

Modelling framework for invasive pests: Emerald ash borer as a case study

Project Final Report



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Policy question: How can modelling aid preparation for potential bark beetle and wood borer invasion of Scotland?

Addressed by:

- Reviewing suitability of modelling results and frameworks in literature
- Recommendations on how these could be rapidly adapted for Scottish and UK plant health context
- Case study on Emerald ash borer to exemplify approach

1. Abstract

We conducted a systematic review of existing scientific articles which were specific to modelling approaches that predict the spread of wood borer insects. Using robust inclusion criteria to filter relevant articles we identified potential threats to Scotland that included Emerald ash borer (EAB), Eurasian spruce bark beetle, and various beetle species. In total we identified 1,655 articles with 66 focussed on EAB. No articles or models for Bronze birch borer were identified. We classified EAB studies by modelling approach (deterministic/mathematical; statistical; agent-based; and simulation based) and processes included dispersal and population dynamics or abundance of pest; Environmental factors, e.g. landscape or temperature data; and economic impacts, e.g. direct costs of implementing control methods. With particular reference to Scotland and the rest of the UK we used our findings about EAB to illustrate how modelling can be used to prepare for potential invasion e.g. in terms of assessing areas most vulnerable to establishment following introduction and how rapidly spread might occur following establishment. Much data needed for developing models to inform preparation for control of an EAB outbreak in Scotland is available including: Ash inventory and distribution maps (Centre for Ecology and Hydrology/Countryside Survey); EAB dispersal and demographic data (from research articles conducted in the USA/Canada through the United States Dept. Agriculture Forest Service and/or Canadian Forest Service), economic data relevant to ash (via a 2013 report about *Hymenoscyphus fraxineus* [causal agent of ash dieback] impact conducted by Defra). However, information and data related to the life history of EAB, i.e. factors that affect the dynamics of its life cycle are scarce and better life history data would make models more reliable. We found no models for the spread the EAB within Europe, including within the UK and no modelling studies concerning the dual threat to ash from EAB and *H. fraxineus*.

We therefore propose that models of wood borer species are developed which aid decision making from a policy perspective by highlighting the high-risk host species and susceptible regions. Models that predict the rate of spread of wood borers should also be developed to inform containment strategies at the national level. We also propose that models examining multiple threats to host species be developed e.g. EAB-*H. fraxineus* models. Such models should be generic enough to allow different host-threat species to be modelled should the need arise.

2. Executive Summary

This report is based on a literature review of modelling for bark beetle invasions globally and presents a summary of the information found along with our recommendations for further action.

2.1 *Bark beetle & wood borer pests – background*

Wood boring insects (hereby referred to as wood borers)¹, including bark beetles, represent a serious potential threat to Scottish forestry and tree health more widely. This is exemplified by Emerald ash borer (EAB) (*Agrilus planipennis*), which is a future threat to Scotland's ash trees (*Fraxinus excelsior*). The economic and societal damage from EAB in the USA is estimated to have cost US \$10.7-25 billion (McCullough & Mercader, 2012; Kovacs, et al., 2010). The pest is currently absent in the UK. However, EAB is spreading from the Moscow region through western Russia posing an increased threat to ash within Europe (Orlova-Bienkowskaja, 2014; Straw, Williams, Kulinich, & Gninenko, 2013) [Note: References are provided at end of the report].

2.2 *The role of modelling*

Models can be used to develop options for surveillance and control and are cheap compared to costs of real-world control operations. Therefore, even small resultant improvements are likely to be cost effective. All wood borer species require a host tree species with which to complete their life cycle but can have different life history and dispersal characteristics. However, many existing models for these share similar characteristics. It should be possible to design a sufficiently generic yet flexible modelling framework for wood borers that can be specified and parameterised for particular species and conditions as required. We were able to highlight potential models, identify what data would be required to further develop the models for Scotland and identify gaps in the research that are pertinent to Scotland.

2.3 *Recommendations*

As a first step towards a general model-based risk assessment for wood borer threats to Scotland we recommend:

- Models for the spread of EAB be modified for Scotland and the wider UK.
- Modified models be used to aid policy decisions and strategy required to prepare for an outbreak e.g. where to focus preventative resources most effectively and/or Map areas at high risk of an infestation establishing that could act as a “beach head” for a sustained invasion.

In the medium term we also propose to:

- Work towards a more general wood borer model that could be used for other pest species.
 - Case study: Given the information available for EAB we propose using an EAB model as a first approximation for Bronze birch borer (BBB) for which there is relatively little available information. This seems reasonable as EAB and BBB share attack characteristics despite requiring a different host.
- Develop model(s) to assess EAB outbreak impact including effects of ongoing *H. fraxineus* outbreak (ash dieback). Predictions for ash tree health and mortality (at risk from both threats) would aid development of policies and strategies for ash conservation. This research would benefit Scotland, rest of UK and continental Europe.

3. Introduction

Plant health in Scotland faces challenges posed by invasive plant pest and pathogen species. The economic, societal and ecological damage caused by such problems have been estimated as £15b for the current ash dieback epidemic (Kew, 2016; Hill, et al., 2019). Control of such potential threats is further complicated by difficulties associated with detection and delays

¹ Taxonomically bark beetles e.g. Eurasian spruce beetle, are “true weevils”, whereas wood-boring insects e.g. Emerald ash borer, are not. However, both taxonomic families bore larval galleries beneath tree bark to complete their life cycle and are considered wood borers.

between establishment of pests and any following action. Constant monitoring of invasion fronts is resource intensive, e.g. requiring wide-ranging surveys, whereas mathematical or statistical modelling can use existing data to inform or predict the spread of any threat that can be used to assess likely impacts and support and better target surveillance and control. The need to have a reliable modelling framework for any potential invasion is crucial for pre-emptive policy. For example, models can be used to identify or rank areas in terms of focal points from which a pest or pathogen, if introduced there, could best establish, i.e. develop a viable population capable of seeding new areas. An effective strategy prior to invasion will ensure resources are deployed effectively and efficiently to best mitigate negative effects of invasions. Mitigation is most likely effective during the early stages of invasion and therefore early detection is critical.

By reviewing the scientific literature, models can be identified for customisation to Scotland's needs, relevant to any particular pest, and/or new models can be developed. Critical information can also be identified e.g. data or parameter values that might be used to enhance the capabilities of these models in terms of precision and scope. Such models could then be used to inform policy and develop effective strategies to counteract potential impacts on plant health in a range of sectors including forestry, environment, horticulture and agriculture.

Woodland and forests cover over 1.4m hectares of Scotland, which is 18% of total land cover. Under new targets, Scotland's forest and woodland cover is set to increase to 21% by 2032. To meet with Scottish Forestry's 50-year vision, three main objectives must be met within 10 years:

- Increase forest and woodland's contribution to Scotland's sustainable and inclusive economic growth.
- Improve resilience of Scotland's forests and woodlands and increase their contribution to a healthy and high-quality environment.
- Increase use of Scotland's forest and woodland resources to enable more people to improve their health, well-being and life chances.

If these targets are to be met, then we must ensure that we have predictive capabilities for potential wood borer pest outbreaks in order to develop policies and strategies that will mitigate their negative effects on forests and woodlands (Government, Scottish, 2019) .

3.1 Literature review

Bark beetles and wood boring insects, such as the Eurasian spruce bark beetle and EAB, are a serious threat to Scottish forestry, woodlands and horticulture. We therefore conducted a systematic literature review of research surrounding the modelling of wood borer pests. From this review we have highlighted those studies that focussed on EAB. The review was based on a similar EFSA study conducted in collaboration with members of the Centre for Expertise on Animal Disease Outbreaks (EPIC) (MacCalman, et al., 2016). The studies were then categorised by the factors included and the modelling framework used. Taking this approach allowed us to determine which models could be used in a Scottish context and which data would be required to accomplish this.

3.2 Procedure

We developed a systematic procedure for assessing whether articles were useful. The search was conducted within Web of Science™ Core Collection which is known to be reliable (Haddaway, Collins, Coughlin, & Kirk, 2015). We decided against using other databases owned by publishers, e.g. Scopus, in case results were biased. On this basis, Google Scholar was also excluded since the search algorithm is influenced by previous searches and the method used by the algorithm is hidden from users.

We compiled a list of terms that would highlight relevant articles related to bark beetles and modelling from their published titles and abstracts. The list of search terms was sorted into the following categories:

- wood borer beetles
- forest
- modelling
- risk
- climate
- economic
- introduction
- establishment
- spread

We then used combinations of the above terms (and synonyms) to collect articles that were then assessed as useful based on our inclusion criteria. The inclusion criteria were constructed so that we could find articles that:

- included wood borers
- had some form of modelling component
- were recent (within the last 14 years, i.e. since 2006)
- had original research (only scientific articles and reports were considered whereas book chapters and conference abstracts were excluded)

Further details of the systematic search procedure and inclusion criteria are given in Appendix A.

3.3 Literature review results

The search was conducted on 29th March 2019 and included studies from 1st January 2006 up until the date of the search. The search produced 1,655 articles for inspection using our inclusion criteria. After filtering those articles, using their titles and abstracts, we found that 318 were worthy of examination in more detail. We found the following species categorisation within the literature as:

- 107 articles on Mountain pine beetle – *Dendroctonus ponderosae*
- 78 articles on Eurasian spruce bark beetle – *Ips typographus*
- 66 articles on EAB – *Agrilus planipennis*
- 1 article on Great spruce bark beetle – *Dendroctonus micans*
- 40 articles on various *Dendroctonus* species
- 0 articles were on Bronze birch borer – *Agrilus anxius*
- 11 articles were irrelevant or were not accessible
- 13 articles included studies on species that were spread across the above categories and required deeper searches.

Each of the articles were examined to determine whether they contained information useful for developing a modelling framework. We examined the articles on EAB in greater detail due to the urgent threat that this pest poses to Scotland and the results are summarised below.

4. Emerald ash borer

Emerald ash borer (EAB) is a wood borer beetle native to north-eastern Asia that feeds on ash trees (*Fraxinus*) as well as requiring ash to complete its life cycle. Adults bore through the outer layer of bark and deposit eggs within the phloem of the tree, on which the larvae then

feed until emergence as adults. The larvae create galleries underneath the bark in relative safety from predators. Within its native range EAB feeds on the native *Fraxinus* species, with infestation and mortality considered low (Valenta, Moser, Kapeller, & Essl, 2017). Within its introduced range, infestations and mortality are considered high (Valenta, Moser, Kapeller, & Essl, 2017). In severe infestations the larvae consume large amounts of phloem that effectively girdle the tree, with death occurring in a few years (Klooster, et al., 2014).

An infestation was first reported in Detroit in 2002 and 2003 and had spread to 25 US states and 2 Canadian provinces by 2015 – the entire north-eastern United States, becoming a serious pest to the native ash populations. EAB has also been reported in western Russia and using common ash (*Fraxinus excelsior*) as a host (Haack, et al., 2002; Baranchikov, Mozolevskaya, Yurchenko, & Kenis, 2008). Unlike its native range, *Fraxinus* species within the USA and Russia are highly susceptible, creating conditions for extensive infestations (Valenta, Moser, Kapeller, & Essl, 2017). By 2011, the Animal and Plant Health Inspection Service (APHIS) in the USA had spent US\$30 million per year since 2008 in efforts to minimise the damage caused by EAB. However, this figure is expected to grow (Kovacs, et al., 2010). Total estimates over a ten-year period have predicted costs ranging from US\$10.7 to 12.5 billion (Kovacs, et al., 2011). In the USA, there have also been reports of infestations of EAB in *Chionanthus virginicus*, which is a species used within British horticulture (Cipollini, 2015). Experimental evidence that EAB can feed on European olive, *Olea europaea*, has also been found (Cipollini, Rigsby, & Peterson, 2017) (Cipollini D. R., 2015).

Information about the westward spread of EAB from European Russia is scarce. The main host species in the UK is common ash but it is unknown whether two other ash species in Europe, the Southern European flowering ash (*Fraxinus ornus*) and the Narrow-leaved ash (*Fraxinus angustifolia*), are suitable hosts, the latter of which is wide-spread across the UK (Valenta, Moser, Kapeller, & Essl, 2017). The natural spread rate has been estimated at 6-10 km/year but EAB has actually advanced a total of 460 km in 10 years (Orlova-Bienkowskaja, 2014; Straw, Williams, Kulinich, & Gninenko, 2013). This discrepancy could have arisen because EAB was already present but undetected or from human-mediated dispersal. For example, EAB was discovered near the railway station at Michurinsk but was apparently absent from surrounding forested areas, which suggests they may have “hitch-hiked” on railway cars from other infested areas (Orlova-Bienkowskaja, 2014).

Symptoms of infestation include defoliation of leaves and leaf dieback as well as small D-shaped exit holes where adults emerge from the bark – see figure 1. Methods of controlling the spread of EAB include: tree felling and replanting, use of insecticides (*azadirachtin*, *imidacloprid*, *emamectin benzoate*, *dinotefuran*) (Herms & McCullough, 2014), and biological control (*Spathius agrili*, *Tetrastichus planipennisi*, and *Oobius agrili*, *Spathius galinae*) (Bauer, Duan, Gould, & Van Driesche, 2015). A procedure called SLow Ash Mortality (SLAM) (McCullough & Mercader, 2012) has been effective at slowing the spread of EAB although these measures do not eradicate the pests from affected regions. Therefore, being as prepared as is possible for immediate action, should there be an EAB discovery in the UK, is advisable.



Figure 1 – Symptoms of EAB infestation. Left *Agrilus planipennis* (emerald ash borer); exit hole from which an adult beetle has emerged; note the characteristic 'D' shape. Right: *Agrilus planipennis* (emerald ash borer); damage to an ash tree in the USA. Note thinning of the crown and browning of the foliage. ©David Cappaert/Bugwood.org - CC BY-NC 3.0 US

Links to web-based information sources about EAB can be found within Table 1.

Table 1 List of information sources of EAB

Resource	Description	Access
Forest Research	Details of EAB facts, e.g. how to report a sighting	https://www.forestresearch.gov.uk/tools-and-resources/pest-and-disease-resources/emerald-ash-borer/
UK pest risk register	Details of risk levels, potential hosts, pathways in the UK.	https://secure.fera.defra.gov.uk/p/hiw/riskRegister/search “Emerald ash borer”
Emerald ash borer information network	International information source about EAB based in the USA. Regularly updated with related research articles.	http://www.emeraldashborer.info

CABI invasive species compendium	International information source related to EAB. Contains many related research articles.	https://www.cabi.org/isc/datasheet/3780
USDA EAB datasets	Datasets collected by USDA related to EAB, e.g. risk maps of USA, genomic data	https://data.nal.usda.gov/search "Agrilus planipennis"
EAB UK contingency plan	Forest Research EAB contingency plan as of 2017	https://www.forestresearch.gov.uk/.../EABContingencyPlanUpdated26-09-2017.pdf
EPPO procedures of control	EPPO <i>Agrilus planipennis</i> : procedures for official control	https://gd.eppo.int/taxon/AGRLP L/documents
PREPSYS project	Forest Research research project for EAB	https://www.forestresearch.gov.uk/research/prepsys/

4.1 Categorising findings

We found 66 articles on EAB of which 30 contained modelling frameworks which could potentially be further developed for Scotland. The remainder of the articles were not related to modelling EAB and instead included reviews (many of the modelling articles within review papers were already highlighted for inspection by the literature review), experimental research or were solely examining ash regeneration and environmental effects that occurred after the arrival of EAB. A summary of the types of models and their characteristics are given in table 2.

Table 2-- Type of model and a description of the type

Type of model	Model type description
Deterministic Mathematical Models	Using equations to describe physical system that can best be interpreted quantitatively. Models can be parameterised with real data, but lack realistic landscape features. Analysis can provide conditions which determine different long-term dynamics.
Statistical models	Typically use empirical /correlative models to represent dynamics. Models require real data to estimate parameters for development of a descriptive model. Real landscape features are implicit within the data. Models can provide predictions based on previous behaviour of the physical system. Uncertainty can be quantified.
Simulation models (using iterative methods)	Model uses simple rules iterated over fixed time periods to develop predictions. Can be parameterised with real data. Real landscape features or data can be included. Models provide predictions for short or long-term dynamics, but causation of model outcomes are difficult to discern. Stochastic processes can be included.
Agent-based models (ABMs), also known as individual-based models (IBMs)	Models have the same description as simulation models since ABMs are simulations, but more detailed and complex. ABMs model the behaviour of individual organisms (agents) to make local predictions.

4.2 Modelled processes of interest

We further categorised the models to determine whether they included the following mechanistic factors:

- Dispersal/spread.
- Population dynamics or population densities.
- Environmental or climate.
- Economic.

Two of the most important factors related to assessing risks from an invading organism are dispersal and population dynamics. Taken together, dispersal and population dynamics constitute spread models. However, not all studies include dispersal or population dynamics and to develop useful models for risk assessment would require some information relating to either or both of these characteristics. Solely dispersal models were also included within the spread category. It is widely known that spread is influenced by environmental factors, including information from landscape, e.g. presence of host, and climate variation, e.g. temperature. An additional factor that is potentially critical to risk assessment is economic impact. We therefore also included modelling of economic impacts from invasion to find methods applicable to Scotland.

4.3 Summary of findings

Using our categorisation above we found that no methodology was favoured overall, with many studies using combinations of methods, e.g. a combination of statistical and simulation methods. There was a preference for predicting future spread of EAB with few studies modelling the general biology of EAB dynamics, e.g. models that predicted effects of climate on growth. Despite our best efforts at categorisation, most of the studies showed considerable overlap between the processes of interest, e.g. spread and population demographics or spread and economic impacts. Most examined a combination of two, with few examining three, and none examining all four processes. We provide a brief summary of the main messages here and provide more detail in appendices B-E. A cross tabulation of modelling techniques and model focus according to the above categorisations is shown in table 3.

4.3.1 Dispersal/spread models

Many of the models examined ‘spread’ using a variety of methods. The most popular of these used some form of dispersal kernel (a probability distribution that an organism disperses a particular distance). The most direct approach for modelling dispersal is to use a dispersal kernel. A dispersal kernel is a type of mathematical function describing probabilities or rates associated with organisms, e.g. an individual wood borer, moving from their current location to another, where typically local movements have higher probabilities than more distant movements. Dispersal kernels can be chosen (assumed shape and parameters) or parameterised from data (Lutscher & Musgrave, 2017; Kovacs, et al., 2010; Kovacs, et al., 2011). The most popular use of a dispersal kernel was the negative exponential parameterised in (Kovacs, et al., 2010), which other studies used to determine spread (Mercader, et al., 2016; Kovacs, et al., 2011). An example of the negative exponential dispersal kernel is given in figure 3.

Other researchers used fixed probabilities of dispersal, often within cellular models. These models use real landscape data that is divided into cells in which a population in one cell has a defined probability of infesting neighbouring cells. Anderson and Dragičević developed such a method through agent-based models (Anderson & Dragičević, 2016; Anderson & Dragičević, 2018; Anderson & Dragicevic, 2016; Anderson & Dragičević, 2015).

Gravity models have also been used in similar cellular environments. These models weight the distance between cells and establish a probability of dispersing that is maximal for neighbouring cells and decreases with distance away from the originating cell with a weighting given to population size. It is a method used by several studies for spread between regions within the USA (Prasad, et al., 2010).

The spread of EAB is associated with anthropogenic factors such as trade routes or the movement of firewood. Modelling methods exist to examine firewood as a factor, often by adding in additional probabilities of long-distance dispersal. Models using network approaches have also been developed to take account of road systems (Yemshanov, Koch, Barry Lyons, Ducey, & Koehler, 2012; Prasad, et al., 2010). However, patterns of EAB dispersal and spread are not well understood (Siegert, Mercader, & McCullough, 2015).

4.3.2 Population dynamics and demographics

A few limited studies modelled demographics, parameterising growth and carrying capacity (BenDor & Metcalf, 2006; McDermott & Finnoff, 2016). However, availability of data on the life history and demographics of EAB, which is important for modelling population dynamics, was generally limited. We are aware that Forest Research is collaborating with researchers in eastern North America examining life cycles and temperature dependency with respect to UK climate.

Many studies either used abundance data or presence-absence data to model EAB demographics to determine probability of spread from one location to another (Prasad, et al., 2010; Yemshanov, Koch, Barry Lyons, Ducey, & Koehler, 2012; Mercader, Siegert, & McCullough, 2012). This type of spatial demographic modelling was popular among simulation, ABM and software implementation of mathematical modelling approaches, e.g. STELLA or SME (BenDor & Metcalf, 2006; BenDor, Metcalf, Fontenot, Sangunett, & Hannon, 2006). This preference most likely reflects relative availability of spatial presence-absence.

4.3.3 Environmental modelling

We found that modelling impact of environmental variables on EAB was used extensively within Agent-based and simulation studies. This was achieved primarily using geographic information system (GIS) tools and data for real landscapes to develop predictions of future infestations. GIS allows geographic data (e.g. climatic conditions, species distributions, environmental data) to be stored, manipulated and analysed spatially in relation to real landscapes. Using GIS tools to assess data on ash distribution is useful for predicting future spread of EAB within real landscapes. Agent-based and simulation studies used either local sampling or forest inventories to collect ash distribution data. Environmental features were often measured using GIS data on the areas under investigation. See appendices D and E for detail.

We found two studies that used species distribution maps of EAB in its native range to estimate its climatic limits/requirements. This approach, whilst not without limitations, enables locations outside the endemic range to be characterised in terms of climatic suitability for EAB with resulting climate suitability maps considered as risk maps for vulnerability to invasion by EAB (Sobek-Swant, Kluza, Cuddington, & Lyons, 2012; Liang & Fei, 2014). Both studies used specially developed software MaxEnt and GARP, along with IPCC climate data/scenarios, to conduct their studies. These methods can also be used within the statistical programming language R using the appropriate packages (R Core Team, 2013; Hijmans, Phillips, Leathwick, & Elith, 2017).

We found one study that used aerial imagery alongside an ABM to determine local dynamics of EAB. The satellite imagery was used alongside presence-absence data to develop a model that could use such remote sensing data to track and predict EAB infestations (Zhang, Hu, & Robinson, 2014). Satellite imagery was used to diagnose symptoms of EAB infestation from tree canopies, which were then confirmed through field sampling.

4.3.4 Economic impacts

Economic analyses of EAB infestation and predictions were widespread. Many such studies focused on cost-benefit analysis scenarios related to implementing control procedures such as SLOW Ash Mortality (SLAM) (McCullough & Mercader, 2012). This strategy is applied within the USA to slow ash mortality from EAB infestation with an integrated combination of chemical treatment, tree girdling and utilising ash. The majority were predominately deterministic mathematical models that determined the economic value of a single ash tree, which was scaled up to the spatial scale of the study. Factors considered included direct costs, e.g. tree felling, health costs due to air pollution, and depreciation of house prices from reduced desirability associated with dead or dying trees (Epanchin-Niell & Liebhold, 2015;

Jones & McDermott, 2015; Jones, McDermott, & Chermak, 2016; Jones & McDermott, 2018; Kovacs, Haight, Mercader, & McCullough, 2014).

Also noted was the “EAB cost calculator” developed by Purdue University that will calculate the costs of EAB infestation over 25 years while providing management options (Sadof, Hughes, Witte, Peterson, & Ginzler, 2017). This tool requires ash inventory data and estimates of the cost of tree felling and replacement of ash.

Two authors explicitly examined costs of allocating surveillance resources optimally within the constraints of (say, annual) budgets which could prove useful (Yemshanov, Koch, Barry Lyons, Ducey, & Koehler, 2012; Yemshanov, et al., 2014; Withrow, Smith, Koch, & Yemshanov, 2015; Yemshanov, et al., 2015)

Table 3 -- Cross tabulation of modelling techniques and modelled processes of interest

Modelled process vs modelling technique	Spread	Population dynamics	Environmental	Economic impacts
<i>Deterministic mathematical models</i>	Dispersal kernels Gravity models (dispersal to closer locations more likely than farther locations)	Logistic-like growth	Good/bad habitat EAB-ash coupled equations	Cost-benefit analysis Terms for EAB control
<i>Statistical</i>	Probability of dispersal Empirical models fitted to field data	Estimations of population density from ash inventories Fitted models to field data Linear regression of collected field data	Temperature variations Air pollutant factors	Healthcare cost impacts Predicted reduced cost through control
<i>ABM/IBM</i>	Probability of dispersal (fixed or dispersal kernel)	Estimation of population density from ash inventories	GIS layers from physical locations	EAB cost calculator
<i>Simulation</i>	Probability of dispersal (fixed or dispersal kernel)	Estimation of population density from ash inventories	GIS layers from physical locations Generated cells	

4.4 What would be required for modelling EAB in Scotland?

If EAB arrived in Scotland there would be a great deal of uncertainty about how the insect would spread until its behaviour in Scottish conditions was observed; however, international experience suggests that the earliest possible action needs to be taken if there is to be any hope of eradication. However, we can use what details are available from the USA, assuming that its spread dynamics will be similar, to make informed predictions and enhance preparedness.

4.4.1 Suitability models

Approaches that could be taken include development of spatial models that simply seek to quantify suitability for EAB across Scotland, i.e. following introduction of EAB in locations where it is likely to establish viable populations capable of spreading to other areas. Such

models could be based on climate suitability and or habitat characteristics, most notably the distribution of ash trees. As noted, information on life history and demographic parameters is limited.

However, using the approach of (Sobek-Swant, Kluza, Cuddington, & Lyons, 2012; Liang & Fei, 2014) to develop an EAB suitability map for Scotland describing suitable locations for the pest, would require ash distributions and climate information, e.g. as available from WorldClim (Fick & Hijmans, 2017) or the Met Office. Such suitability maps could be improved as more life history data related to climate becomes available e.g. previously mentioned Forest Research projects in North America. The Scottish climate is markedly different from continental USA. Therefore, it is unclear how different EAB population dynamics would be in Scotland compared with those in the USA. However, we can use the limited parameterisations developed for modelling USA EAB population dynamics as a first approximation of how the beetle will behave in Scotland/the UK. In the event of EAB successfully establishing, presence-absence data from surveys can be used for coarse scale modelling, e.g. council boundaries, as has been conducted in the USA. Using aerial identification methods could prove problematic for identifying EAB since the symptoms of infestation are similar to ash dieback, which would mean that field surveys and citizen science observations would be a more reliable method of determining EAB presence.

We will require information related to ash populations in Scotland, e.g. ash distribution, typical distribution of tree trunk dimensions. Another important factor is *H. fraxineus* infection status, as any tree infested is likely to be stressed and at higher risk of EAB attack. Fortunately, data on *H. fraxineus* infection status exists (Maskell, Henrys, Norton, Smart, & Wood, 2013), including within the Forest Research open data archives and from Defra conducted studies of ash and *H. fraxineus* that have recorded information helpful to model construction (Defra, 2013).

A national-scale model can be constructed by dividing the Scottish landscape into a grid of locations such as that in figure 2. Such a model can be informed using ash inventories, e.g. CEH /Countryside Survey (Maskell, Henrys, Norton, Smart, & Wood, 2013), although such data is subject to uncertainty and may become outdated.

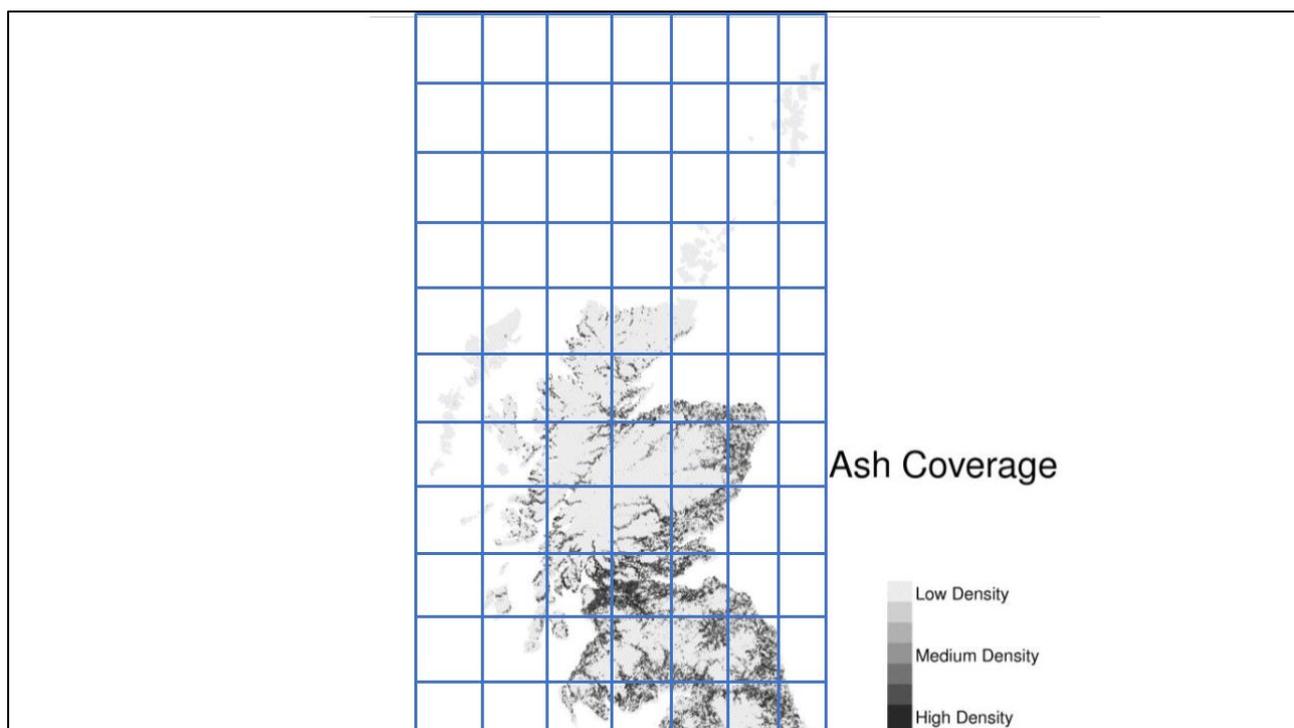


Figure 2 - Dividing Scotland into a suitable grid structure for national level analysis. Grid boundaries are illustrative and would likely be on a 10x10km scale. Image taken from Maskell, 2013

4.4.2 Spread models: combining suitability with dispersal

Spread models combine suitability information with model components that represent dispersal of the organism from one location to another. Probability of successful dispersal and establishment will depend on distance between source and destination and the suitability of both; highly suitable source locations are likely to produce greater numbers of dispersers and these are more likely to establish in a more suitable destination. In addition, distance can be measured in various ways, e.g. straight-line or by connectivity of road networks etc.

Dispersal data has been used to parameterise dispersal kernels, which we can use to our advantage. Other methods for human-aided dispersal that have been devised for use in the USA and Canada can also be considered.

Human-mediated modes of dispersal were an important factor within many studies. In the USA ash firewood, which was transported between forested locations and used as campfire fuel, was found to be an important vector for EAB spread. Such a scenario is unlikely within the UK, however, transportation networks have been shown to facilitate EAB invasions (Orlova-Bienkowskaja, 2014). Road maps for transport links could also be used from Ordnance Survey or Transport Scotland. It would also be useful to attain information related to movement of ash, such as nursery locations and sawmills, from Scottish Forestry, Forestry and Land Scotland, Forestry Commission and Forest Research.

Crucially, if an outbreak was recorded in the rest of the UK (or in Scotland), availability of times and locations of observed infestations would be useful in testing spread models and in informing improved estimates of the rate of spread to update models.

As shown by a pilot study conducted by the Plant Health Centre, models for spatial and temporal spread of invasive species across landscapes can be adapted to model the spread of bark beetles (Catterall, Cook, Marion, Butler, & Hulme, 2012). These use statistical techniques to simultaneously estimate dispersal kernels (reflecting human and other modes of dispersal) and suitability maps from data on observed spread, such as presence absence data in space

and time, along with climate and habitat data e.g. ash tree distributions. These models also quantify uncertainty in predictions and could potentially be applied to available data from the USA, with the resulting models used to predict both suitability and dispersal in the UK, including Scotland. Updating these with data from other locations invaded by EAB, including the UK, would also be possible. This approach could be applied to other pest species.

Parameterisations from research in the USA could then be used to determine a dispersal kernel for EAB dispersal from an infested cell to the surrounding cells. Due to the lack of information related to the life history of the borer, the distance from core infested cells has been used to determine abundance in neighbouring cells. An illustrative graphic is shown in figure 4.

Parameterisations could be provided from studies conducted in the USA. EAB densities have been calculated from field experiments that estimated the number of EAB larvae within trees, which are scaled to forest stands for an overall population density.

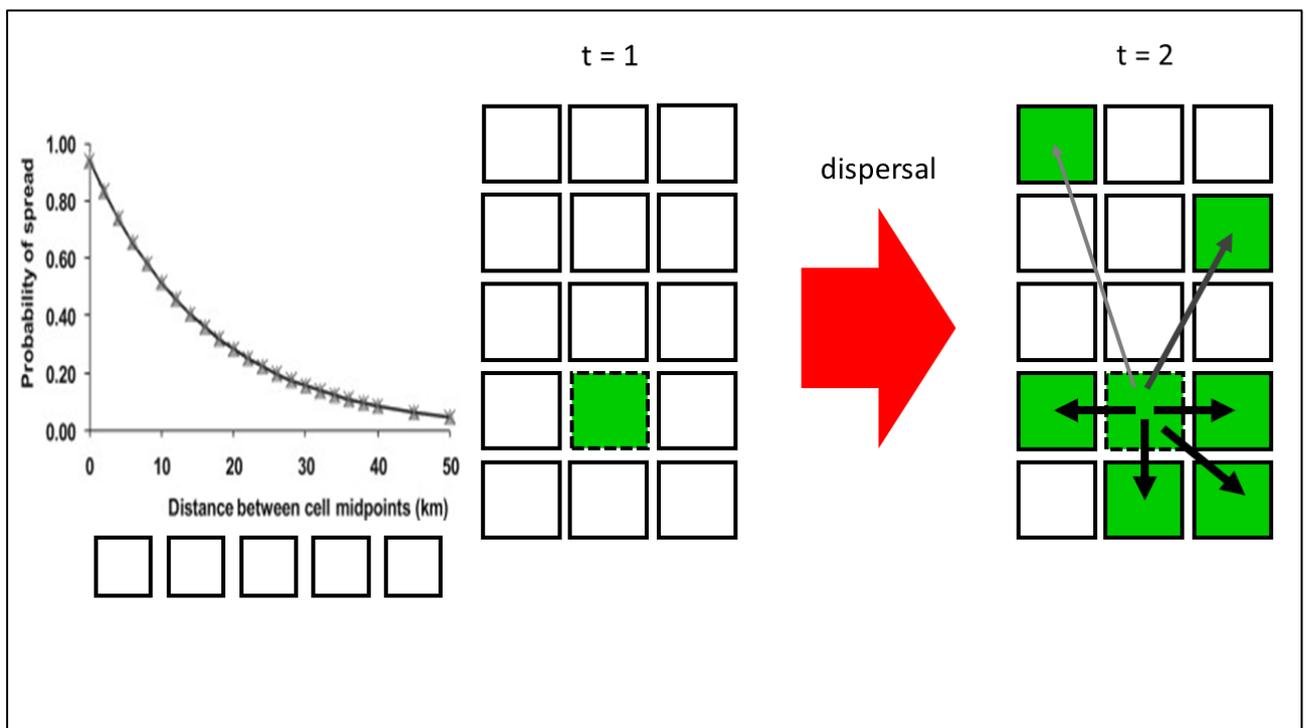


Figure 3 - Illustrative description of dispersal of EAB. Cells associated to the landscape are given a fixed length into which the dispersal kernel is divided. Dispersal kernel gives a probability of movement from one cell to another over a generation. Thicker, darker arrows represent more individuals dispersing. Lighter, thinner arrows represent fewer individuals dispersing. Dispersal kernel given in 1-D but can be scaled into 2-D. Dispersal kernel given in (Kovacs et al. 2011).

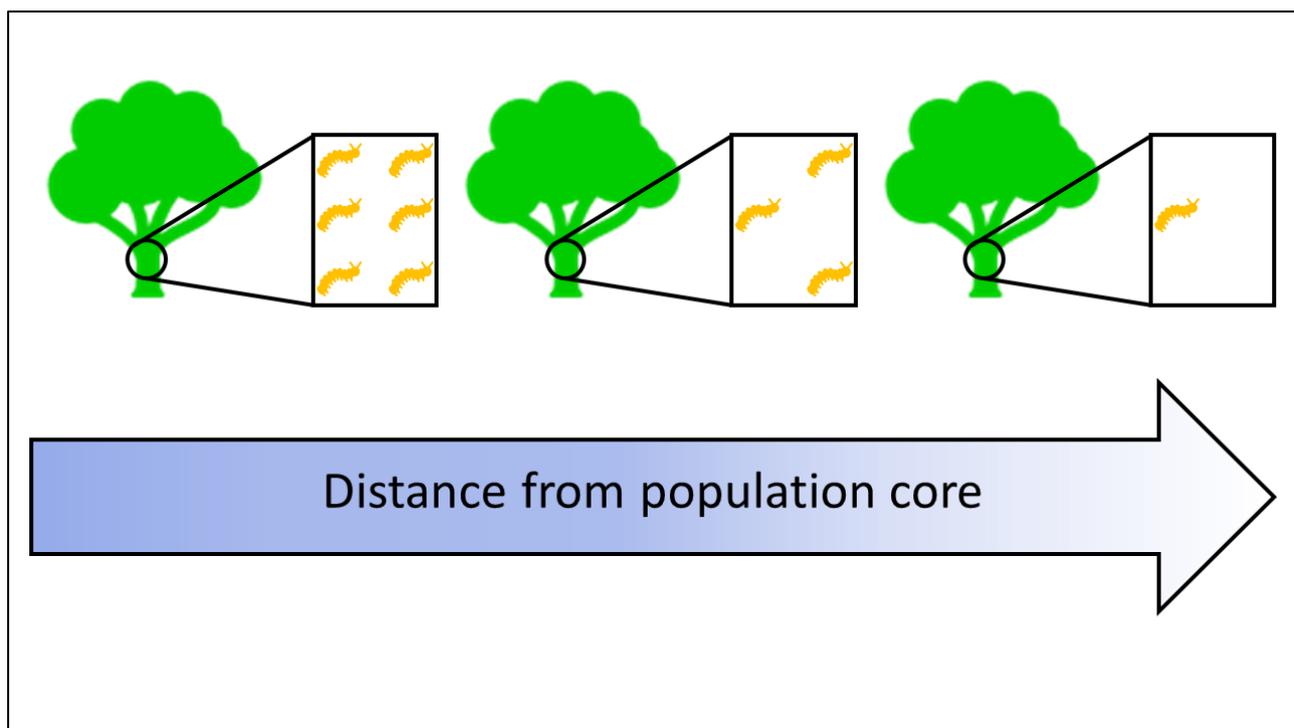


Figure 4 - Illustration of how population density of EAB decreases with increasing distance from range core. Due to the lack of life history data about EAB, this type of estimation is used frequently when predicting abundances.

4.4.3 Environmental effects

Environmental effects are discussed under 4.4.1 Suitability models

4.4.4 Economic impact

Defra studies have examined the economic impacts of ash from *H. fraxineus*, which could be informative for assessing economic impacts of EAB (Defra, 2013). The type of data within these reports is the same as those used for economic impact assessment from EAB related ash mortality within current models used in the USA.

To develop cost-benefit analyses of outbreak control we would require information related to budgets, council boundary maps, and costs of insecticide within the UK. Information about the efficacy of insecticides would be required from the scientific literature or from contacting municipalities where insecticides are used to control EAB.

Further economic analyses related to health or house price depreciations would require information from NHS Scotland related to air pollution and UK House Price Index reports from HM Land Registry.

Economic impacts of EAB are attainable. Due to the outbreak of *H. fraxineus*, there have been economic assessments of ash trees and the threat that is posed by this pathogen. These reports would form a basis for the value of ash, with the outputs of our predictions used to determine the cost of ash loss from EAB.

4.4.5 Accessibility of existing models and data

Much of the methodology and data for modelling an EAB invasion is accessible, with the exceptions of software designed specifically for use in the USA, e.g. EAB cost calculator (Sadof, Hughes, Witte, Peterson, & Ginzel, 2017). Access to formats such as STELLA or SME (see Appendix D) would require contacting the authors of the article for further details to determine how to modify such frameworks for use in Scotland.

4.4.6 Knowledge gaps related to Scotland and the UK

Throughout this study we were able to ascertain methods to model EAB invasion but we were also able to identify gaps within the literature relevant to Scotland and the UK. The first notable absence was any articles that studied the effects of a simultaneous EAB and ash dieback attack. Since UK ash is currently afflicted by *H. fraxineus*, it should be a priority to research the impact of an additional contemporaneous outbreak of EAB. Forest Research is conducting dieback resistance trials which, if stands survive the fungal pathogen, may be vulnerable to EAB infestation. Additionally, research about the dual risk of EAB-*H. fraxineus* is being conducted at the Royal Botanic Gardens Kew.

Life history data from EAB within its native range is scarce. Almost all of the data has been collected within the invaded regions in the USA. This poses a problem when developing models since, during an invasion, evolutionary pressure is most intense and can alter the biology of the organism. As a result, any estimates used within a model for Scotland based on those from the USA will have additional uncertainty within any predictions. If models of spread are developed using data from the USA using common global environmental variables e.g. WorldClim climatic variables, then they can be tested on the ongoing invasion in Russia. Taking such an approach would then provide much more reliable model outputs projected for Scotland.

4.5 Utility of literature review and models as an approach

Bark beetle species share similar life history traits, i.e. requiring a host tree to form galleries, where the beetles lay eggs that develop into larvae and, subsequently, consume xylem vessels to complete their life cycle. Therefore, models developed for EAB could be used, at least as the basis for models of other pests with similar characteristics, e.g. Eurasian spruce bark beetle (*Ips typographus*). Developing a model for EAB which has general features that are transferable to other species is crucial to this strategy. There will be caveats specific to each species, e.g. one brood per year as in EAB (Herms & McCullough, 2014) and potentially 2-3 broods per year for European Spruce bark beetle (Zumr & Soldan, 1981), which will require additional research, e.g. to assess the sensitivity of model predictions to these differences and uncertainties in parameterisations for particular species. The value of such a general approach is that development of models each bark beetle species will not require a complete restart.

A good example is the Bronze birch borer (BBB) for which we found no articles related to modelling. Due to the similarity between EAB and BBB, we could use models for the former as a first approximation to any BBB outbreak within Scotland. We would require information from Scottish Forestry, Forestry and Land Scotland, Forestry Commission and Forest Research related to birch distributions. The literature could also be examined for life history and demographic data for BBB to modify parametrisation of EAB models accordingly.

The literature review conducted allows identification of features for each of the pests investigated, informing rapid adjustment of developed models. By continually updating the literature search, models can be strengthened as more advanced approaches and more reliable data become available.

4.6 Recommendations

Based on our investigation, we would recommend that models for EAB be developed, with enough generality to be interchangeable with other species. We recommend:

- A risk map of EAB suitable locations within Scotland be developed under current conditions and possible future climate scenarios. This will provide an indication of the areas where EAB outbreaks are more likely to establish and facilitate invasion.
- A predictive model be developed that describes EAB invasion dynamics relevant to Scotland. In developing this model, we would propose to make the descriptive features

of the model as general and interchangeable with other species as possible. We would then have access to a tool that can be most adapted to model any wood borer pest.

- The approaches and tools developed would likely be relevant to quantitative assessment of other pests that have invaded regions outside their native range and pose a potential risk to Scotland/ rest of UK.
- To further develop collaborations and networks between stakeholders, research organisations, government, and policy makers to develop coherent and well-informed strategy for pest arrival.
- Further research into mathematical predictions of ash tree health under a simultaneous EAB and *H. fraxineus* attack is conducted. It is currently unclear how ash will respond to a dual attack and the subsequent impacts. Intuition would say both EAB and *H. fraxineus* will have a negative impact. Understanding how ash population health will evolve is important for developing conservation strategies in Scotland and the UK but also in Europe as a whole.

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Appendix A - Systematic search and inclusion procedure

We conducted a systematic search of the scientific literature for modelling papers which focussed on wood boring species. We used a standard approach of developing a list a search terms related to modelling and wood boring insects and an appropriate inclusion criterion for

review. We used an existing EFSA report which members of Centre for Expertise on Animal Disease Outbreaks (EPIC) collaborated on as a basis (MacCalman, et al., 2016).

The procedure involves creating a list of search terms and searching databases which contain articles of scientific research to find those which are relevant to a review. A list of search terms to be used to search within the database are concocted and used in conjunction to provide a list of articles for inspection. Each entry of the list contains the title and abstract of the article which are then inspected against the inclusion criteria to determine if the full article should be inspected. We then determine if the article is useful for the review at the full text level and take notes of the information provided in tables (whichever tables they are in the main doc)

Search terms

The search terms were categorised into themes to help define the appropriate search terms and synonyms for these terms which would allow a wide variety of articles. The themes and search terms are given in Table A.1.

Table A 1 - Search terms used within the systematic search

Theme	Search term
Wood borer	coleoptera scolytinae bupresidea chrysomeloidea xylophageous bark beetle wood borer/ing forest pest tree boring Ips typographus 8 toothed spruce bark beetle emerald ash borer Agrilus planipennis broze birch borer Agrilus anxius great spruce bark beetle Dendroctonus micans
Forest	forest tree Pineacea stand pine ash birch oak elm forestry forest ecology/ecosystem windthrow forest system
Models	modelling cellular automata simulation stratification forecast stochastic deterministic qualitative quantitative statistical

	<p>equations relation GIS</p>
Risk	<p>probability impact likelihood effect forecast prediction</p>
Introduction	<p>outbreak incursion infestation emergence invasion endemic vulnerability penetration</p>
Establishment	<p>fixation resilience sustainability threshold robustness percolation prevalence stability persistence steady state adaptation growth</p>
Spread	<p>spread dispersal movement invasion diffusion human mediated percolation long distance event reaction jump process flight dispersal kernel transport time evolution</p>
Climate	<p>climate change drought climate breakdown precipitation thermal sum climate model degree days windthrow carbon emissions storm incidence scenario analysis extreme temperature seasonal change</p>
Economic	<p>forest economics cost-benefit analysis economic ecological economics intervention</p>

	management strategy ecosystem services sustainability intervention timber economic value economic analysis
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Search strategy

We used the database Web of Science (WoS) to conduct the search for relevant articles. WoS is not the only database, however, it has been found that other databases are not as reliable as WoS due to biases (cite study). Each of the themes and associated search terms were entered individually and then grouped according to theme to make sorting and grouping themes together more efficient. Searching within WoS requires Boolean logic to group terms together, e.g. AND, OR, NOT. It should be noted that the operator NEAR/X will link two search terms that appear within X words of one another; and "*" is the wildcard operator which when added to the end of a term will include all terms that finish in different characters e.g. economic* will search for economic, economics, economical etc.

We had searched for the terms in the following way:

1. Bark Beetles AND (Introduction OR establishment OR spread) AND modelling
2. Bark Beetles AND forest AND (Introduction OR establishment OR spread) AND modelling.
3. Bark Beetles AND forest AND (Modelling OR risk)
4. Bark Beetles AND forest AND Modelling AND risk
5. Bark beetles AND risk AND modelling
6. Bark Beetles AND forest AND Risk
7. Bark Beetles AND climate AND (modelling OR Risk)
8. Bark Beetles AND climate AND modelling AND Risk
9. Bark Beetles AND economic AND (modelling OR risk)
10. Bark Beetles AND economic AND modelling AND risk
11. Bark Beetles AND (Introduction OR establishment OR spread) AND (modelling OR risk) AND climate
12. Bark Beetles AND (Introduction OR establishment OR spread) AND modelling AND risk AND climate
13. Bark Beetles AND forest AND (Introduction OR establishment OR spread) AND (modelling OR risk) AND economic
14. Bark Beetles AND forest AND (Introduction OR establishment OR spread) AND modelling AND risk AND economic

We conducted several searches on 28th March 2019 to find articles which would be of use to us.

Table A 2 -- counts of articles with search themes and search terms. Search number is given to follow combinational searches

Total number of articles	Theme	Search terms	Search number
63,692	Wood borer	TS = ((Coleopter* OR scolytinae OR Bupresidea OR chrysomeloidea OR "bark beetle" OR "wood boring" OR "wood borer" OR "tree borer" OR	1

		ips typographus OR "8 toothed spruce" OR "emerald ash borer" OR "agrilus planipennis" OR "bronze birch borer" OR "agrilus anxius" OR "great spruce bark beetle" OR "dendroctonus micans") OR (xylopha* AND (beetl* OR coleopter*))	
9654,485	Forest	TS = (Forest* OR tree OR "pineacea" OR (stand NEAR\5 (tree OR forest*)) OR "pine" OR "ash" OR "birch" OR "oak" OR "elm" OR "spruce" OR forest eco* OR forest system OR windthrow)	2
12,605,363	Modelling	TS = ("mathematical model" OR model* OR "cellular automata" OR simulat* OR stratification OR forecast OR stochastic OR deterministic OR qualitative OR quantitative OR statistical model OR equations OR GIS OR relation)	3
12,255,146	Risk	TS = (Probabil* OR impact OR effect OR forecast OR likelihood OR prediction)	4
2,126,022	Introduction	TS = (Outbreak OR incursi* OR infest* OR emerge* OR invasi* OR endemic OR vulnerab* OR penetrat*)	5
8,413,085	Establishment	TS = (fixation OR resilien* OR sustainab* OR threshold OR robust* OR percolat* OR prevalen* OR stability OR persist* OR "steady state" OR adapt* OR growth)	6
6,989,127	Spread	TS = (spread* OR dispers* OR movement OR invas* OR diffusion OR "human mediated" OR percolat* OR ("long distance" AND (dispers* OR event)) OR reaction OR "jump process" OR flight OR "dispersal kernel" OR transport* OR time evol*)	7
966,668	Climate	TS = (climate change OR drought OR climate breakdown OR precipit* OR "thermal sum" OR climate model OR "degree days" OR windthrow OR carbon emission* OR storm incidence OR "scenario analysis" OR extreme temperature* OR seasonal change)	8
5,642,999	Economic	TS = (Forest economics OR cost-benefit analysis OR economic* OR ecological economics OR intervention OR management OR strategy OR ecosystem services OR sustainab* OR interven* OR timber OR economic value OR economic analysis)	9

These terms were then grouped together in the following way

Table A 3 -- counts of articles with search themes and search terms. Search number is given to follow combinational searches

Search number	Total Articles	Combination of searches
10	20,648,826	4 OR 3
11	14,954,214	7 OR 6 OR 5
12	4,472	11 AND 3 AND 1
13	11,129	11 AND 10 AND 1
14	3,902	11 AND 10 AND 2 AND 1
15	1,753	11 AND 3 AND 2 AND 1
16	6,023	10 AND 2 AND 1
17	1,319	4 AND 3 AND 2 AND 1
18	3,332	4 AND 3 AND 1
19	4,761	4 AND 2 AND 1
20	1,880	10 AND 8 AND 1
21	710	8 AND 4 AND 3 AND 1
22	1,177	9 AND 4 AND 3 AND 1
23	5,449	10 AND 9 AND 1
24	1,418	11 AND 10 AND 8 AND 1
25	1,512	11 AND 9 AND 3 AND 1
26	2,090	10 AND 9 AND 2 AND 1
27	1,023	10 AND 8 AND 2 AND 1
28	6,426,577	9 OR 8
29	1,933	28 AND 11 AND 10 AND 2 AND 1
30	1,926	#28 #AND #11 AND #10 AND #2 AND #1 Refined by: DOCUMENT TYPES: (ARTICLE OR PROCEEDINGS PAPER OR REVIEW)
31	1,655	#28 AND #11 AND #10 AND #2 AND #1 Refined by: DOCUMENT TYPES: (ARTICLE OR PROCEEDINGS PAPER OR REVIEW) AND PUBLICATION YEARS: (2019 OR 2011 OR 2018 OR 2010 OR 2017 OR 2009 OR 2016 OR

		2008 OR 2015 OR 2007 OR 2014 OR 2006 OR 2013 OR 2012)
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The final search was conducted using search number 31 with 1,655 articles to examine.

Inclusion criteria

The criteria for articles to be inspected were to include those which used some form of modelling which were related directly to wood boring insects.

Before defining a set of inclusion criteria, we first outlined an exclusion criterion to remove irrelevant articles, or those which we justified to be reasonable exclusions. The exclusion criteria for articles were those which:

- were not written in English
- published pre-2006 (to include only the most recent advances)
- had no abstract available
- were not sources of primary research e.g. peer-reviewed articles, conference proceedings, research reports, dissertation, or thesis
- the research subject was unrelated to bark beetles
- the modelling within articles was unrelated to wood borers
- the articles were empirical, observational, etc. unless modelling accompanied the measurements.

We then created assessment criteria based first on a title inspection, then by abstract, and finally by examining the full text article to determine if the article was useful. During a sweep if any of the search terms were explicitly mentioned in the assessment stage then the articles were to be retained. If there were any doubts about an article matching any of the criteria, then it was kept until the next round of assessment to be ruled out.

Title assessment

We examined the titles to determine if the articles were about wood borers which is in the fields of biology, ecology, or environmental sciences. Therefore, we removed any articles which were not within those fields. The title assessment was conducted alongside the first sweep of the abstracts.

Abstract assessment 1

The articles were to be included for the next level of inspection was designed to retain only articles related to wood borer species. Articles were retained if:

- The abstract mentioned wood boring species
 - Articles which examined fungi or nematodes that are strongly related to wood boring beetles were retained
 - Articles which examine species which a not wood borers are excluded e.g. ground beetles.
 - We specifically exclude saproxylic beetles because they feed on dead or fallen trees, rather than attack live and or weakened trees
 - Weevils that attack leaves, or buds, or fruits were excluded due to the population dynamics being fundamentally different to those of wood borers – even if dispersal is similar.
- Articles which examines species assemblages which are unrelated to wood borer dynamics were excluded.

Abstract Assessment 2

The articles were to be included for full text inspection if the remainder examined some aspect of modelling. Articles were retained if:

- Articles which contain any modelling components
 - Articles which conducted simulations, predictive statistics, specialised simulation software, used mathematical equations or relations were to be retained.
 - Articles which mentioned “theoretical” were to be retained due to strong association with mathematical modelling.
- Articles which predict risk of infestation, or economic impacts of wood borer species are to be retained.
- Articles which conduct empirical, observational, or survey studies are to be excluded
 - Articles which have a modelling component as a result of the above experiments etc. are to be retained.
 - Articles which use GIS-type software or modelling related to wood borer distribution changes are to be retained.
 - Articles which conduct standard statistical testing on empirical data which are not predictive are to be excluded.

Full text assessment

The full text assessment was to further distil abstract assessment 2 into a table which took note of the species, process of interest which was modelled, the techniques used, and the purpose of the modelling. The full text criteria were the same as that of abstract assessment 2, however, at full text level inclusion of articles was clearer than by abstract.

Review articles

If a review article was identified, then the references were extracted from the article and inspected using the inclusion criteria.

Appendix B - Deterministic mathematical models

Probability of emerald ash borer impact for Canadian cities and North America: a deterministic mathematical model – Cuddington et al., 2018

Use a deterministic mathematical model to predict EAB distributions based on cold weather mortality. They claim a -30 centigrade for effective mortality, however Scotland will not likely see temperatures this low.

They determine the probability of pupae death from cold expose using logistic regression with random effects (R package: glmer/lme4).

To develop under-bark temperatures, they used timeseries data with 24 time points, with some location modifications. Citations within.

They use a Newtonian cooling model of

$$Tree_i = Tree_i - 1 + k(Air_i - Tree_i)$$

where $Tree_i$ is the underbark temperature at given hour i , Air_i is the air temperature at hour i , and k , is the fitted cooling constant.

They have expanded on this with an urban heat effect which includes a fitted parameter U

$$Tree_i = Tree_i - 1 + k((Air_i + U) - Tree_i)$$

Annual Regression model for minimum underbark temperature

Two annual regression models were also fitted, linear and non-linear.

$$\text{Linear: } Tree_{ij} = m * AirMin_{ij} + b_i * city_i + \epsilon_{ij}$$

$$\text{Non-linear: } Tree_{ij} = a_i * city_i + b_i * \exp(c * AirMin_{ij}) + \epsilon_{ij}$$

where $Tree_{ij}$, is the underbark temperature for city i , at year j , $Airmin$, is the minimum annual air temperature, m , is the slope and b , the intercept of the regression models, and ϵ , is the error term.

Mortality predictions in Canadian urban centres

The above predictions were then used to determine a 99% and 75% probability of cold induced mortality by fitting either a normal distribution, or a generalised extreme value distribution given by

$$f(x) = \exp\left(-\left[1 + \frac{\xi(x - \mu)}{\sigma}\right]^{\frac{-1}{\xi}}\right)$$

where μ is a location parameter, σ is a scale parameter, and ξ is a shape parameter. They used gridded climate data, interpolated using ANUSPLIN from Natural Resources Canada. This was then used to calculate 99% and 75% mortality events using the raster package in R and mapped onto ArcGIS.

Behavioural responses to resource heterogeneity can accelerate biological invasions – Lutscher and Musgrave, 2017

They use a spatio-temporal integro-difference equation to simulate results. The parameters for the dispersal kernel and demographics are parameterised (citations within).

The model simulates good and bad patches of habitat, and has 2 parameters for diffusion coefficients D_1, D_2 and oviposition rates, α_1, α_2 . The authors introduce a parameter $z \in [-1, 1]$ which indicates preference for a patch, where $z > 0$ indicates preference for good patches. There is a probability of moving to a good patch as $\frac{1+z}{2}$ and $\frac{1-z}{2}$ for a good patch. A patch is considered good if it had positive consequences for growth, and a bad patch if there are negative consequences for growth. The landscape consists of periodically alternating between good and bad patches l_1 and l_2 with period $l = l_1 + l_2$. For homogeneous conditions, either $l_1, l_2 = 0$.

The spatio-temporal model is given by

$$E_{t+1} = \int_{\Omega} K(x, y) \frac{r}{2} \left(1 - e^{-\frac{P_t(y)}{P}}\right) s E_t(y) dy$$

$$P_{t+1} = P_t(x) e^{-w s E_t(x)}$$

$$K(x, y) = \frac{a}{2} e^{-a}$$

where E_t is number of eggs per kilometre, P_t is the area of phloem per kilometre, $K(x - y)$ is the dispersal kernel, $\frac{1}{a}$ is the mean dispersal distance, t is year, s is probability eggs survive to hatch, r average number of eggs per emergent female, w indicates a stronger negative impact

on phloem by larvae, and \bar{P} indicates a higher phloem requirement for successful larval development.

The authors simulate under differing scenarios and calculate the speed of invasion. They find that heterogeneous environments can increase the rate of advance of EAB.

PLAN or get SLAM'ed: Optimal management of invasive species in the presence of indirect health externalities – Jones et al., 2016

The authors describe a current control strategy for EAB known as SLAM (SLow Ash Mortality). SLAM is a strategy of combining insecticide, girdling of trees and phloem reduction. This has proven successful in carefully controlled experiments, but is claimed to be practically ineffective. They propose pre-emptive planting of new saplings with resistance alongside susceptibles – PLAN.

This is an ecosystem services framework and bioeconomic model to explore both SLAM and PLAN strategies, as well as health benefits.

The model consists of susceptible and resistant trees a_n, a_r . Resistant trees are age-structured into adults and juveniles a_{ra}, a_{rj} . Juveniles grow logistically with intrinsic rate r and are bounded by a carrying capacity K , which is the maximum biomass ash trees could achieve in a given climatic/physiographic zone, and transition into adults at a given rate θ . The model is given by

$$\begin{aligned} \dot{a}_{rj}(t) &= (1 - \theta) \left[r a_{rj}(t) \left(1 - \frac{a_{rj}(t)}{K} \right) \right] + m(t) \\ \dot{a}_{ra}(t) &= \theta a_{rj}(t) - \varphi a_{ra}(t) \\ \dot{a}_n(t) &= (1 - \varphi) g a_n(t) \left(1 - \frac{a_n(t)}{K(e(z(t)))} \right) \end{aligned}$$

where $m(t)$ is additionally planted trees according to a management decision, r is the intrinsic rate of growth of natives, φ is natural mortality. EAB affect the trees through carrying capacity $K(e)$. Biological and chemical controls and treatments are quantified by $z(t)$, which reduces the borer numbers, $e(z(t))$. Therefore, $K(e(z(t)))$ can be conceptualised as management controls the the effects that the borers have on tree stand carrying capacities, i.e. K can be controlled through $z(t)$.

The authors work within a framework of health benefits from ash in terms of improved air quality. Air quality is modelled as a function of ash trees, $w(a_n(t), a_r(t))$ where trees improve air quality, i.e. $w_{an}, w_{ara} > 0$. Health status is a function of air quality and an exogenous composite health good, c , representing all other health goods that an agent could consume – various parameters within the article. The current health status is given by $h(c, w(a_n(t), a_{ra}(t)))$. Further details for the inspiration and framework are given within the article. The authors define a social benefit function given as

$$B(v(a_n(t), a_{rj}(t), a_{ra}(t)), h(c, w(a_n(t), a_{ra}(t))), y)$$

where $v(\cdot)$ is a function of environmental and aesthetical quality, human health impacts via air quality, $h(\cdot)$, and a composite of other ecosystem service flows provided by trees, y . Social benefits are increasing in environmental quality and health status when $B_v, B_h > 0$. Accounting for cost planting replacement trees $c(m(t))$, and treating EAB, $d(z(t))$, the present value net social benefits (NPV) is given by

$e^{-\delta t} \left[B \left(v \left(a_n(t), a_{rj}(t), a_{ra}(t) \right), h \left(c, w \left(a_n(t), a_{ra}(t) \right) \right), y \right) - c(m(t)) - d(z(t)) \right]$
where δ is a non-negative discount factor.

The above characterise a bioeconomic dynamical optimisation problem that can be solved using optimal control theory where the NPV is optimised subject to the other constraints. The remainder of the paper discusses in detail how to parameterise the model and data sources they had used to do so. The authors then simulate their results to compare SLAM and PLAN strategies.

Impact of repeated human introductions and the Allee effect on invasive spread – Mc Dermott and Finnoff, (2016)

The authors use a predator prey model established by (Ludwig et al. 1978), and note that human mediated assistance to EAB invasions is not well understood. They take an approach of modelling the dynamics of average bark surface area (m^2) of ash trees in one acre stands a , the health of the stand, s , and the population density of EAB, e . The governing equations are given by

$$\dot{a} = \frac{da}{dt} = r_a a \left(1 - \frac{ak_s}{k_a s} \right)$$

where r_a is the intrinsic rate of growth of the stand, k_a is the carrying capacity of the stand, and $\frac{k_s}{s}$ accounts for the stress on the tree. The variable $z(t)$ can be interpreted as 0 for a dead tree, and 1 for a perfectly healthy tree. As $\frac{k_s}{s}$ approaches 1, the carrying capacity of ash trees increases. The dynamics of tree health are given by

$$\dot{s} = \frac{ds}{dt} = r_s s \left(1 - \frac{s}{k_s} \right) - p \left(\frac{e}{a} \right) \frac{s^2}{T_s^2 + s^2}$$

where the first term represents the growth of ash tree health, $p \left(\frac{e}{a} \right)$ is the stress endured by Ash as a result of EAB infestation where $\dot{s} = \frac{ds}{dt} = r_s s \left(1 - \frac{s}{k_s} \right) - p \left(\frac{e}{a} \right) \frac{s^2}{T_s^2 + s^2}$ is the rate of energy consumption in the form of phloem, and $\frac{s^2}{T_s^2 + s^2}$ accounts for the decline in ash tree quality. A reduction in ash tree quality then reduces predation, which must be below a certain threshold value T_s . The dynamics which govern EAB are given as

$$\dot{e} = \frac{de}{dt} = r_e e \left(1 - \frac{e}{k_e a} \frac{T_s^2 + s^2}{s^2} \right) \left(\frac{e}{K_{crit} a} - 1 \right) - \beta a \frac{e^2}{(\alpha' a)^2 + e^2} + (\theta * driving).$$

The first term represents the growth of EAB which is limited by their carrying capacity with respect to ash., and declining ash quality, $\frac{T_s^2 + s^2}{s^2}$. The second term accounts for a strong Allee effect where growth is negative below a certain population density, K_{crit} . The third term is predation from woodpeckers, further details of woodpecker predation parameters are within the paper. The final term accounts for human mediated introductions and is the expected number of EAB introduced through economic activity. Their choice of model is influenced by Inverson et al. (2008) and Poland and McCullough (2006).

They simulate these results using parameterisations to assess scenarios with differing Allee effects. They also include a crude economic analysis in the form of a previous analysis (Sydnor et al., 2007) to calculate the economic value of ash per metre squared and interpret this through ash densities.

Their findings can be summarised as smaller Allee effects are costlier and less effective management of EAB is. Introducing economic activity in the form of $\theta * driving$, allows some form of control over the Allee effect, i.e. decreasing this term can bring the EAB population to below the Allee threshold.

Linking environmental management to health outcomes: a case study of emerald ash borer – Jones and McDermott, 2015

This article is an earlier study by the lead author of “**PLAN or get SLAM’ed: Optimal management of invasive species in the presence of indirect health externalities – Jones et al., 2016**” detailed above. Therefore, we will take the most recent work as a potential framework for future projects and use this article to reinforce the legitimacy of the approach.

Optimal allocation of invasive species surveillance with the maximum expected coverage concept – Yemshanov et al., 2015

This article examines human-mediated dispersal of EAB from campgrounds – not immediately obvious if this has direct applications to Scotland – which were used to develop monitoring methods within a surveillance budget. The main objective was to develop a model to determine where best to use surveillance methods based on proposed introduction sites.

The model is based on a surveillance programme within a landscape consisting of N locations, with I origin locations for the pest, and J destinations for which the pest is absent. The surveillance budget is given as C to allocate survey resources to uninvaded locations J . There is an assumption that the decision-maker can estimate survey costs, c_j , at individual locations $j, j \in J$. However, due to budget constraints, only a subset $M \subset J$ can ever be conducted.

Areas of infestation i and pest free j are connected pair-wise by a rate p_{ij} at which EAB could spread from invaded to uninvaded territory. Such values of p_{ij} are to be developed through prior knowledge – the authors scale this value such that $p_{ij} \in [0,1]$. Thus, anticipated spread rates form a $I \times J$ matrix of the $p_{ij}, i \in I, j \in J$ values, which corresponds to a bipartite network of spread vectors. They make an assumption that the spatial resolution examined is too coarse to account for natural spread, and that spread is only due to human-mediated instances. The authors have also made the simplifying assumption that p_{ij} is independent of adjacent locations.

To account for decisions to monitor EAB at an uninvaded location, the authors introduce a binary decision variable x_j which takes the value 1 when surveyed, and 0 when not. Therefore, the likelihood that an invader has spread into an uninvaded location and is missed by the surveying is given by

$$\prod_{j \in J} (1 - p_{ij} x_j)$$

and the likelihood that EAB spreads from location i and is not covered by any one of the surveys is

$$1 - \prod_{j=1}^J (1 - p_{ij} x_j).$$

To allocate the best use of resources is then an allocation problem to maximise the expected number of source locations covered by surveys, which is given by

$$\tau_{MECP} = \text{Max} \sum_{i=1}^I (1 - \prod_{j=1}^J (1 - p_{ij} x_j)) \text{ such that } \sum_{j=1}^J c_j x_j \leq C, x_j \in \{0,1\}, \forall j \in J. \quad (1)$$

The MECP model is taken from conservation research, more specifically, from determining where best to place nature reserves for maximal impact (Camm et al., 2002, Arthur et al., 2004).

The authors then implement a propagule pressure framework to the MECP model. Propagule pressure (PP) is a metric used within invasion biology to measure incoming invaders to a particular location. The premise is that more invaders entering a location increases the probability of that invader establishing there.

The first method referred to as PP1 is the expected number of individuals arriving at an uninvaded location from an already invaded location given as the sum of pest arrival rates

$$\sum_{i=1}^I (p_{ij})_j \quad \forall j \in J$$

which when integrated to equation (1) gives

$$\tau_{PP1} = \text{Max} \sum_{j=1}^J \left(\left[\sum_{i=1}^I (p_{ij}) \right]_j x_j \right).$$

The second method referred to as PP2 estimates the expected number of invasives to spread to a vacant location from one or more source locations, which when integrated into equation (1) is given by

$$\tau_{PP2} = \text{Max} \sum_{j=1}^J \left(\left[1 - \prod_{i=1}^I (1 - p_{ij}) \right]_j x_j \right)$$

These models are then used with geographical data to determine different strategies for creating a monitoring network in real locations. The models converged, however, budget constraints did have an impact on the outcome of the monitoring network – something which could be rigid when applying strategy. They found that the MECP model and the PP model optimal solutions were based on topological properties of the spread network. The PP models allocate more monitoring to areas with expected high spread rates. If there is low correlation between spread rates and connectivity between locations, then the MECP model will maximize survey effort from as many invaded locations as possible. Which models would be best used is dependent on the objective of the surveys.

Benefits of invasion prevention: Effects of time lags, spread rates, and damage persistence – Epanchin-Niell and Liebold, 2015

The authors examine several factors that influence the long-term damages from invasive species, and the benefits of prevention, or eradication. They investigate spread rates, invasion range sizes, and geographic distribution of resources and use these to determine the influence of spread and damage lags and the impacts of persistence within invaded territory. EAB is one of 3 species used as a case study for their models.

The authors develop a spread model based on diffusion by Shigesada and Kawasaki (Shigesada and Kawasaki, 1997). They assume radial spread which has a time dependent lag period and is given by

$$radius(t) = \begin{cases} 0 & t \leq lag1 \\ v_0(t - lag1) + v_1(t - lag1)^2 & lag1 \leq t \leq T_{max} \\ \sqrt{\frac{A}{\pi}} t \geq T_{max} & \end{cases}$$

where $lag1$ is the lag before the species begins spreading, and T_{max} is the time taken for the species to spread across its entire potential range from the time of introduction. Note that v_0 and v_1 are parameters that determine spread. Constant radial spread with no long-distance dispersal events corresponds to $v_1 = 0$. To calculate the invasion area I at time t is then $I(t) = \pi * radius(t)$.

The authors then define another lag, $lag2$, which is the time lag between the introduction of the species and the commencement of damages. They assume that damages per area, $D \left(\frac{\$}{km^2} \right)$, is constant, and thus increases as the invasion area does, i.e. cost of damage is proportional to species spread. The authors make the assumption that damage persists for some period of time, P , such that damages per time period equal $\frac{D}{P}$. They calculate total cost of non-discounted damage, i.e. no control programmes, at time t by

$$Damage_t = \sum_{s=t-lag2-P-1}^{t-lag2} \frac{D}{P} * NewAreaInvaded(s)$$

where $NewAreaInvaded(t)$ is the new area invaded at time t . The total present value of expected damages allowing for discounting through control programmes is given by

$$PVDamage_{total} = \sum_{t=1}^{\infty} \sum_{s=t+lag2}^{t+lag2+P-1} \frac{D}{P} * NewAreaInvaded(s) \frac{1}{(1+r)^s}$$

where $\frac{1}{(1+r)^s}$ is the discount factor and r the discount rate.

The authors develop 3 models by altering the parameters v_0 and v_1 . Model A is for constant radial spread, $v_1 = 0$; model B has parameters $v_0 = ModelA, v_1 \neq 0$; model C has parameters $v_0 \neq ModelA, v_1 \neq 0$, but is parameterised such that the average rate of spread over T_{max} is the same as that of model A. For model C, although the initial rate of spread is slower than model A, the non-zero parameter $v_1 \neq 0$ allows for an acceleration of spreading. Parameter values are located in supplementary material.

The purpose of the model is to highlight that preventative measures can reduce damages incurred over time. The use empirical data 3 forest pests: Gypsy moth, Hemlock wooly adelgid, and EAB, to illustrate this. Their models predict that A and C are similar, with C being the least damaging, and model B as the worst case, as would be expected from their parameter choices.

There is no silver bullet: The value of diversification in planning invasive species surveillance – Yemshanov et al., 2014.

The authors develop a short-term allocation of pest surveillance resources as a portfolio valuation problem – a branch of theory associated to financial investment. The purpose is to provide assistance to pest managers for effective allocation of resources when planning a surveillance programme.

To protect an area, say Scotland, the geographic area is separated into smaller locations or regions, m , with potential survey locations, y , each characterised by an estimate of the likely outcome of a survey, ξ . The distributions of potential survey outcomes ξ are estimated prior to survey planning. This would involve estimating the probability of an invading pest, such as the survey locations proximity to a previously infested area.

For each individual region $j = 1, 2, \dots, m$, the authors constructed a cumulative distribution of the expected survey outcomes from the location-specific ξ values generated within the invasion model (located in appendix A of the article). The cumulative distributions were then sampled at 20 successively increasing percentile points equally spaced on the interval $[0,1]$. Each survey region, j is then characterised by a set I_j of distribution values I_j at sampled percentage points. Sampling points were identical across all regions which allowed the comparison of sets for any two regions, i.e. I_j and I_i for regions j and i .

The authors then introduce the proportion of total survey resources allocated to each location as ω_j , where $\omega_j \in [0,1]$. To find the mean performance of all surveys over all regions, \bar{I} they first calculated the mean survey performance r from the set I_j and multiplied this quantity with ω_j which gives

$$\bar{I} = \sum_{j=1}^m \omega_j \bar{I}_j \text{ where } \sum_{j=1}^m \omega_j = 1.$$

The article lists calculations for the standard deviation, co-variance between regions, and the total variation of the surveys, V , which we have omitted. Due to the sensitivity of pairwise correlations of performance, the authors account for diversification with a Euclidean distance between expected survey performance given by

$$D = \sum_{j=1}^m \sum_{\substack{i=1 \\ i \neq j}}^m \omega_j \omega_i d_{ji} \text{ where } d_{ji} = \sum_{\substack{k=1 \\ i \neq j}}^N (I_{kj} - I_{ik})^2$$

where I_{ik} and I_{jk} are survey performance values in sets I_i and I_{jk} respectively, and N is the number of elements in the sets. The similarity measure d_{ji} then finds the regions with high expectation of pest arrival and dissimilar distributions of expected invasion outcomes from different regions. By surveying more dissimilar regions in terms of the variation in predicted survey performance values I_j , this would cover more diverse landscape conditions and potentially increase the opportunity to detect pests in unanticipated regions.

The authors then formulate the survey allocation problem of finding the optimal allocation of total surveillance resources among m regions represented as a proportion ω_j to each region that minimises survey variance, V , while meeting the desired level of survey performance, $I^* = \bar{I}$ and diversification, $D^* = D$, given by

$$\underset{\omega_j}{\operatorname{argmin}} [V] \text{ such that } \sum_{j=1}^m \omega_j = 1 \text{ and } \omega_j \in (0, h_{max}]$$

where h_{max} is the limit of the proportion of resources which are allowed in any individual region.

This optimisation problem was then evaluated for 3 resources allocation approaches: equal resources allocation, i.e. $\omega_j = \frac{1}{m}$; resource allocation weighted for the mean performance value \bar{I}_j ; and the final method is choosing ω_j such that the variance contributions from each location are equal – which involves solving numerically.

The authors apply this technique to a survey system in Canada and use the outputs of a model (details in appendix B, similar to **Optimal allocation of invasive species surveillance with the maximum expected coverage concept – Yemshanov et al., 2015**) to determine the ξ values. The method does not account for spatially explicit factors which could influence the spread of EAB, and favours locations with lower variance in survey location performance. The third method described performed the best with much of the resources surrounding areas adjacent with EAB infestation. Method 3 also allocated more resources to areas that would not be expected to invasion targets for EAB than models 1 and 2.

Modelling interactions between forest pest invasions and human decisions regarding firewood transport restrictions – Barlow et al., 2014.

The authors develop a SIR model for invasive forest pests, the Asian Long Horn, and EAB. They include human mediated transport in the form of a social decision model related to firewood transport.

The authors begin with describing tree dynamics given by

$$\begin{aligned}\frac{dS_i}{dt} &= rS_i \left(1 - \frac{S_i + I_i}{K_i}\right) - AS_i I_i \phi(I_i) \\ \frac{dI_i}{dt} &= -\varepsilon I_i + AS_i I_i \phi(I_i)\end{aligned}$$

where $i = 1, 2$, and

$$\phi(I_i) = \begin{cases} 0 & \text{if } I_i < a \\ 1 & \text{if } I_i \geq a \end{cases}$$

S_i and I_i are the susceptible and infested trees in patch i respectively, r is the intrinsic rate of growth for the trees, K_i is the carrying capacity of the trees within patch i , A is the transmission rate of the pest, and ε is the death rate of infested trees. The term $\phi(I_i)$ represents effects which can affect slow tree growth when the tree densities are sufficiently small, e.g. an Allee effect. The authors also claim that this expression can – albeit imperfectly – capture stochastic “fadeout” effects which would emerge more naturally within a fully stochastic model. The authors determine that multi-patch models behave qualitatively the same as a 2-patch system and thus restrict discussion to the 2-patch case.

The authors introduce a social influence model which accounts for positive and negative decisions regarding firewood. The model quantifies social influence using a pay-off function for buying firewood locally within the patch, given by

$$P_l = -C_l + n(L_i - 0.5),$$

or transporting the firewood form another patch, given by

$$P_t = -C_t + n(0.5 - L_i) - fI_i.$$

Here, n represents the strength of social norms, C_l is the direct economic cost of purchasing local firewood and burning within the patch, C_t is the direct economic cost of buying firewood and transporting it to be burned in another patch, L_i is the proportion of individuals who adhere to firewood transport restrictions in patch i , and f is a proportionality constant controlling for the impact of infestation levels on individual decisions. If $L_i > 0$, then there is a positive pay-off for adopting the socially dominant strategy, and if $L_i < 0$ there is a penalty. In the equation for P_t there is always a penalty associated with concern for causing a new infestation.

There is more detail within this article, but I believe it to be poorly written and/or incorrect amounting in confusion with regards to the methodology. Therefore, we shall only revisit this article in the event we decide to use this method.

A bioeconomic analysis of an emerald ash borer invasion of an urban forest with multiple jurisdictions – Kovacs et al., 2014

The authors determine a bioeconomic model for mitigation strategies in urban forests infested by EAB in Minnesota, USA, using real data. They examine the obstacles of regional funding between local authorities, centralised authorities, and private land ownership. Their model is used to aid decision makers on the best course of action regarding EAB spread and infestation when management of, and access to, resources and information has differing administration levels.

The authors model the spatial-dynamics of EAB by focusing on the population of ash that are potential hosts for the pest. They use a map grid representation of spatially explicit growth and dispersal of EAB. The landscape is divided into m square cells of equal area with a single land use. Each cell classifies ash trees into an ownership class, n , which is either public or private. The model quantifies ash into area (m^2) of phloem which can be converted into tree numbers depending on the size of the trees. The susceptible phloem in site i with ownership status j at year t as $S_{ij}(t)$. They assume that susceptible trees are treated with a pesticide with 100% effectiveness for 2 years and are quantified by $R_{ij}(t)$. Additional control methods introduced are phloem treated in Spring as $X_{ij}(t)$, and susceptible trees removed in the Autumn as $Y_{ij}(t)$. The amount of phloem consumed by larval EAB between spring and summer periods $t - 1$ is given as $G_{ij}(t)$. Insecticide treatment and trees felled remove phloem available to EAB and the cumulative amount removed is $L_{ij}(t)$, whereas the cumulative amount removed by EAB consumption is $C_{ij}(t)$. The governing equations are then given as

$$\begin{aligned}
 S_{ij}(t) &= S_{ij}(t-1) - X_{ij}(t) - Y_{ij}(t) - G_{ij}(t) + X_{ij}(t-2) \\
 C_{ij}(t) &= C_{ij}(t-1) + G_{ij}(t) \\
 R_{ij}(t) &= R_{ij}(t-1) + X_{ij}(t) - X_{ij}(t-2) \\
 L_{ij}(t) &= L_{ij}(t-1) + Y_{ij}(t) \\
 G_{ij}(t) &= \left(S_{ij}(t-1) - X_{ij}(t) - Y_{ij}(t) + X_{ij}(t-2) \right) \left(\frac{r \sum_{k=1}^m p_{ik} \sum_{j=1}^n \mu G_{kj}(t-1)}{\mu \sum_{j=1}^n (S_{ij}(t-1) + R_{ij}(t-1))} \right)
 \end{aligned}$$

where L_i is the expected proportion of adults that emerge within site k and move to site i and is a negative exponential function of the distances between sites i and k . The number of adults which emerge from site k is $\mu G_{kj}(t-1)$ where μ is the average number of adults per m^2 . The annual population growth rate is given by r . The parameters r and μ are estimated from the articles (Mercader et al. 2011) and (Mc Cullough and Seigert, 2007) respectively.

The above equations are then optimised under economic conditions derived in the same manner as that of **PLAN or get SLAM'ed: Optimal management of invasive species in the presence of indirect health externalities – Jones et al., 2016**, and will therefore be omitted. Articles of parameterisations within their model, such as the economic value of a single ash tree, are contained within the article.

The authors test their model using 5 management strategies which were available for each of the municipalities and conducted sensitivity analyses afterwards. The strategies were: no management, aggregate budget across municipalities, local budgets, aggregate budgets removal only, aggregate budget insecticide only.

Their main findings were that aggregating budgets between municipalities using both removal of infested ash and insecticide was the most effective strategy at cost-effective control of EAB.

Economic analysis of emerald ash borer (coleoptera: buprestidae) management options – Vannatta et al., 2012.

The authors develop an economic model using existing ash tree populations on the University of Wisconsin-Stevens Point campus to quantify net values of urban ash populations under several management strategies. The examined pre-emptive removal, pre-emptive removal and replacement, and insecticide treatment. All strategies were compared with a no management approach.

The authors used an ash tree mortality model given by

$$1 - \left[\frac{R_n - R_e}{1 + e^{4-\gamma n}} \right] + N_a$$

where R_n is the annual survival rate (%) of ash when EAB is present, R_e is the ash survival rate (%) after a tipping point when EAB is present, r , years since arrival of EAB, N_a is the natural death rate of EAB free ash trees. The tipping point is cited to be an EAB population infestation level where mortality of ash is approximately 20% (Knight et al., 2007). Details of the parameterisation are within the article.

The economic evaluation is based on two methods: CTLA and i-Tree Streets programs deducting the costs of tree management. The authors evaluate the value of lost trees using the following functions

$$\begin{aligned} VR_i &= \left\langle \sum_{t=1}^n \left[\frac{V_c}{(1+d)^t} - \frac{C_m}{(1+d)^t} - \frac{C_t}{(1+d)^t} - \frac{C_r}{(1+d)^t} - \frac{C_p}{(1+d)^t} \right] \right\rangle \\ VR_i &= \left\langle \sum_{t=1}^n \left[\frac{V_i}{(1+d)^t} - \frac{C_m}{(1+d)^t} - \frac{C_t}{(1+d)^t} - \frac{C_r}{(1+d)^t} - \frac{C_p}{(1+d)^t} \right] \right\rangle \\ VL_i &= \left\langle \sum_{t=1}^n \left[\frac{V_c}{(1+d)^t} - \frac{C_m}{(1+d)^t} - \frac{C_t}{(1+d)^t} - \frac{C_r}{(1+d)^t} - \frac{C_p}{(1+d)^t} \right] \right\rangle \\ VL_i &= \left\langle \sum_{t=1}^n \left[\frac{V_i}{(1+d)^t} - \frac{C_m}{(1+d)^t} - \frac{C_t}{(1+d)^t} - \frac{C_r}{(1+d)^t} - \frac{C_p}{(1+d)^t} \right] \right\rangle \end{aligned}$$

where VR_i is the net annual value remaining for management option i , VL_i is the net annual value lost for management option i , V_c is the CTLA valuation, V_i is the i-Tree valuation, C_m is the management cost, C_t insecticide treatment cost, C_r cost of removing ash trees, C_p is the cost of planting new ash trees, and d is the discount cost. The angled brackets refer to the inner product for real numbers.

The authors then simulate these models over a period of 20 years (20-time steps) and rank the outcomes of each management option in order of desirability (details within the article) in a Goeller scorecard (Goeller, 1988). To determine how sensitive the input variables were to the outcome, the authors conducted a sensitivity analysis to each of the input values.

The authors develop a framework for taking decisions about EAB that have different outcomes and determine the cost. This allows managers to choose methods for EAB control based on the desired outcome, rather than a catch-all strategy.

Appendix C - Statistical and risk models

Maintaining ecosystem properties after loss of ash in Great Britain – Hill, et al., 2019

The authors develop a risk map for loss of ecosystem functioning for the destruction of ash trees from ash dieback, or EAB. A map is produced mapping the risk of other species with similar, or reliant on, traits of ash trees. Although this article does not specifically model risk from EAB, it was highlighted as potentially useful when developing similar models.

Tree shade, temperature, and human health: evidence from invasive species induced deforestation – Jones, 2018

The authors develop a regression model to estimate the relation between defoliation of ash trees and the impacts on temperature increase. This is then further examined in the realm of temperature effects on health, and more specifically, the economic value of mortality and morbidity due to temperature.

The authors include fixed effects to determine the causal effects of EAB on temperature, namely that temperature in different counties vary seasonally, which can also be independent of annual variance. They also account for urban heating effects which can be different from rural areas. They also account for observable weather characteristics which are known determinants of temperature. The baseline econometric model is given by

$$Temp_{ct} = \alpha + \beta_1 EAB_{ct} + \beta_2 X'_{ct} + \delta_{state-month} + \theta_{year} + \mu_{urban} + \epsilon_{ct}$$

where $Temp_{ct}$ is one of several measures of temperature in county c in month t , EAB_{ct} is an indicator variable (0/1) for EAB detection, X'_{ct} is a vector of non-linear weather characteristics, $\delta_{state-month}$ is the state-month fixed effect, θ_{year} is the year fixed effect, μ_{urban} is the urban indicator variable, and ϵ_{ct} is the idiosyncratic error term. The term of interest is β_1 , which is the effect of EAB detection, and thus, shade loss on temperature.

The authors also introduce a distributed lag model due to ash mortality increasing as the severity of the infestation, and damage accruing since the time of detection occurred. This adjusted model is given by

$$Temp_{ct} = \alpha + \sum_{j=0}^{12} \beta_{t-j} Yr EAB_{ct-j} + \beta_2 X'_{ct} + \delta_{state-month} + \theta_{year} + \mu_{urban} + \epsilon_{ct}$$

Here temperature is regressed on 12 years of lags and the variables of interest are the 12 coefficients β_{t-j} . Standard errors in all models were clustered at the county level to allow for spatial correlation.

The results from the regression analysis are then input into a mathematical model used in Jones et al., (2016) (see Appendix B).

The authors then examine cases related to the heterogeneity of the data, such as socio-economic background under the assumption that lower ash coverage is correlated to lower economic income and lower health. Their results suggest that defoliation from EAB has significant human health impacts and economic impacts lost from tree shade.

Health impacts of invasive species through altered natural environment: assessing air pollution sinks – Jones and McDermott, 2018

The authors use a regression model mechanistically similar to **Tree shade, temperature, and human health: evidence from invasive species induced deforestation – Jones, 2018** to estimate the human mortality rate from air pollution sinks attributable to EAB. The authors find that detection of EAB is associated with air pollution sinks which affect human mortality cases.

The base model is given by

$$Mort_{ict} = \beta_0 + \beta_1 Pollut_{ict} + X'_{ct} \delta + \gamma_{cs} + \pi_t + \mu_{ct}$$

where $Mort_{ict}$ is either the respiratory or cardiovascular age-adjusted mortality rate (per 100,000) for pollutant type i , measured in county c , in year t , $Pollut_{ict}$ is the ambient concentration of the pollutants in each county at a particular year, X'_{ct} is a vector of time-varying weather, socioeconomic, and demographic characteristics in the county and year that could affect mortality rates, γ_{cs} are countyXstate fixed effects that control time-invariant, unobserved determinants of mortality for individuals resident in a particular county and state, π_t are time fixed effects to control for unobserved changes in rates of mortality over time, and μ_{ct} is the error term. The coefficients of interest β_1 estimates the effect of a unit increase in pollution concentration in an EAB-infested county on the average respiratory or cardiovascular mortality rate.

The authors also introduce models which address the issue that pollutants make be driven externally and determine an estimate for these. The authors also address the case when there is a lag due to ash dying, whereas the model detailed above is for instantaneous effects from infestation. The effects from EAB are translated into economic costs from cardio-respiratory mortality costs using a cost-benefit analysis.

Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate – Iverson et al., 2016

The authors use another model (Prasad et al., 2009, see Appendix D) to determine the risk of spread from EAB short and long-distance dispersal. The model accounts for estimates of EAB abundance, ash abundance, traffic intensity and other parameters for major roads, campground size and usage, distance from the core infested zone, wood products industry size and type of wood usage, and human density. The article is an assessment of how well the model predicted risk of EAB infestation after 10 years.

The authors then update the inputs with various data sources from the USDA Forest Service (Climate Change Atlas, Forest Inventory and Analysis) They then use the estimates to determine how well the model predicted risk using linear regression to find a good match ($R^2=0.45$, $P<7e^{-12}$). The Climate Change Analysis tools had to be modified using literature described in the article because it is a statistical model which excludes ecosystem processes, such as disturbance. The authors developed a scoring system to then modify DISTRIB model outputs (DISTRIB no on USDA Forest Services site).

Ultimately, the authors were concerned with ash replacement species as a result of EAB which we shall omit.

Cost of potential emerald ash borer damage in U.S. communities, 2009-2019 – Kovacs et al., 2010.

The authors develop a statistical model of EAB using forestry data from different municipalities and a probabilistic spread of EAB which accounts for the rate of detections. These results are then used to determine costs of control strategies: no action, remove trees, remove and replant trees, and to add insecticide that protects from EAB damage. The cost

estimates come from a calculator with the following link (<http://www.entm.purdue.edu/EAB/>).

The spread model is a negative exponential between geographic locations within grids. The grid has been constructed from census data into 23x25 km² areas. The spread model between grids is given by

$$p = 0.94e^{-0.06d}$$

where p is the probability of spread and d is the distance between cell midpoints in km. The parameterisation of the negative exponential model was conducted using a series of Bernoulli trials with further details within the article. The results were simulated across the grid 500 times across 500 permutations of both p and d . Due to the predictive nature of the model, the authors conduct a sensitivity analysis for ash distribution from potential site to be developed in future.

The influence of satellite populations of emerald ash borer on projected economic costs in U.S. communities, 2010-2020 – Kovacs et al., 2011

This article is an updated version of **Cost of potential emerald ash borer damage in U.S. communities, 2009-2019 – Kovacs et al., 2010** with the addition of satellite populations which have a reduced probability of dispersing to adjacent cells. It is assumed that beetles are unlikely to spread beyond 20km, and human transport has created the satellites. We shall therefore omit details since the model is the same, however, additional data has been added.

Dispersal of the emerald ash borer, *Agrilus planipennis*, in newly colonised sites – Mercader et al., 2009

This article fits 3 statistical models to collected field data related to EAB to determine a dispersal function. The authors took 2 known sites of infestation and felled trees into bins of 10m from the point of origin where 0m was within 5m, and outwardly expanding in 10m from there. They fitted densities from their collected larvae to 3 functions: Ricker model, negative exponential model, and inverse power model. They found that the negative exponential was the best fitting model for predicting the densities from the tree felled sites using AIC criterion. All three models were parameterised from the data. This model is used throughout the literature as a dispersal kernel for EAB based on this study.

Estimating potential emerald ash borer (Coleoptera: Buprestidae) populations using ash inventory data – Mc Culloch and Siegert, 2007

This article uses field data from two infested counties in Michigan from felled trees to estimate the densities of EAB in 3 different ash species based on the *diameter at breast height (DBH)* measurement. The authors then fit regression models for: linear, power, exponential, and second order polynomial parameter. They found that the second-order polynomial fit best to the data, however, no model selection data was conducted. These estimates were used as a proxy for phloem area which can then be used to calculate potential EAB sites and carrying capacities. The measurements were then scaled and used on ash inventories to determine how much destruction can be attributed to EAB. They had found that trees with $DBH \geq 26cm$ made up 6% of all ash trees, but could account for 55-65% of the total EAB production at each of their samples sites. The authors also found that 75-80% of ash trees where $DBH \leq 13cm$ could only have contributed to less than 12% of the potential production. This paper continually appears within the cited literature as justification for the method of statistically determining EAB densities.

Patterns in the within-tree distribution of emerald ash borer *Agrilus planipennis* (Fairemaire) in young, green-ash plantations of south-western Ontario, Canada – Timms et al., 2006.

This article uses field data collected from 32 sites in Ontario, Canada, to predict densities of EAB from collected ash trees. The authors use a technique known as upper boundary regression (see citations and details within) to estimate relationships between each of their chosen density parameters: stem diameter, bark thickness, and height above ground. They then use linear and non-linear (quadratic) regression models to make estimates from the data. They also develop a model for probability of infestation using presence-absence data from their samples and modelled this against stem diameter using logistic regression to create a predictive model for EAB occurrence. They also conducted a Pearson's correlation analysis to identify correlations between their different measured variables. The authors also conducted a compass analysis which suggested that south east areas of the trees were most densely populated with EAB.

They authors found that all 3 variables were highly correlated when infested with EAB, suggesting that at least one of them is a main predictor for EAB presence. The authors suggest that bark thickness is the most likely explanatory variable for EAB presence.

Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America – Muirhead et al., 2005.

This article develops a dispersal model with the probability of infestation from data collected in Michigan, USA. The authors use an exponential decay function relating the probability of settling to the centroid of a pre-defined area. The model is phenomenological, i.e. no particular assumptions are made about the flight of the borer, other than flight being the main dispersal method. The authors define the probability of an area remaining pest free is given by

$$P_j = \prod_i \left[1 - \frac{\exp(-bx_{ij})}{d_i} \right]$$

where P_j is the joint probability that the borer fails to disperse from all infested sub-counties i to destination j , x_{ij} is the Euclidean distance from source i to non-infested region j , b is the estimated coefficient of the exponential slope, and d_i is a normalising constant given by $d_i = \sum \exp(-bx_{ij})$. Scaling the probability in such a way allows P_j to determine the relative risk of infestation between 0 and 1. The coefficient b can then be estimated by finding the minimum value of the maximum likelihood function.

Long-distance dispersal was modelled based on two scenarios of human-mediated transport. The first was by using logistic regression weighted by the log-transformed human population size of cells and distance from infested cells. The second used the same method but with log-transformed distance from the epicentre of the first infestation site. Both methods were used to attribute the distance to the human population size.

The authors also used a gravity model to estimate human-mediated long-distance dispersal events to firewood and campsites throughout the study region. Data was provided from a program of intercepted firewood within quarantine zones and the model is given by

$$w = \alpha c d^{-\beta}$$

where w is the number of wood bundles, c is the number of campsites, d is the shortest road distance from the park to the epicentre of infestation, and β and α are variables estimated using non-linear regression and least-squares regression.

These estimates were then used in conjunction with arcGIS to develop a prediction of spread across infested regions.

Appendix D - Agent based modelling/cellular automata/software/imagery methods

The following publications use the same agent-based models (a.k.a. individual-based models) and are published by the same authors. Therefore, we shall list the publications and briefly describe the modelling framework to be determined for use. Such models are computationally intensive and are only capable of local dynamics (within a township) and have limited use for describing nationwide dynamics or predictions, which is our primary interest.

Network-agent based model for simulating the dynamic spatial network structure of complex ecological systems – Anderson and Dragičević, 2018

Geospatial pest-parasitoid agent based model for optimizing biological control of forest insect infestation – Anderson and Dragičević, 2016

A geosimulation approach for data scarce environments: modeling dynamics of forest insect infestation across different landscapes – Anderson and Dragičević, 2016

An agent-based modeling approach to represent infestation dynamics of the emerald ash borer beetle – Anderson and Dragičević, 2015

Agent based models are synonymous with individual based models in the realms of ecology. These methods track the dynamics of individuals rather than population level modelling. Inferences are made from the results of ABMs to the population level. The benefits of using such an approach is that all manner of detail can be accounted for, however, the trade-off is that understanding what factors and parameters are driving the dynamics are difficult to determine.

These models have been constructed using software called Recursive Porous Agent Simulation Toolkit (Repast). The model uses a combination of arcGIS landscape data, and recursive dynamics for both beetle and tree dynamics. The entire life cycle of EAB is captured through each of its 4 instars including dispersal. These recursive steps are parameterised from available data. Much of the dynamics within these particular articles are controlled using fixed probabilities, such as, chance of establishing in a satellite population 30%.

The results are then compared against real past infestation data to validate the model. A risk map was then developed to predict the likelihood of future infestation.

Early detection of emerald ash borer infestation using multisourced data: a case study in the town of Oakville, Ontario, Canda – Zhang and Robinson, 2014

This article uses aerial imagery to determine the position of infested trees from crown dieback. Th authors use a suite of different aerial imagery tools to calculate a score of infestation: healthy; low infest.; medium infest.; and high infest. The score is attained by taking distance from known infestation sites within 24km and assessing the damage to tree crowns by chlorophyll content to provide the score.

Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change – Liang and Fei, 2014

This article uses known climate predictions from the IPCC to model the species distribution of EAB across the North American continent. The authors use maximum entropy models (Maxent, software) to determine an optimum estimate of the probability distribution of EAB range. The authors use known climatic conditions from the native range of EAB since knowledge about the beetle's environmental physiology. They use IPCC climate predictions for 4 different carbon emission scenarios, two for 2020, and two for 2050, in addition to current climatic information. The EAB distribution is then layered onto known ash tree distributions to provide suitability for the borer.

Potential distribution of emerald ash borer: what can we learn from ecological niche models using Maxent and GARP? – Sobek-Swant et al., 2012

This article uses both maximum entropy models (Maxent) and genetic algorithm models (GARP) as software packages to determine species distributions of EAB. Both model frameworks used arcGIS to examine environmental variables from WorldClim. The variables of interest were mean annual temperature, mean annual precipitation, mean winter temperature, and mean winter precipitation. The ranges of EAB and ash trees was then overlapped to determine likelihoods of EAB. Data was only used for current climatic conditions. The models were also run over their native range in the Far East. This was conducted due to little information about EAB within its native range.

The authors noted that GARP performed better than Maxent at predicting already invaded regions. They account this to GARP being more effective at dealing with spatial bias than Maxent. They also note that GARP has been criticised in the past for a high number of false positives. They note that Maxent has been better at extrapolating new invasion sites. Using both and comparing would be advised.

Modelling the invasive emerald ash borer risk of spread using a spatially explicit cellular model – Prasad et al., 2009

This article develops a cellular automata model for the spread of EAB and is one of the major sources for recent research of EAB spread and infestation. The model accounts for local dispersal, and long-distance dispersal, as well as accounting for demographics, stochasticity, and anthropogenic factors. This makes this method appealing for use in Scotland. The authors use GIS data to create weightings related to anthropogenic factors, such as, road networks, and human population density. The model requires landscape data for ash distribution (taken here from USDA FIA records, or Landsat aerial data), known EAB distribution from field data, road locations and traffic density, campground sites, wood industry sites, and human population densities.

The authors use a gravity model for dispersal, and an inverse power law for whether a cell becomes infested. Due to the extensive detail required for this approach, we refer the reader to the article.

Appendix E - Simulation/decision support methods

Strategic removal of host trees in isolated, satellite infestations of emerald ash borer can reduce population growth – Fahrner et al., 2017

This article develops a simulation model parameterised from real data to determine the effectiveness of removing infested, or at-risk trees slows EAB population growth – and by extension, spread. The authors collected ash tree measurements of the diameter at breast height and used to estimate carrying capacity of a single tree. Measurements for EAB growth were taken from other articles cited within. To gain suitable parameters, the real data was then used to draw values from Gaussian distributions centred on the estimated mean and standard

deviations for use within the simulation. The authors also used the same approach for signs of predation of EAB by woodpeckers using data from their collected sites.

Each simulation was conducted with each of the different management scenarios: current strategy, no removal, removal at signs of predation, randomly removed, voltinism, no removal with voltinism, instant removal of trees equivalent to cumulative current strategy, random removal where phloem area was equivalent to current strategy.

The authors also conducted sensitivity analysis on the current and no tree removal strategies. Each of the scenarios was then compared with respect to proportional reduction in EAB production using mixed-effects models (R, lme4).

The role of restoration in the prevention of a large-scale native species loss: case study of the invasive emerald ash borer – Berry et al., 2017

This article investigates the possibility of invasion of EAB in Denver, Colorado, USA given that the nearby metropolitan area of Boulder, Colorado is infested. The authors develop a cost-benefit analysis for potential interventions from the SLAM procedure. They quantify the net benefits after the invasion in already invaded regions, and then determine cost-benefit before the invasion in Denver to predict the potential difference from intervention. The authors use empirical estimations for a background hazard function for invasion, previous literature to determine the benefits from ash, and calibrate parameters for their effectiveness of prevention, and effective hazard rate terms. Further details of the functional form can be seen within the article.

The authors then solve an optimisation problem given biological and fiscal constraints to determine which strategy is most beneficial. Their models were also subject to sensitivity analysis.

Estimating local spread of recently established emerald ash borer, *Agrilus planipennis*, infestations and the potential to influence it with a systematic insecticide and girdled ash trees – Mercader et al., 2016

This article uses a combination of collected EAB infestation data collected from previous years and use of simulation model from a previous article by the same authors (currently behind a paywall). This study was conducted in two separate sites in Michigan, USA. This project examined the implementation of the SLAM protocol.

The landscape is divided into grid cells for the purpose of the simulation. The authors determine a dispersal function determined by the presence of EAB using distance between cells which is based on a negative exponential function with an additional parameter which was estimated to find the best fitting dispersal function to previous data. The authors also include an estimation of expected detection within a cell which is dependent on the dispersal function with an additional weighting with respect to the condition of the ash tree.

The authors then compare their simulations with observed effects using linear least squares regression. There were two simulation models accounted for: no SLAM protocol, and SLAM protocol included – for which additional parameters and variables were added to account for.

Managing outbreaks of invasive species – a new method to prioritize pre-emptive quarantine efforts across large geographic regions – Withrow et al., 2015

This article examines a cost-benefit suitability analysis for pre-emptive quarantine for EAB in the North Eastern, USA, and bordering Canada. The authors develop a model that assesses risk of infestation from bordering counties and builds predictions iteratively. The model

requires presence-absence data for EAB at the county level in addition to suitability of hosts, quantified as a parameter accounting for as EAB hazard. The dispersal kernel for EAB is a parameterised Gaussian that is treated as a probability of dispersing from one county into the others. They account for human mediated dispersal by weighting the kernel by the amplitude of the distribution, i.e. increasing the amplitude will adjust the kernel such that some EAB will disperse farther.

The authors used non-linear regression to estimate the parameters for EAB expansion which were also subject to a sensitivity analysis. The spread model is then subject to a cost-benefit analysis to determine which counties are suitable for pre-emptive quarantine procedures.

Evaluating short term simulations of a forest stand invaded by emerald ash borer – Levin-Nielsen and Rieseke, 2015

The authors use a software program called “Forest Vegetation Simulator” (FVS) alongside field data collected from a forest in Northern Kentucky, USA. They collected field data to use within their study to determine the short-term dynamics of EAB induced mortality using FVS. They collected data in 2010 and 2012 and compared the outputs of the model to determine the impact EAB had over that time period. The data were then categorised for analysis at the tree level, and the plot level (0.0004 ha). There were no further details of FVS stated other than information informing us that it is regionally parameterised for the USA. Therefore, we should not expect that there is a similar variant for the UK, or Scotland. Details of the handbook are cited within, but have not been examined for relevance to the UK or Scotland.

Estimating the influence of population density and dispersal behaviour on the ability to detect and monitor *Agrilus planipennis* (Coleoptera: Buprestidae) populations – Mercader et al., 2012

This article uses simulations in an attempt to link population densities of EAB and detection probability. The authors use a model detailed in **Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis* – Mercader, 2011** and field data from three separate sites in Michigan, USA. The authors use the collected data to estimate larval densities within their sites and use the parameterised model to estimate the spread of EAB. They then compared these estimates with data collected in their sites. This article differs from **Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis* – Mercader, 2011** in that the dispersal kernel was altered to accommodate differing percentages of the population which engage in long distance dispersal events. They used repeated Bernoulli trials for each individual cell to determine the probability that EAB would be detected in the surveyed cell.

Evaluation of potential strategies to Slow Ash Mortality (SLAM) caused by the emerald ash borer (*Agrilus planipennis*): SLAM in an urban forest – McCullough and Mercader, 2011.

This article uses simulations to predict the effectiveness of insecticide used with SLAM protocol over a 10-year period. The authors refer to a previous model detailed in **Influence of foraging behavior and host spatial distribution on the localized spread of the emerald ash borer, *Agrilus planipennis* – Mercader, 2011**. They made changes to the model which allowed EAB individuals to disperse among trees within the same year allowing the females to visit and oviposit more than one ash tree. In doing so would also allow more realistic dynamics for individual EAB mortality from the insecticide treated leaves. Additionally, by modelling individual trees, the dispersal of EAB within the simulation is tracked better than within a coarser resolution. The authors used data from previous studies to parameterise their models – citations within. The authors examined scenarios of SLAM

procedure: no insecticide, applying insecticide on an increasing proportional scale to ash populations; targeting ash trees close to points of introduction; assuming private ash trees were not treated, but municipally owned tree were. They also included a cost-benefit analysis by pricing an individual tree and scaling the costs to the larger populations.

They found that no treatment was the most costly, followed by 10% of ash treated. The remaining treatments of 20-50% of ash had similar costs.

A dominance-based approach to map risks of ecological invasions in the presence of severe uncertainty – Yemshanov et al., 2011

This article models long-distance EAB spread via road transport links while assessing the uncertainty of infestation. The results were then used to develop a risk map for Eastern Canada. The model is based on a model developed by **There is no silver bullet: The value of diversification in planning invasive species surveillance. -- Yemshanov et al., 2014** which we refer the reader to. This model differs from the previous by including stochastic terms for each node determined by the EAB transmission rates. They then use second-order stochastic dominance to rank each node that is a route of transmission. These ranks are then used to create a risk map for transmission rates of EAB.

The influence of satellite populations of emerald ash borer on projected economic costs in U.S. communities, 2010-2020 – Kovacs et al., 2011.

This article uses an identical approach to the Kovacs et al. 2010 except they have re-parameterised the negative exponential kernel to include satellite populations. Therefore, we shall omit the details and use both articles in conjunction should the need arise.

Influence of foraging behaviour and host spatial distribution on the localised spread of the emerald ash borer, *Agilus planipennis* – Mercader et al., 2009

The model developed in this article has been a basis for other studies, therefore, we shall take a more detailed approach here. This article examines the effects of EAB foraging behaviour and distribution of ash on spread rates. The authors develop a spatially explicit coupled map lattice model with each cells accounting for the area of ash phloem available to EAB. The model can account for phloem levels from real inserted data. The model takes account of larval development, dispersal of fertilised adult females, and population growth encompassing oviposition and survival.

Larval development parameters were calculated from collected data and a functional relationship was statistically derived from logarithmic regression, further details within. Dispersal from each cell at time $t + 1$ is given by

$$N_{t+1}^i = \sum_{j=1}^n N_t^j \frac{e^{-bD_{ji}}}{\sum_{j=1}^{n+1} e^{-bD_{ji}}}$$

where N_t^j is the number of individuals present in cell j at time t , b is the parameter estimated in Mercader et al., 2009 (negative exponential distribution), and D_{ji} is the distance between cell j and cell i . To account for foraging behaviour, the authors adjust the equation with the addition of two parameters: one to simulate the attraction to resources, and another to control attraction to another neighbouring cell relative to the currently occupied cell.

Population growth is accounted for using a step function that is dependent on the consumption of phloem and is given by

$$N_t^i = \begin{cases} r^0 N_t^i, r^0 N_t^i \leq \frac{A_t^i}{C} \\ \frac{A_t^i}{C}, r^0 N_t^i < \frac{A_t^i}{C} \end{cases}$$

where C is the consumption rate in m^2 per individual, r^0 is the population growth rate, and A_t^i is the quantity of phloem present in cell i at time t . The parameter estimate for the population growth rate was conducted using data from previous publications between growing years and estimated using bootstrapping methods.

Using the above model the authors were able to adjust parameters and the simulation environment to examine 5 forms of foraging behaviour: unbiased; avoidance of ash devoid cells; bias towards the highest ash phloem within 200m; bias towards the highest concentration of ash phloem irrespective of their current position; and bias towards cells with the highest stressed ash. The final behaviour involved implementing the bias after phloem was reduced beyond a threshold value.

The entire methodology to develop this framework is within appendices within the article, including a script of the code performed in the programming environment R.

Modelling the spread of emerald ash borer – BenDor et al., 2006

This article uses software packages spatial modeling environment (SME) and STELLA which the authors admit to requiring some technical knowledge to use. They combine these software approaches with data from arcGIS to determine environmental factors relevant to EAB in Illinois, USA. Each aspect of the model is parameterised from other studies (citations within). This particular framework is one of the earliest modelling attempts of EAB infestation (infestation recognised in 2002) and it is therefore recommended that readers consult this article for information and use more recent developments when modelling EAB.

The spatial dynamics of invasive species spread – BenDor and Metcalf, 2006

This article uses the same modelling framework as **Modelling the spread of emerald ash borer – BenDor et al., 2006** and we ask the reader to refer to this section.

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