result in establishment of new populations. The
423 importance of arrival timing is supported by several theoretical studies that show its
424 impact on establishment success across taxa (Jerde and Lewis 2007; Leung et al. 2012;
425 Pili et al. 2024a). For example, in cane toads, *Rhinella marina*, timing of arrival relative
426 to breeding phenology is important in the establishment success of small founding
427 populations (Pili et al. 2024b). Similarly, seasonal restrictions were employed for forest
428 products to reduce the movement risk of the pine shoot beetle, *Tomicus piniperda*, in the
429 early 2000's (Poland et al. 2002). Therefore, implementing seasonal restrictions on the
430 movement of firewood could reduce the risk of establishment of populations to new
431 regions. The Government of Canada now defines high (April 1-September) and low risk

(October 1-March 31) periods and restricts the movement of many types of ash products moving out of regulated areas (Canadian Food Inspection Agency 2026a). While transport of ash firewood from regulated areas always remains prohibited, the transport of ash firewood remains unrestricted outside regulated areas. Despite prohibition of firewood transport, EAB continues to disperse to new counties and provinces across Canada (Canadian Food Inspection Agency 2026b), probably due to lack of surveillance of firewood movement.

We additionally found that arrival risk is high near large population centres, making travelling distance an important predictor in EAB establishment. EAB, like many species, 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, the most important means by which new regional foci of expansion are established (Ward et al. 2020). Our results suggest that there is value in predicting where new populations are more likely to establish. Understanding transport mechanisms can help: for EAB, transportation risk can remain high even for some areas far from large population centres, because those areas have attractions that bring in campers. Eastern New Brunswick and the northern Kespukwitk region in Nova Scotia are good examples of regions that have many large campgrounds (Caouette 2024). It is important to determine such areas as priority for surveillance of new populations of EAB in the Maritimes.

Our model does not include ash abundance as a parameter of EAB arrival or establishment, despite that being theoretically important for invasive species survival and

454 establishment (Jerde and Lewis 2007; Leung et al. 2012; Duncan 2016). Instead, we
455 visually compared the distribution of ash density to our EAB arrival risk model. This
456 omission from our model could overestimate the probability of EAB establishment in
457 areas with low ash abundance, such as the northern tip of Prince Edward Island, and may
458 underestimate establishment probabilities in areas of high ash abundance, such as the
459 Wolastoq River Valley. Future models should incorporate the distribution of ash trees
460 near campgrounds (from forest composition data; e.g. Beaudoin et al. 2014) to include
461 the probability that emerging EAB will find a suitable host for mating and oviposition.

462 Ash distribution data will be important for another reason as well: areas with
463 abundant ash, but with low risk of EAB transportation and establishment may act as
464 refugia for ash populations as the invasion continues to spread (Selwood and Zimmer
465 2020). These regions may retain mature trees and a large amount of genetic diversity
466 which could contribute to future ash recovery. One such area is the northwestern
467 Wolastoq River Valley, which has a high proportion of ash but contains only a few
468 campgrounds and is far from major population centres. Such refugia may be especially
469 important for black ash, which is commonly found in wet soils near rivers and is an
470 important source of wood fibre for Indigenous communities for basket weaving,
471 snowshoe frames, and canoe ribs (COSEWIC 2018). The northwestern Wolastoq River
472 Valley may also be important for conservation because all three Maritime ash species are
473 at the northeastern edge of their North American distribution there, which may make
474 these populations better adapted to extreme climatic events (Rehm et al. 2015). However,
475 this potential refugium may still be at risk of EAB dispersal from established populations

476 in the north near Edmundston and to the southeast around Fredericton. These areas
477 should be monitored and protected as they are important for cultural and ecological
478 conservation.

479 Wood movement for home heating may also vector forest insect dispersal (Solano et
480 al. 2021), and in the Maritimes firewood accounts for approximately a quarter of fuels
481 used for heating homes (Statistics Canada 2013). While our model considers firewood
482 transportation for recreation, it does not consider household heating. However, we
483 suggest that including wood transport for home heating would not significantly change
484 the establishment probability of EAB, because wood for heating homes is transported less
485 frequently and over shorter distances than recreational firewood (United States
486 Department of Agriculture Animal and Plant Health Inspection Service 2010).

487 Educational campaigns, such as providing flyers or writing emails to campground
488 users, can potentially decrease long distance dispersal (Solano et al. 2022). However,
489 modelling of firewood transport from Ontario, Quebec and Manitoba has shown that
490 unless the rate of spread is slow and intervention strategies are well-funded,
491 transportation of infested firewood is unlikely to decrease (Jentsch et al. 2020). We
492 believe that EAB spread may be slower in the Maritimes because human population
493 density is lower than in other regions of North America. However, a significant
494 investment in education and enforcement would still be required to slow the spread of the
495 beetle.

Overall, our study indicates that by incorporating transportation, insect survival, and population dynamics into risk assessment models, we can more accurately predict dispersal and spread of invasive forest insects in new habitats.

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748

Figures and Tables

Table 1. Equations used in the model development with equation numbers referenced in the text.

Equation Reference	Equation
1a	$O_i = r\ P_i\ s\ b$
1b	$O = [O_1\ O_2\ \vdots\ O_n\ ]$
2a	$A_{ij} = C_j\ 2^{-\frac{d_{ij}}{100}}$
2b	$I_{ij} = O_i A_{ij}$
2c	$I_j = \sum_{i=1}^{n} O_i\ A_{ij}$
3a	$B_{ik} = P_i\ M_{ik}$
3b	$TB_k = B_{1k} + B_{2k} + \cdots + B_{nk}$
4a	$N = \frac{1}{1 + e^{0.135(a_d - a_p)}}$
4b	$F = -0.009x + 2.22$
4c	$H = FN$

4d	$R_j = \left(\frac{\beta}{2\sigma\Gamma\left(\frac{1}{\beta}\right)}\right) exp\left(-\left(\frac{V-7.483}{\sigma}\right)^{\beta}\right)$
5a	$W_j = HI_j$
5b	$E = \frac{1}{1+e^{(W_0 - W_j)}}$

752

753 Table 2. Establishment characteristics of the emerald ash borer for four scenarios of risk

754 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)

755

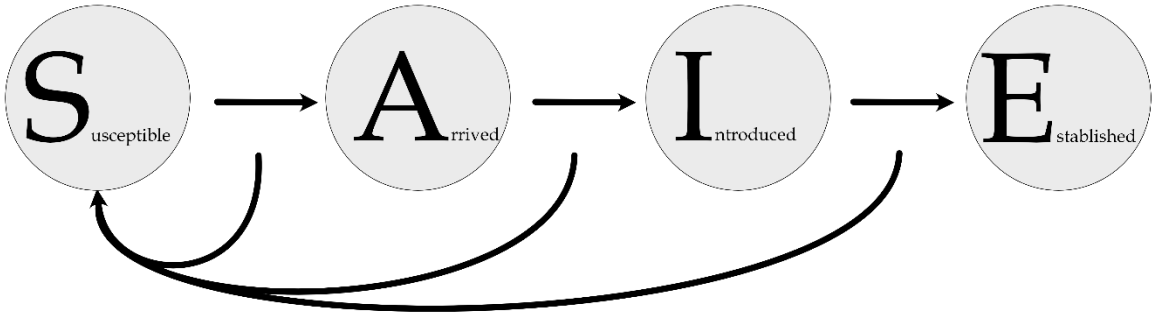
756

757 Table 3. ANOVA table measuring the impact for two establishment characteristics,

758 timing of firewood arrival and Allee effect threshold.

	Sum of squares	df	F-statistic	P-value
Timing of firewood arrival	57.1	1	75,697.5	1.0E-6
Allee effect threshold	250.7	1	332,624.2	1.0E-6
Interaction of timing of firewood arrival and Allee effect threshold	28.4	1	37,702.9	1.0E-6
Residual	3.0	3996		

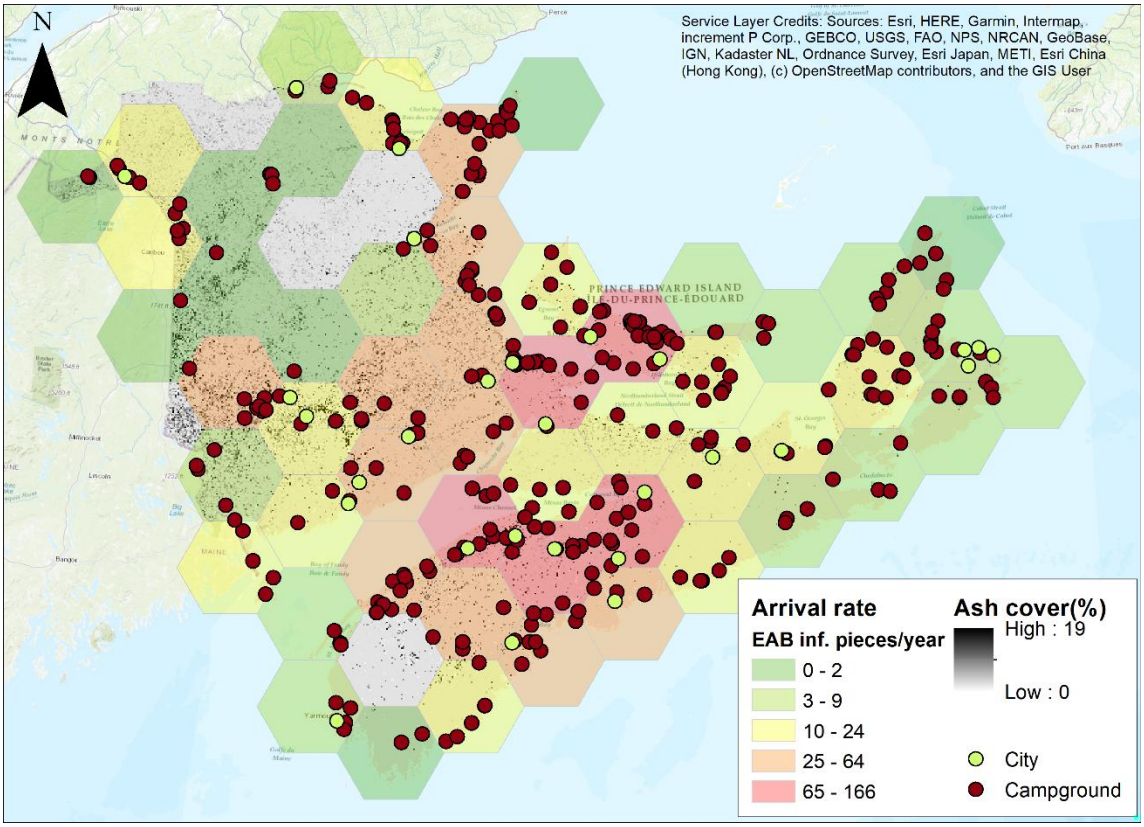
759



760

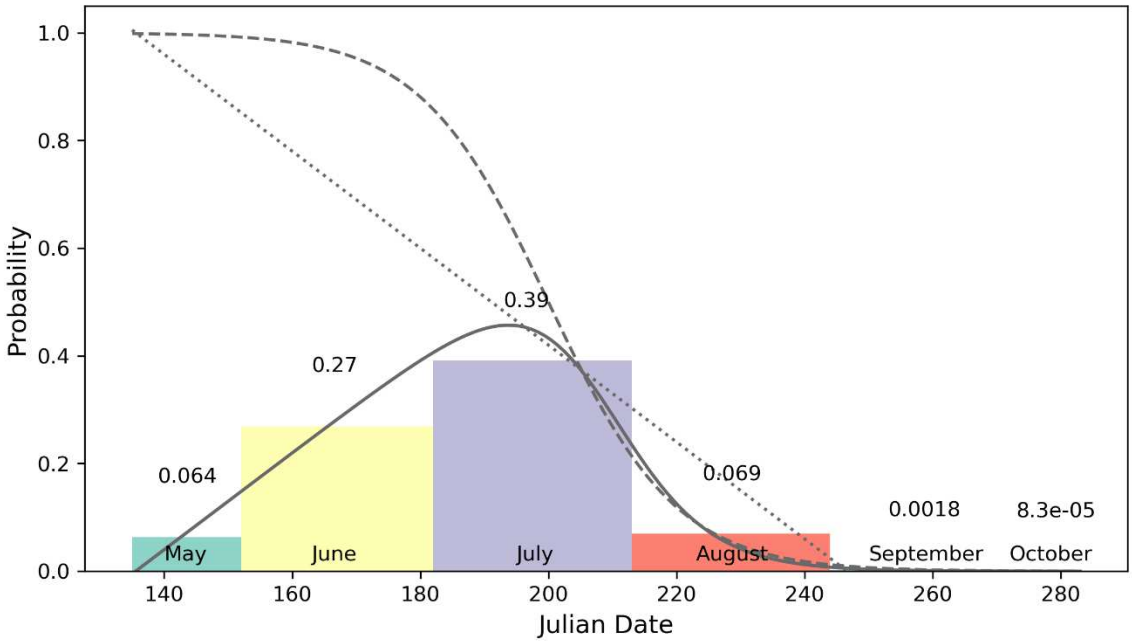
761 Figure 1. Steps in emerald ash borer establishment into a new location . “Arrived” is the
762 probability that a piece of ash-infested firewood is transported from a city to a
763 campground. “Introduced” is the probability that emerald ash borer can survive in
764 firewood based on the timing of arrival at a new location. “Established” is the probability
765 that there are sufficient individuals from introductions to surpass the Allee threshold and
766 establish.

767

768 

769 Figure 2. Probability of EAB introduction into Maritime provinces - New Brunswick,
770 Prince Edward Island, and Nova Scotia. Green dots represent cities with a population >
771 5,000. Red dots are campgrounds. Colours of hexagons indicate the mean arrival rate of
772 EAB-infested firewood pieces each year. Percent of ash forest cover is represented as a
773 greyscale of square grid cells measuring 1 km^2.

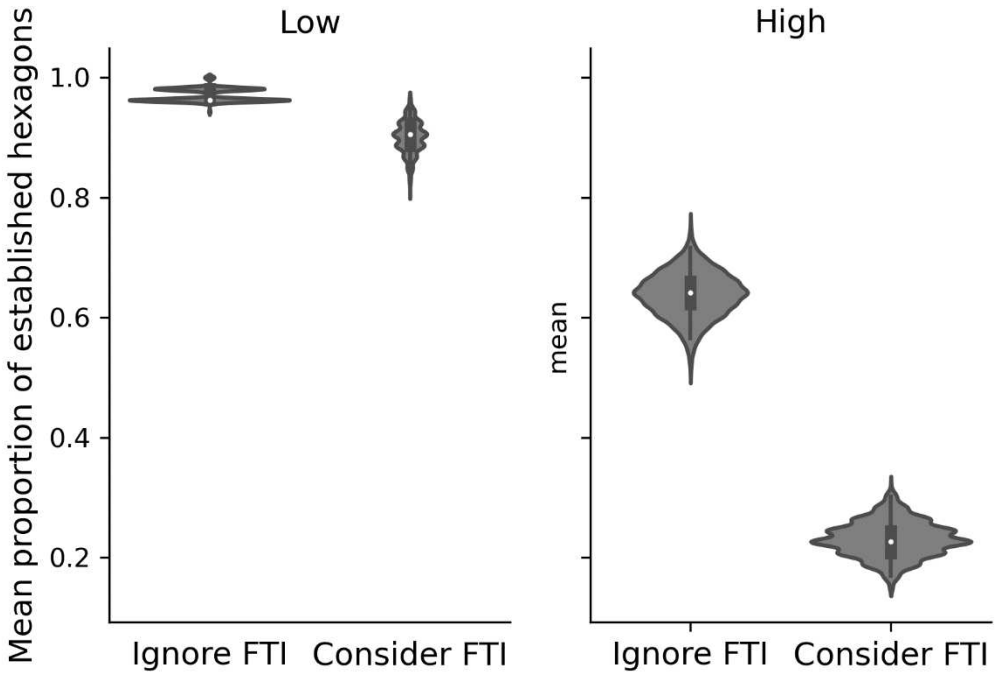
774



775

776 Figure 3. Temporal patterns of EAB introduction probability from firewood. Lines
777 represent the product of the proportion of emerald ash borer left to emerge (dashed line)
778 and probability that firewood is burnt before the end of emerald ash borer emergence
779 (dotted line). These are combined to calculate the probability that emerald ash borer
780 emerges from unburnt firewood (solid line) at a given arrival date. Bars represent the
781 mean monthly probability of emerald ash borer emergence from unburnt firewood, with
782 the value represented above each bar.

783



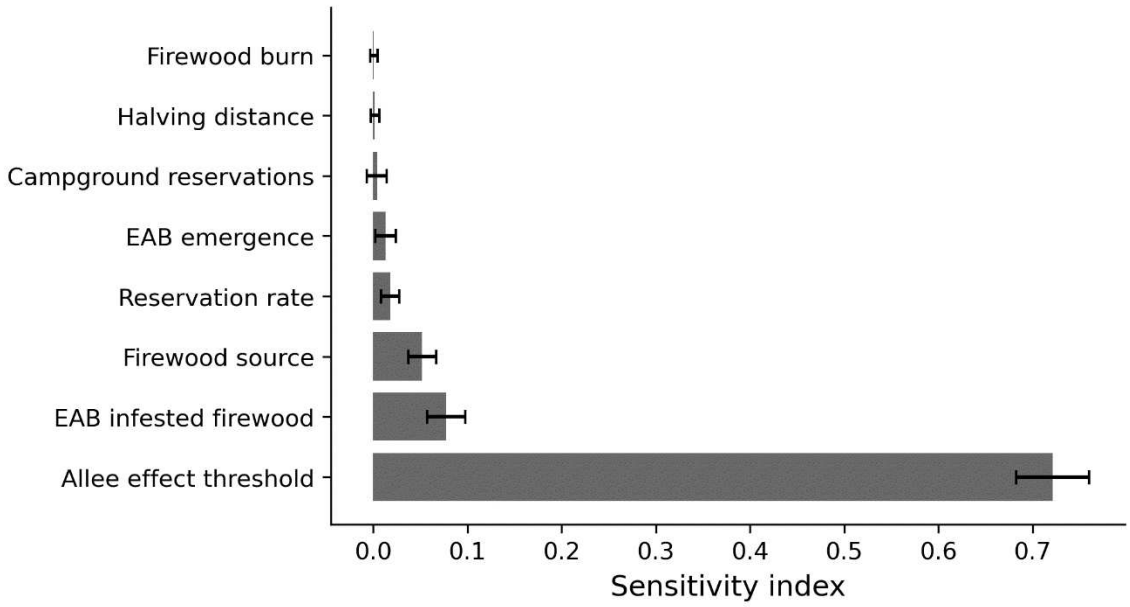
784

785 Figure 4. Mean proportion of established hexagons under four scenarios of timing of

786 firewood arrival and the Allee threshold. “Low” and “high” represent the strength of the

787 Allee threshold. FTI is timing of firewood arrival.

788



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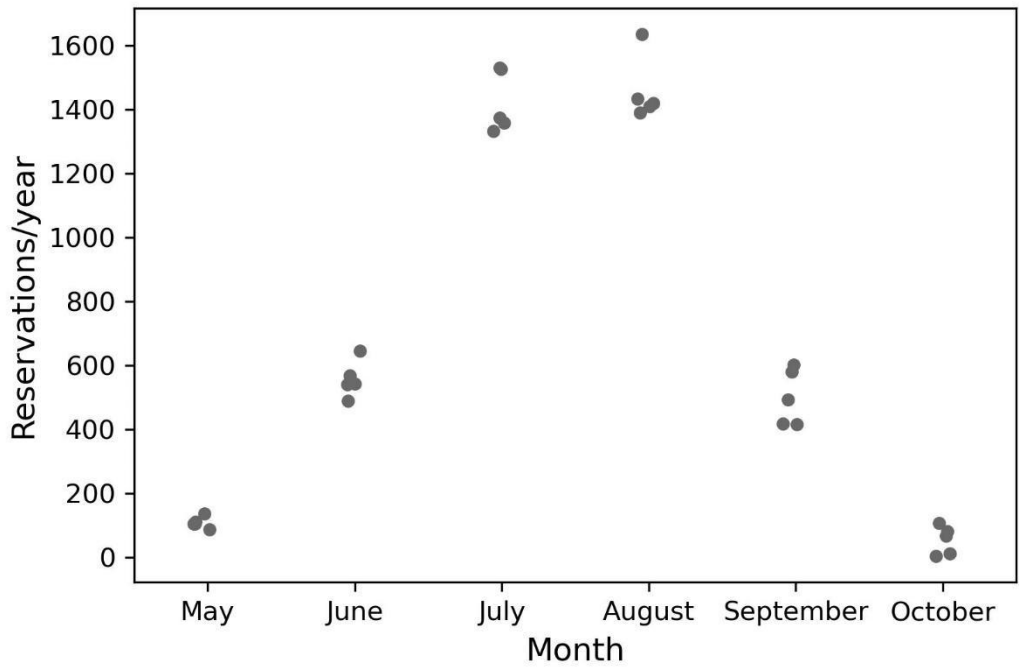
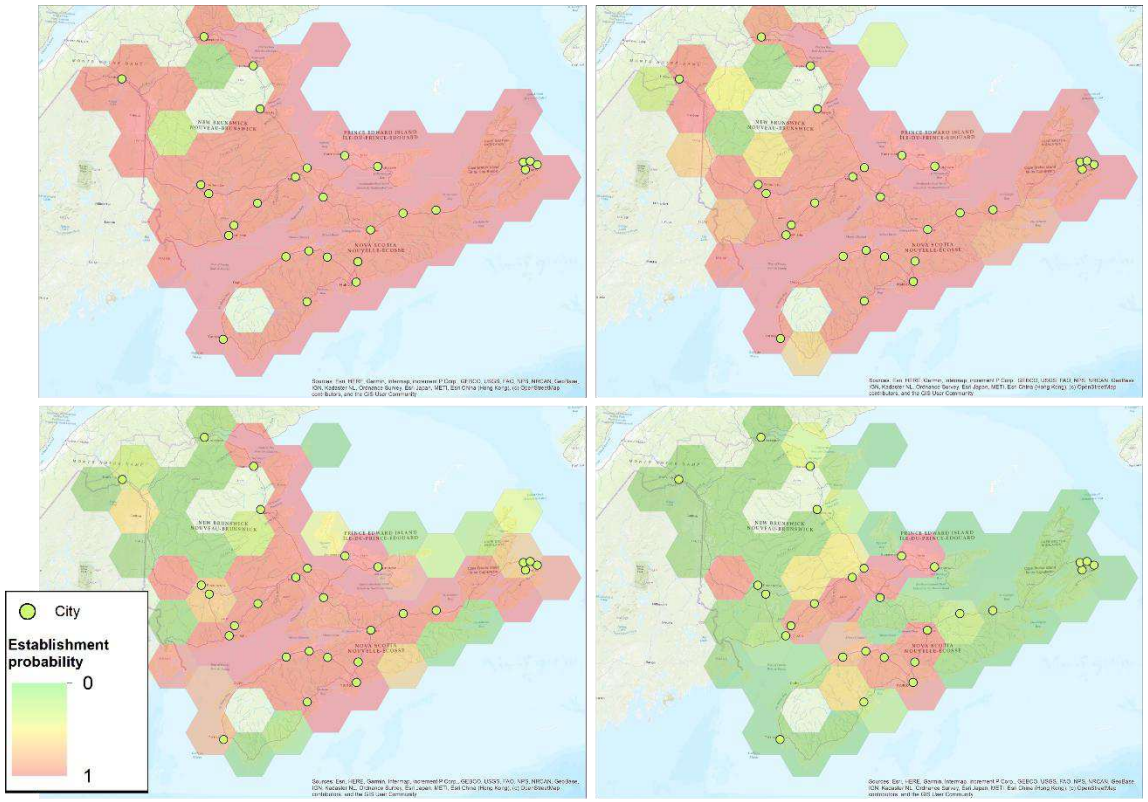
790 Figure 5. Sensitivity index of model parameters from the global sensitivity analysis run
791 for 20 000 replications. See supplementary table 1 for an explanation of parameters. Error
792 bars represent 95% confidence intervals

Supplementary Materials



Supplementary Figure 1. Monthly camping reservations made by campers from New Brunswick provincial parks between 2015 and 2020. Each dot represents the monthly reservations made per year.



Supplementary figure 2. Four scenarios of timing of firewood arrival and Allee threshold on establishment of 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; and d) High Allee effect threshold, consider timing of firewood arrival.

803 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 (D_{ij})	50km	400 km	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 (b)	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 (s)	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 (r)	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 (W_0)	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: σ) (2: β)	(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 (F)	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 (a_p)	-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

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

Halving distance: Literature has shown that campers travel more than 100 km 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.

Statements and Declarations

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Conflicts of interest

The authors have no relevant financial or non-financial interests to disclose

Data Availability

The Authors have provided an anonymized GitHub repository for the review process available here: https://anonymous.4open.science/r/EAB_Establishment_Model-EFF3/. Coding files may still have identifiers in them.

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