

## Review

# Pathway models for analysing and managing the introduction of alien plant pests—an overview and categorization



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## ABSTRACT

Alien plant pests are introduced into new areas at unprecedented rates through global trade, transport, tourism and travel, threatening biodiversity and agriculture. Increasingly, the movement and introduction of pests is analysed with pathway models to provide risk managers with quantitative estimates of introduction risks and effectiveness of management options. Pathway models vary greatly in mathematical form, level of detail, treatment of uncertainty and variability, as well as terminology. We conducted an overview and cluster analysis of pathway models to guide risk assessors, risk managers and model developers. We performed divisive hierarchical clustering on models retrieved from the peer-reviewed and grey literature to characterise and categorize the currently used modelling approaches. We distinguish two clusters of models based on product volume flows and two clusters of models based on the movement of individual agents. The first cluster of flow-based models describes a flow of infested material from origins to destinations according to fixed partitioning coefficients. These deterministic models can account for consequences of parameter variability and uncertainty. The second and third clusters of pathway models incorporate stochasticity in processes, and are respectively flow-based or agent-based. Models in the fourth cluster account for interactions between agents and nodes in the pathway. Conceptually, there are no fundamental differences between epidemic network models and this last cluster of pathway models. The choice of pathway model depends on the aim of the risk assessment, the available time, expertise and data. Models in clusters 2, 3, and 4 add sophistication and insight in variability to pathway analysis, but under time and data constraints, key objectives of risk assessors and managers can be addressed with models in cluster 1. The four clusters represent a comprehensive and fit for purpose toolbox of models.

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Abbreviations: RRO, risk reduction option.

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## 1. Introduction

Biodiversity and agriculture are threatened by increasing rates of introduction of non-indigenous plant pests (i.e. taxa of microorganisms and herbivores encompassing arthropods, as well as vertebrates) (Kenis et al., 2009; Blackburn et al., 2014; Roy et al., 2014; Bebbier, 2015; Lovett et al., 2016). The main reasons for the higher rates of introduction are increasing global trade, transport, travel and tourism which enable species to overcome natural dispersal barriers and expand into new territories (Meyerson and Reaser, 2002; Hulme, 2009; Drake and Mandrak, 2010; Siegert et al., 2014). Authorities responsible for biosecurity need to assess and compare the introduction risks associated with different pathways of pest introduction (Hulme, 2009). Risk managers need to weigh costs and benefits of alternative risk management options. Pathway models provide a tool to make risk assessments quantitative, transparent and more reproducible (Hennessey, 2004; OIE, 2004; Vose, 2008; EFSA, 2009; Devorshak, 2012), thereby strengthening the scientific basis of risk assessment as well as risk management.

In this paper, we adopt the pathway definition of Richardson et al. (2010): “The combination of processes and opportunities resulting in the movement of propagules from one area to another, including aspects of the vectors involved, features of the original and recipient environments, and the nature and timing of what exactly is moved”. Pathway models simulate the movement of propagules or their vectors (carriers) from a source along path with segments that are distinguished by discrete points to one or more points within a geographic area of concern. Pathway models quantify the number of pest propagules that might be moved into an area of concern (hereafter referred to as exposure). Most models can describe the outcome of several scenarios by modifying model inputs or management options, such as effects of changes to inspection, processing and transport, that may affect processes represented within the model. Such scenarios can support risk management decisions. Some models furthermore enable a spatially explicit characterization of exposure, informing on the scope for spatial differentiation of management (Colunga-Garcia and Haack, 2015).

Many pathway models account for uncertainty or variability in one form or another. Uncertainty is defined by EFSA (2015) as “limitations in knowledge”. Uncertainty in the context of pathway modelling can pertain to model inputs, model structure, or model parameters. Such uncertainty can be reduced by additional research or data collection. However, uncertainty can also pertain to future events predicted by a pathway model that are subject to variability in e.g. trade volume or in biological or weather processes affecting infestation rates of traded product. Variability is defined simply as non-constancy of a process or process outcome (Warren-Hicks and Hart, 2010). Variability is not reducible by research, but

variability may be characterised by surveillance and monitoring. Stochasticity is a way to represent variability in parameters or process outcomes with probability models (e.g. Vose, 2008).

Variability and uncertainty are not strictly separated in the literature, primarily because the former (variability) contributes to the latter (uncertainty): imperfect knowledge about future events. Despite uncertainty, quantification of expected exposure with a pathway model can help focus discussions about risk mitigation on facts and figures instead of risk perceptions. Quantification of uncertainty about exposure estimates can help target research and data collection efforts (including surveillance and monitoring) to reduce this uncertainty. Quantification of uncertainty about predictions of the future can point to either a need for research on processes or on a need for real time monitoring, to observe ongoing phenomena that cannot be well predicted. Analysing pathway models can assist in deciding what is needed to reduce uncertainty.

Two other approaches that are used to analyse the introduction of invasive pests are epidemic network models and gravity models (e.g. Bossenbroek et al., 2001; Jeger et al., 2007). Epidemic network models study an epidemic process in a network by characterising the contact patterns between susceptible infected, and immune individuals (Keeling and Eames, 2005). The contact patterns can be based, among others, on physical contact or movement of propagules. Gravity models describe the movement of agents (e.g. propagules or their vectors) in a system as a function of the characteristics of the source and the destination and the distance between the two (Bossenbroek et al., 2001). Whilst gravity models originate from Newtonian physics and have been widely applied to model trade flows, as well as human migration and mobility patterns (Simini et al., 2012), network epidemic models have their root in complexity science and have now become popular in human and animal epidemiology, with some applications in plant disease epidemiology (Moslonka-Lefebvre et al., 2011).

The number and diversity of pathway models in pest risk analysis are increasing rapidly (e.g., Benninga et al., 2012; Pains and Yemshanov, 2012; Ma et al., 2012). Therefore, several questions arise: (1) what types of pathway models are there?; (2) how can the models be categorized?; (3) what type of model is the most suitable for a given risk assessment purpose?; and (4) how are pathway models connected to related approaches such as epidemic network models and gravity models?

We searched the literature to retrieve pathway models for plant pest risk analysis, and characterised these with objective criteria to describe the current state of the art. We then categorized the models using statistical clustering. This analysis focuses on the mathematical aspects of the models, to bring order to the apparent chaotic diversity of approaches. Terminology is reviewed critically.

## 2. Methods

Characterization and categorization of the pathway models followed three general steps. First, we developed a common terminology to describe pathway models, epidemic network models and gravity models. Next, we described a set of objective criteria to characterise each pathway model that was found through a literature search. Finally, a clustering method was used to categorize the pathway models to a limited number of groups.

### 2.1. Pathway model terminology

We used terminology from graph theory to describe pathway models (Table 1, Banks et al., 2015). In pathway models, nodes represent spatial locations or categories of spatial locations relevant to the introduction process of the carrier or the pest. Examples of nodes are import locations, storage and packing houses and nurseries. For example, for the processing of imported logs into lumber, the logs might first arrive at a port of entry (node 1), be moved to a storage area (node 2), and processed at a mill (node 3). The lumber might be sold to a furniture manufacturer (node 4), and the waste might be used for pavement of garden paths (Douma et al., 2015). Nodes are connected by links (also called edges) which represent movement or other processes that modify the location, state or amount of what is moved. Such processes are for instance: treatment, processing, inspection and transport. Process outcomes include acceptance/rejection of a consignment at import and a change in location due to transport. For example, imported logs transported to a storage location after being inspected at the port of entry. A series of connected nodes is called a path, and the overall collection of paths is a graph or network. Individual agents (e.g. propagules or consignments of plant product) flow through this network from a place of production (source) to a place of consumption or waste disposal in the area of destination. Exposure is represented by propagules of the pest (e.g. egg-laying female insects, fungal spores) transferring to hosts in the area of concern.

**Table 1**  
Glossary with definition of terms used in this paper.

| Term               | Explanation                                                                                                                                                                                                                                                                              |
|--------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Agent              | An entity that is characterised by a set of attributes. In the context of pathway models, an agent may be a propagule of a non-indigenous plant pest or the vector that may move those propagules from one area to another. An agent is fully defined by its attribute values            |
| Attribute          | A property of an agent that can be measured at any node along the path and which may change when the agent moves through the network                                                                                                                                                     |
| Carrier            | A product which may carry propagules of a non-indigenous plant pest or a vehicle that may carry such a potentially infested product. Both product and vehicle provide a vector for propagules. For example, a log infested with pine wood nematodes or a truck loaded with infested logs |
| Consignment        | A quantity of a product that is traded, typically commercially, between a source and destination area                                                                                                                                                                                    |
| Edge               | See link                                                                                                                                                                                                                                                                                 |
| Entry              | The movement of a pest into an area where it is not yet present or present but not widely distributed and being officially controlled (FAO, 1996)                                                                                                                                        |
| Exposure           | The number of propagules that arrive in a given area and time window. Also known as propagule pressure                                                                                                                                                                                   |
| Flow               | A population of agents moving from a source area to a target area within a given time period, e.g. one year                                                                                                                                                                              |
| Network            | A collection of paths                                                                                                                                                                                                                                                                    |
| Node               | A point in space and time at which the state of the agent or the amount of infested material can be measured                                                                                                                                                                             |
| Path               | A set of linked nodes                                                                                                                                                                                                                                                                    |
| Pest               | Any species, strain or biotype of plant, animal or pathogenic agent injurious to plants or plant products (FAO, 1996)                                                                                                                                                                    |
| Process outcomes   | Anything that can change the attribute value/amount of infested material. Processes may have stochastic outcomes                                                                                                                                                                         |
| Propagule          | A unit of inoculum of a pest (Agrios, 2005)                                                                                                                                                                                                                                              |
| Link               | A process that affects the location or condition of infested material or the state of the agent that transits from one node to another. See process outcomes (also called edge)                                                                                                          |
| State of the agent | A specific combination of agent's attribute values                                                                                                                                                                                                                                       |
| Spread             | Expansion of the geographical distribution of a pest within an area (FAO, 1996)                                                                                                                                                                                                          |
| Uncertainty        | Imperfect knowledge about a property                                                                                                                                                                                                                                                     |
| Variability        | The existence of natural or anthropogenic variation in a property                                                                                                                                                                                                                        |
| Vector             | The means that carries a propagule                                                                                                                                                                                                                                                       |

### 2.2. Describing epidemic network models and gravity models

Epidemic network models are models (of any kind) that describe the transmission of diseases in networks. A network consists of a series of objects (nodes) that are interconnected by links (representing the relationship between the nodes). In this case, nodes represent individuals or populations of the pest or the host (Brooks et al., 2008; Cox et al., 2013). The nodes can have attributes (e.g. susceptible/exposed/infectious), and the infection status of a node depends on the probability of infection transmission due to links from other nodes (as well as the infection status of the same node at a previous time step of the simulation). The links that connect the nodes can represent various relationships and processes.

In gravity models nodes represent spatial locations or categories of spatial locations relevant to the movement of the carrier or the pest. Nodes have attributes that describe the infection status of the node, and their attractiveness to moving agents. Attractiveness of the node is often approximated by the some relevant characteristics of the node, such as the size of a lake, water quality etc (see Muirhead et al., 2011 for various of other proxies). Links represent the movement of agents. The movement rate of agents is based on the force of attraction exerted on the agent, which in turn is based on the distance of a node to the origin and the attractiveness (“weight”) of the nodes (Muirhead and MacIsaac, 2011).

### 2.3. Review of the literature

We reviewed the literature as per Woodcock et al. (2014) (Appendix S1 of Supplementary information) to find existing pathway models related to plant health. We limit our selection to plant health to keep the analysis tractable and focussed. In short, the ‘Web of Science’ database was queried on the 9th of July 2014 using multiple sets of keywords to retrieve papers that describe pathway models for plant pests. We excluded models that predicted movement/dispersal of plant pests in continuous space; e.g.; through diffusion or dispersal kernels. Further references were identified by checking reference lists of already found papers. In addition; the Google search engine was used to find additional pathway models in the grey (i.e. non-peer reviewed) literature.

**Table 2**

Characteristics used to describe pathway models (also used for the cluster analysis). See for a glossary Table 1.

| Nr. | Description of model feature                                                                                                                                 | Result (Abbreviation)                                                                                                                                                | Feature used in cluster analysis (weight) |
|-----|--------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------|
| 1)  | Name of model                                                                                                                                                |                                                                                                                                                                      | 0                                         |
| 2)  | Purpose                                                                                                                                                      |                                                                                                                                                                      | 0                                         |
| 3)  | Domain of application                                                                                                                                        |                                                                                                                                                                      | 0                                         |
| 4)  | Starting point and endpoint of the pathway                                                                                                                   |                                                                                                                                                                      | 0                                         |
| 5)  | How is exposure evaluated?                                                                                                                                   | <b>Relative or Absolute</b>                                                                                                                                          | 0                                         |
| 6)  | What is moving along the nodes?                                                                                                                              | Agents ( <b>A</b> ), or a flow of matter not distinguishing the agents ( <b>F</b> )                                                                                  | 1                                         |
| 7)  | Do the attribute values of the agents affect the process outcomes? For example does the infestation level of the agent determine probability to be detected. | <b>Yes or No</b>                                                                                                                                                     | 1                                         |
| 8)  | Do nodes affect the attributes of the individual? For example, can a moving consignment become infected when it passes an infected retailer?                 | <b>Yes or No</b>                                                                                                                                                     | 1                                         |
| 9)  | How are processes/relations (links) quantified?                                                                                                              | <b>Quantitative or other</b>                                                                                                                                         | 1                                         |
| 10) | How are processes/relations (links) modelled?                                                                                                                | Functions with stochastic ( <b>ST</b> ) or deterministic ( <b>DE</b> ) outcomes.                                                                                     | 1                                         |
| 11) | Is parameter uncertainty and/or variability dealt with?                                                                                                      | <b>Yes or No</b>                                                                                                                                                     | 1                                         |
| 12) | How are the parameters of the processes/relations (links) obtained?                                                                                          | Data derived from direct observations ( <b>DA</b> ), indirect observations (gravity model, <b>GR</b> ), other assumption ( <b>OT</b> ), not specified ( <b>NS</b> ). | 0.5                                       |
| 13) | What does “the pest” represent?                                                                                                                              | One species ( <b>1S</b> ), multiple species ( <b>mS</b> ), group of species ( <b>G</b> )                                                                             | 0.5                                       |
| 14) | What does the carrier represent?                                                                                                                             | one carrier ( <b>1C</b> ), multiple carriers ( <b>mC</b> )                                                                                                           | 0.5                                       |
| 15) | Does a node represent a function at a geographical location (e.g. port of Rotterdam) or a function only (non-spatial ports)                                  | A function at geographical location ( <b>SP</b> ) or a function only ( <b>FU</b> ) or a mixture of both ( <b>MI</b> )                                                | 0.5                                       |
| 16) | Are risk reduction options explored?                                                                                                                         | <b>Yes or No</b>                                                                                                                                                     | 0.5                                       |
| 17) | Is the pathway model part of a larger model?                                                                                                                 | <b>Yes or No</b>                                                                                                                                                     | 0.5                                       |

#### 2.4. Analysis

Each pathway model was described using 17 characteristics (Table 2). The relatedness among model approaches was explored by divisive hierarchical clustering (van Tongeren, 1987). In a first cluster analysis, we focused on the fundamental (mathematical) features of the models. In a second analysis, other, more general features were added, but they were given half weight so as not to overrule the fundamental features (Table 2). The dissimilarity matrix was calculated using Gower's distance, a frequently used measure to handle categorical variables (Gower, 1971).

### 3. Results

The literature search in Web of Science yielded 5,330 publications. Based on the inclusion criteria, 197 papers were studied in detail resulting in the selection of 14 papers that fitted the scope of this review. Nine more relevant papers were found by consulting the references cited in the selected 14 papers and through Google searches. The resulting list of papers is shown in Table 3 (model characteristics are shown in Appendix S3 of Supplementary information). The hierarchical clustering analysis identified four distinct clusters of pathway models (Fig. 1; Appendix S2 of Supplementary information). We decided not to further split cluster 3 for reasons explained below.

The second cluster analysis identified the same clusters that were identified with the first cluster analysis.

#### 3.1. Cluster 1: deterministic flow-based pathway models

The first and largest cluster (9 papers out of 23) consisted of models with a low level of sophistication when compared to models in the other 3 clusters (Fig. 1). These models (numbers 1, 2, 3, 8, 9, 10, 11, 15, 16; Table 3) were based on a trade network and accounted for the size of trade flows. These models did not allow for stochasticity in process outcomes: the traded product

was partitioned over the nodes according to deterministic fractions. Parameters were fixed within one simulation, although they could be drawn from a probability distribution. We refer to them as deterministic flow-based pathway models.

For example, Addo-Bediako et al. (2007) assessed the risk of introduction of the sweet potato weevil (*Cylas formicarius elegantulus* Summers) into the southern United States through shipment of sweet potatoes. In their model, the amount of infested sweet potatoes was determined by, among others, the effectiveness of postharvest treatment and border inspection. The effectiveness of the postharvest treatment was taken from a probability distribution and was multiplied by the incoming amount of infested material (also drawn from a probability distribution) to obtain the amount of infested material after postharvest treatment.

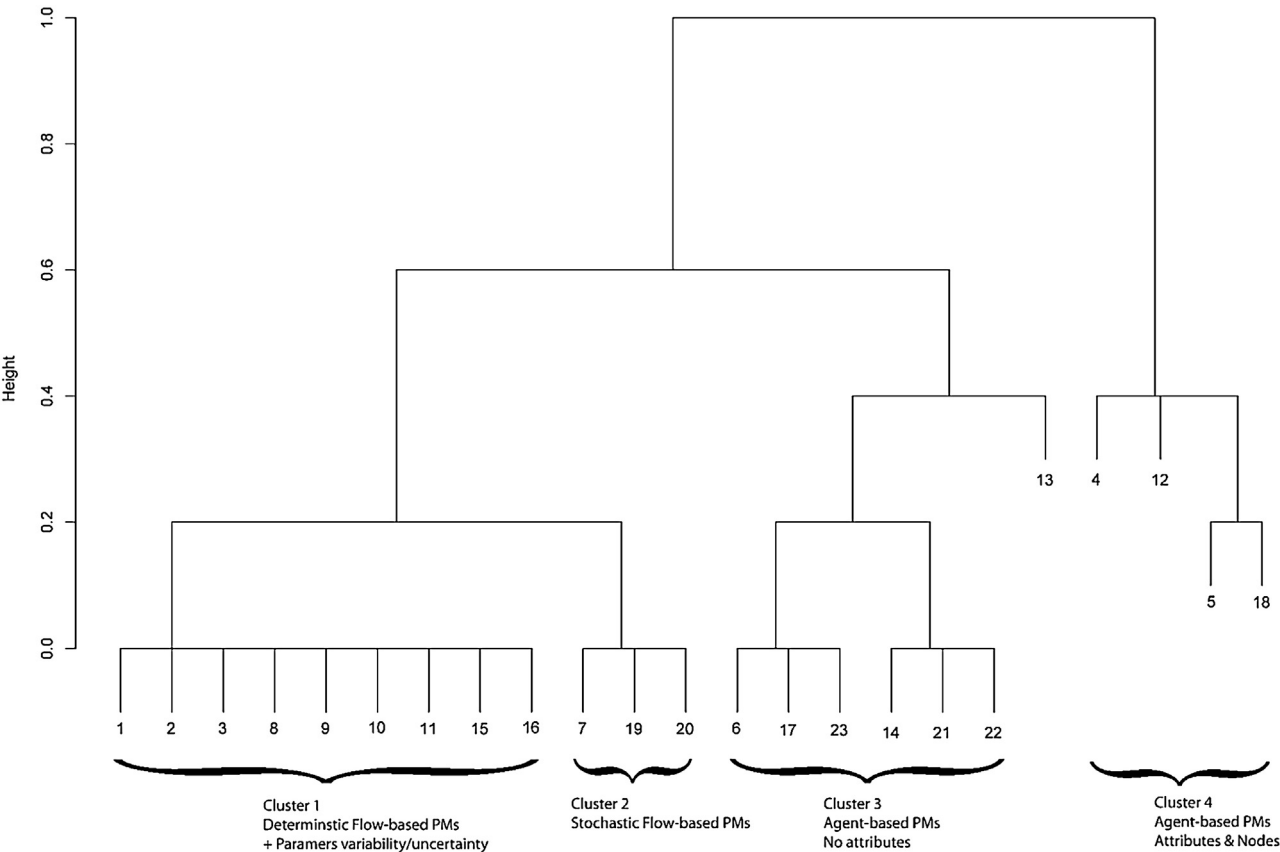
Parameters in this cluster of models were represented in all cases by a distribution of values to represent uncertainty or variability associated with the parameter (e.g. Auclair et al., 2005; Ma et al., 2012). In many cases, parameters were represented by the PERT distribution (a modified Beta distribution, tailored for expert elicitation (Vose, 2008)). Thus, in this cluster, processes were modelled deterministically, while parameters were drawn from distributions. Consequently, by running the model multiple times, the output variable was a distribution of values representing the variation in the parameter values.

#### 3.2. Cluster 2: stochastic flow-based pathway models

The second cluster, which we call stochastic flow-based pathway models, used a stochastic partitioning of trade flows over the nodes (three papers; numbers 7, 19 and 20 in Table 3), thus accounting for randomness in processes. For example, Jerde and Lewis (2007) modelled the number of transported pest propagules as a probabilistic process. The number of transported propagules differed across simulations and was determined by the total number of propagules subject to transport, the probability of transport, and the probability distribution describing the possible outcomes of

**Table 3**  
List of publications retrieved by literature search and used for analysis in this paper.

| Nr | Study                                      | Topic                                                                                                                                                                  |
|----|--------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1  | <a href="#">Addo-Bediako et al. (2007)</a> | Introduction of a potato weevil ( <i>Cylas formicarius elegantulus</i> Summers) in the USA                                                                             |
| 2  | <a href="#">Anonymous (2004)</a>           | Risk associated with pests on apples from New Zealand to Australia                                                                                                     |
| 3  | <a href="#">Auclair et al. (2005)</a>      | Assessment of the risk of introduction of <i>Anoplophora glabripennis</i> (Motschulsky) in municipal solid waste from the quarantine area                              |
| 4  | <a href="#">Benninga et al. (2012)</a>     | Cost-effectiveness of disease control                                                                                                                                  |
| 5  | <a href="#">Breukers et al. (2006)</a>     | Spread of brown rot ( <i>Ralstonia solanacearum</i> biovar 3, race 2) in the potato chain                                                                              |
| 6  | <a href="#">Carrasco et al. (2010)</a>     | Invasion of species in heterogeneous landscapes                                                                                                                        |
| 7  | <a href="#">Caton et al. (2006)</a>        | Introduction of insect pests with air cargo                                                                                                                            |
| 8  | <a href="#">EFSA (2014)</a>                | Entry of <i>Phyllosticta citricarpa</i> ( <i>Guignardia citricarpa</i> Kiely) to Spain on citrus fruit without leaves in commercial trade                              |
| 9  | <a href="#">Fowler et al. (2006)</a>       | Risks to the Southern United States associated with pine shoot beetle ( <i>Tomicus piniperda</i> Linnaeus), on different commodities originating from quarantine areas |
| 10 | <a href="#">Fowler et al. (2008)</a>       | Introduction of Karnal bunt ( <i>Tilletia indica</i> Mitra) with wheat into the EU                                                                                     |
| 11 | <a href="#">Gould et al. (2006)</a>        | Risk of establishment in the contiguous United States by <i>Copitarsia decolora</i> (Guenée) on asparagus from Peru                                                    |
| 12 | <a href="#">Harwood et al. (2009)</a>      | Risk assessment of <i>Phytophthora ramorum</i> (Werres) and <i>Phytophthora kernoviae</i> (Brasier) in the UK through grid-based and network modelling                 |
| 13 | <a href="#">Jerde and Lewis (2007)</a>     | General invasion model. No application to a specific case                                                                                                              |
| 14 | <a href="#">Koch et al. (2014)</a>         | Assess risk of forest pest spread through recreational travel                                                                                                          |
| 15 | <a href="#">Li et al. (2010)</a>           | Introduction risk of exotic fruit flies with fruit and travellers                                                                                                      |
| 16 | <a href="#">Ma et al. (2012)</a>           | Introduction risk of the guava fruit fly ( <i>Bactrocera correcta</i> Bezzi) associated with the importation of host fruit into China                                  |
| 17 | <a href="#">Paini and Yemshanov (2012)</a> | Introduction of Khapra beetle ( <i>Trogoderma granarium</i> Everts) through vessels to Australia ports                                                                 |
| 18 | <a href="#">Rebaudo et al. (2011)</a>      | Human induced spread of invasive species in agricultural areas                                                                                                         |
| 19 | <a href="#">Stanaway et al. (2011)</a>     | Human-mediated dispersal of alien species applied to spiralling whitefly                                                                                               |
| 20 | <a href="#">Stansbury et al. (2002)</a>    | <i>Tilletia indica</i> (Mitra) entering and establishing in W-Australia                                                                                                |
| 21 | <a href="#">Yemshanov et al. (2012b)</a>   | Estimation of rates of human assisted entry of forest pests in Canada                                                                                                  |
| 22 | <a href="#">Yemshanov et al. (2012a)</a>   | Map risks of ecological invasions, illustrated with emerald ash borer ( <i>Agrilus planipennis</i> Fairmaire)                                                          |
| 23 | <a href="#">Yemshanov et al. (2013)</a>    | Exploring uncertainties of human-assisted introductions of alien forest pests                                                                                          |



**Fig. 1.** Dendrogram obtained by divisive hierarchical clustering on the characteristics of the mathematical structure of the model. We distinguish four types of clusters. Cluster 1 includes deterministic flow-based models that include parameter uncertainty or variability. Cluster 2 includes stochastic flow-based models. Cluster 3 includes agent-based pathway models without interaction between the nodes and the agents. Cluster 4 includes agent-based models in which the agent and the nodes interact. The divisive coefficient is 0.93 and measures the degree of clustering. Numbers identify the models and refer to the numbers in Table 3. A glossary of terms is presented in Table 1.

the transport process. The proportions that partition the flow were interpreted as true probabilities. Thus, given a fixed input, the output was stochastic. The size of the flow at one node was determined by the probability that an event occurred and the size of the flow that was subject to that event.

### 3.3. Cluster 3: agent-based models without interaction between agent and nodes

The third cluster consisted of agent-based models that simulated the behaviour of individual “agents” (Grimm, 1999), albeit without interaction between agents and nodes (six papers, numbers 6, 14, 17, 21, 22, 23 in Table 3). The agents in these models were individual propagules or individual carriers carrying propagules. The distinction between agent-based and flow-based is independent of what constitutes the agent; the agent could for example represent an insect, or a branch, packet or container of wood. In agent-based models, the estimate of exposure was obtained by simulating the behaviour of the individual agents (Harwood et al., 2009; Yemshanov et al., 2012b). The fate of an agent in these models was a stochastic realization determined by the randomness in processes acting on it. Multiple simulations (Monte Carlo simulations) resulted in a flow of agents that were spread over the network enabling the calculation of exposure as the sum of all propagules getting in contact with the host in the area of concern.

The models in the clusters 2 and 3 give similar predictions, provided that the total amount of infested material that is imported in the flow-based model equals the amount of infested material that is transported by the agents. The predictions are similar because each agent obeys the same behavioural rules and different agents act independently from one another. As a result, the total exposure equals the sum of exposure arising from the individual agents.

Members (6, 17, 23) of the left branch of the third cluster (Fig. 1) included parameter uncertainty in addition to process variability. In contrast, members of the right branch of this cluster (14, 21, 22) included process variability only. For example, members of the left branch would describe pest survival through a binomial distribution with a fixed probability whereas members of the right branch would in addition include variability in the probability of survive. However, to keep the number of clusters limited, we decided not to further split this cluster. Parameter uncertainty or variability was usually modelled using uniform distributions on an interval that was considered relevant for the parameter. The resulting model outcome is a distribution of exposure values that is a combination of stochasticity in processes and parameter variability or uncertainty.

### 3.4. Cluster 4: agent-based model with interaction between agent and nodes

The 4th cluster consisted of agent-based models with interaction between agents and nodes (four papers, numbers 4, 5, 12, 18, Table 3). Interaction may occur, for instance, if i) the agent's attributes determine the path through the network, and ii) the node can act as a reservoir of the pest and transmit the pest to another agent. Adding these features to the pathway requires specifying agent attributes.

An example of the first option is the model developed by Breukers et al. (2006). They included the relationship between the infestation level of a potato consignment and the probability of detection during inspection. In this study, the potato consignment is the agent, and the number of potatoes and the infestation level were attributes of this agent. This led to heavily infested consignments having a greater chance of detection and removal from the trade flow.

The possibility of transfer of the invasive organism from a node to an agent was included in three of the four models in cluster 4.

This reflects reality: an infected node (e.g. a warehouse) could infect an agent (e.g. potato consignment) when it passes that node.

The most complicated pathway models (No 5 & 18) included a two-way movement of propagules between agent and node. For example, a village became infested when visited by infested agents, and a non-infested agent could become infested by visiting an infested village (Rebaudo et al., 2011). Such exchange of propagules between agent and a node adds an extra layer of complexity to exposure assessment since an agent that is moving through the network may affect another agent by infecting a node. This potentially leads to complex emergent behaviour. This type of pathway model shares many properties with epidemic network models, and the border with epidemic network models is fuzzy.

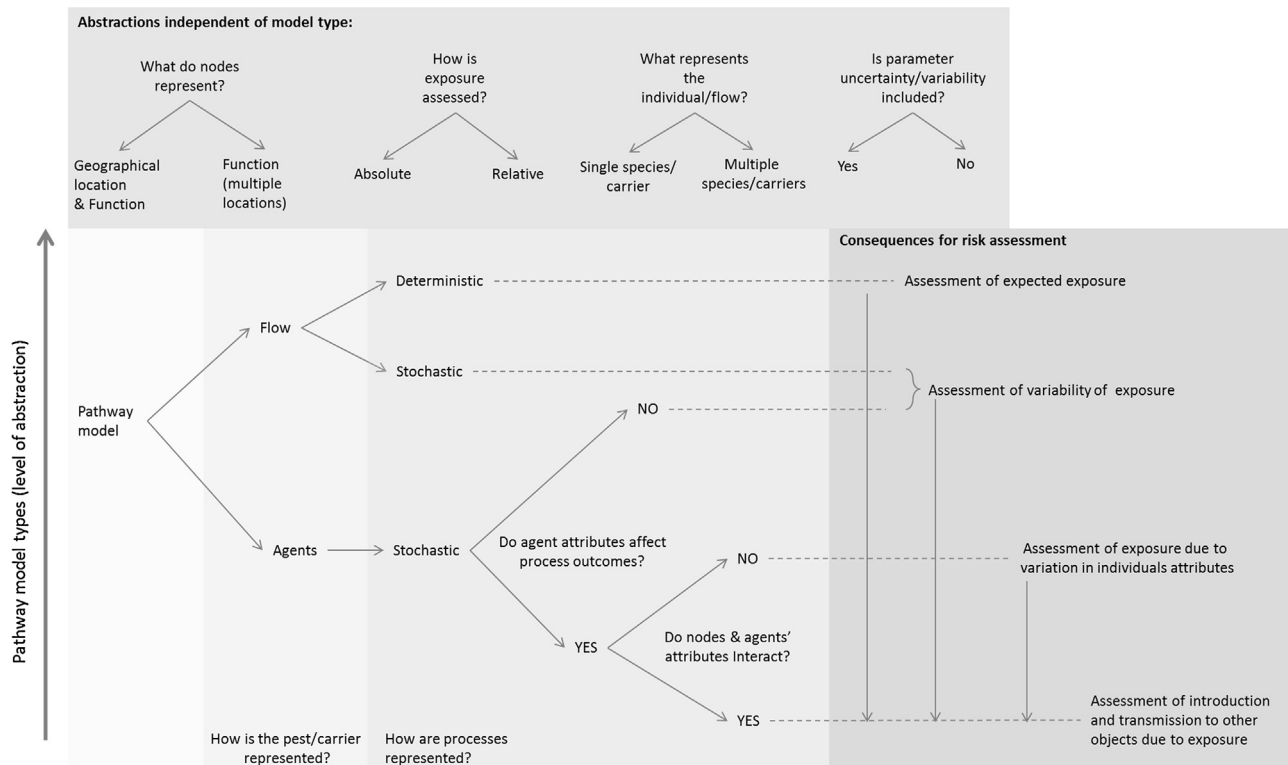
Various model characteristics occurred in all clusters (Fig. 2). In some models, nodes represented an activity at a specified geographical location, while in other models a node represented all geographical locations with a particular activity. In addition, some pathway models modelled a single taxon, others a group of taxa (e.g. insects) or multiple carriers (7 out of 23). This allowed a comparison across those taxa. A more detailed discussion on these characteristics can be found in Appendix S4 of Supplementary information.

## 4. Discussion

This overview and cluster analysis resulted in a categorization of four types of pathway model; (1) deterministic flow-based, (2) stochastic flow-based, (3) agent-based models without interaction between agent and nodes and (4) agent-based with interaction between agent and nodes. Each model is built up from a number of traits (Fig. 2). Deterministic flow-based models (cluster 1) partition the total infested product flow over nodes according to fixed coefficients. Given a set of parameters, these models produce a deterministic outcome of calculated exposure. Given parameter uncertainty or variability, multiple run with such a model can generate variable outcomes, representing either the uncertainty of parameter values (e.g. the level of infestation in the country of origin), variability in these parameter according to site and year (e.g. Fowler et al., 2008), or both. Deterministic flow-based models are the most prevalent kind in the literature, probably because they are the easiest to build. We infer that these models strike a favourable balance between usefulness of the model and resources required to build it (Soliman et al., 2015).

Stochastic flow-based models (cluster 2) account for variability generating processes in the pathway, e.g. the chance process of detecting infestation during inspection at ports (Eschen et al., 2014). Such models produce variable outcomes even with fixed parameters, and are preferred if the emphasis is on quantifying variability in exposure due to variability generating processes. In addition, these models can be easily extended to assess the consequences of parameter variability or uncertainty on exposure by drawing parameter values from probability distributions.

Models of cluster 3 generate variability in processes by simulating individual agents. While the mathematics of applying a probability model to single agents in the models of cluster 3 is somewhat different from the mathematics of applying a probability model to a population of agents (a “flow”; cluster 2), both approaches produce identical results (Douma et al., 2015). They produce a distribution of exposure outcomes for a given set of parameters by accounting for variability generating processes in the pathway. The only difference between the two approaches is that models in cluster 3 produce additional information on the distribution of agent attribute values. Models in cluster 2 do not produce such a distribution because they consider only the total flow, not the agents.



**Fig. 2.** Overview of the diagnostic traits of pathway models. Pathway models can take various forms, each with different features and levels of complexity. Some model abstractions can be made to any pathway model and do not modify the mathematical structure (shown in the dark grey upper block). The four types of pathway models are depicted in the middle (light grey). The consequences of the model type for risk assessment are shown at the right (dark grey).

If agent attributes affect process outcomes but not *vice versa* (cluster 4) the model can—under certain circumstances—be also formulated as a stochastic flow-based model of cluster 2 (Douma et al., 2015). However, the behaviour of a population of interacting agents cannot be easily described without modelling the agents separately (Grimm, 1999). An agent-based approach is most convenient if the modeller aims to take interaction between agents and the effect of agent attributes into account without averaging attribute values over the population, with the inherent risk of bias due to Jensen's inequality (Hilborn and Mangel, 1997).

The time needed to develop a pathway model is related to model complexity. Models in the 4th cluster require most time in terms of model conceptualisation, implementation, data collection, and interpretation. Model complexity increases with the level of detail in which the system is represented. A key challenge is parameterization. Biological characteristics of the pest, pest incidence in commodities as well as the size and dynamics of the commodities' trade are usually not well documented (Robinet et al., 2016 *in press*). Often, data may not be accessible because of commercial interests. For instance disclosure of connectivity data from plant nurseries, wholesalers and retailers appears to be difficult (Dehnen-Schmutz et al., 2010; Pautasso et al., 2010). As a result, proxies are often needed, based on less reliable sources such as expert judgement or (inter)national trade-statistics such as Eurostat. The shortage of precise data weakens the usefulness of pathway modelling. There is an urgent need for increased data collection on plant trade if pathway modelling is to become standard practice in future pest risk assessments (Colunga-García et al., 2013; Eschen et al., 2015).

With greater model complexity the number of parameters increases. For cluster 1, information is only needed on how the flow of infested material is partitioned over the nodes. The second cluster of pathway models requires additional information on the probabilistic processes leading to a stochastic distribution of the

infested flow over the nodes. The third cluster of pathway models requires additional information on the agents carrying the propagules, the variation among the agents (size of consignments, trucks etc.), and the stochastic nature of processes acting on them. Variation in infestation level among infested trade consignments is a highly relevant piece of information. However the authors have not come across examples that report this information. Thus, while it may be possible to conceptualize the model, it is often very difficult to come up with parameter values (but see Gould et al., 2013). Again this stresses the importance of data collection for all nodes of the pathway, in particular the infestation rate of traded consignments. The fourth cluster of pathway models requires data on how the agent and the nodes interact. Information is needed on the probability that an agent becomes infested when passing an infested node, and on the probability that a node becomes infested when an infested agent passes. Depending on the complexity of the model in cluster 4, information is needed on how the characteristics of the agent determine its fate (e.g. how humidity of wood packaging affect the probability of pest survival).

#### 4.1. Pathway models, network models and gravity models

Mathematically and conceptually we did not find fundamental differences between epidemic network models and the cluster 4 pathway models. Some pathway models (5 & 18) in cluster four would fit the definition of epidemic network model.

Nevertheless, two differences appear between pathway models and epidemic network models. First, pathway models are predominantly used to study the entry of an invasive (pest) species when it moves from a source area to a target area, by assessing the exposure at target points. Thus, pathway models are often uni-directional (a sense of direction is implicit in the definition of pathways with a start and end point), while most epidemic network models are

not. In plant disease epidemiology, directionality of flow has been incorporated in various epidemic network models, by using asymmetric adjacency matrices, but these still enable movement of disease propagules in both directions, although at different rates (Moslonka-Lefebvre et al., 2012). Second, pathway models have a strong emphasis—particularly in risk management studies—on the carrier or pest that is moved. Epidemic network models on the other hand tend to focus on disease dynamics, and the state of the nodes (agents or populations of agents that can become infected). A key insight from network epidemic models relevant to pathway models is that, in the case of directed networks, the increase in risk posed by heterogeneity in the number of connections among nodes (i.e. the presence of hubs) is only present if there is a positive correlation between incoming and outgoing links among the nodes of the network (Pautasso and Jeger, 2014). The mathematical similarity between both approaches allows incorporating entry, establishment and spread in the same modelling framework: a pathway model may be used to simulate entry while an epidemic network model can be used to study establishment, spread and epidemiology of the disease within the target area. This is a future opportunity to overcome the – often ecologically difficult to justify – separation of the pest risk assessment in entry, establishment, spread and impact. In fact, the processes of entry and spread may be identical, the only difference being whether they are within the confines of the area of concern (spread) or across its border (entry).

Mathematically and conceptually we did not find fundamental differences between gravity models and pathway models. The clustering procedure corroborated this finding: three models parameterised the movement of pests through a gravity approach (no's 6, 18 and 19), of which one of them was found in cluster four. Indeed, some gravity models are not unidirectional and simulate epidemics and are thus more like epidemic network models. Yet, one subtle difference appeared between pathway models and gravity models. Characteristically, gravity models specify the attractiveness of a node by making specific assumptions on what determines the movement between nodes (Jongejans et al., 2015). Parameterisation of movement rates through a gravity approach is attractive as proxies can be used to predict movement of agents. However, such an approach does not reflect the peculiarities of movement patterns (Kaluza et al., 2010; Duenas and Fagiolo, 2013). Therefore, a pathway model using a gravity approach can best be used as a first approximation when data on movement probabilities are absent.

#### 4.2. The choice of pathway model depends on the aim of the risk assessment

Pathway models are important because they allow systematic analysis of the entry of pests, the identification of critical stages in the pathway, and risk ranking of different pathways of a pest. These models help identifying risk reduction options (RROs) that may be applied in the country of origin, before, during or after shipment or after arrival. Models in each of the four clusters have their strengths and limitations to evaluate pest movement and entry and the effectiveness of RROs.

Deterministic flow-based models (cluster 1) are probably most useful

- 1) For a rapid risk assessment of movement and entry;
- 2) in case of data scarcity and high parameter uncertainty. Parameter uncertainty and variability are the only sources of variation included in these models. Hence variation in exposure is directly related to variability and uncertainty of the underlying parameters;
- 3) for evaluation of RROs that affect the size of the infested flow before the stage where consignments are formed, e.g. pest-free

places of production, pest control during crop growth and pest-adverse harvesting methods and storage conditions;

- 4) to prioritize among pathways or commodities, and to contrast the high-risk and low-risk pathways. For example Fowler et al. (2006) identified the movement of lumber and logs as the main pathways for introducing the pine shoot beetle;
- 5) in a tiered approach. If one commodity is predicted to be of particular concern, a more complex model is needed. A tiered approach helps economize on effort and costs for pathway development. Caution is needed, however. Averaging over large areas or over a long time span without considering variability may lead to results that deviate substantially from more detailed parameterisations, e.g. as a result of Jensen's inequality (Hilborn and Mangel, 1997). Soliman et al. (2012) show how spatial aggregation may result in biases in pest risk assessment.

When the aim of the risk assessors is to study the consequences of stochasticity in process outcomes, stochastic flow-based models (cluster 2) or agent-based models (cluster 3 or 4) are appropriate. Adding stochasticity to the processes in the pathway model has a number of advantages:

- 1) The distribution of exposure values allows to identify worst and best cases of exposure due to inherent randomness of the processes;
- 2) the impact of RROs on the distribution of exposure values may be evaluated. In particular, models from cluster 3 allow evaluating the effect of RROs on the frequency of infested consignments. They may also be used to test whether pest incidence of infested consignments exceeds acceptable levels;
- 3) the addition of stochastic processes can be used to determine when exposure meets the minimum number of propagules needed for successful infestation of a host (similar to Allee effects; Jerde and Lewis, 2007). When stochasticity in process outcomes and parameter uncertainty is included, it helps risk assessors and managers separate these two sources of unpredictability. For instance, this separation allow quantifying the variability originating from randomness in the number of surviving propagules, and the uncertainty that arises from poorly estimating the survival probability. For the latter, more precise estimates could be obtained through research if desirable (Warren-Hicks and Hart, 2010). Several simulation techniques are available to separately simulate the consequences of variability and uncertainty (Pouillot and Delignette-Muller, 2010). We did not come across pathway models that applied either of these techniques.

The models in cluster 4 incorporate variability in the characteristics of agents and nodes. This allows risk assessors to

- 1) make the fate of the agent depend on its characteristics. This feature is necessary when simulating the consequences of variation in the infestation degree, e.g. the probability of detection of the carrier at import inspection or the probability of successful transfer and establishment of the pest as a function of infestation degree;
- 2) model transmission of propagules from nodes to agents. This may be helpful to model post-harvest infection. The idea that nodes infest uninfested material could also be implemented in flow-based pathway models but only if a flow of uninfested material is modelled as well;
- 3) model transmission between agents. This may be helpful to model cross-contamination of carriers;

- 4) identify and evaluate RROs that apply to the consignment, e.g. treatments of consignments before shipment, import inspection and post-entry quarantine.

It may be easier to parameterize some processes at the carrier level than at a flow-based level – provided data are available. For example, it is difficult to estimate what proportion of the infested flow passes border inspection while this naturally follows from an agent-based pathway model – assuming the agent represents a consignment. Only few models in cluster 4 included agent attributes that affected process outcomes. One key reason may be lack of data, time and resources to build models at such a level of detail (Soliman et al., 2015).

## 5. Conclusion

This overview and clustering analysis clarifies that four classes of pathway models may be distinguished in the domain of plant pest risk assessment. There is a continuum of models from comparatively simple (deterministic flow-based; cluster 1) to comparatively complex (stochastic agent-based; cluster 4), where the latter category of models merges with epidemic network models. Similarly, gravity models could be applied in the plant health domain and may be particularly useful when movement data is missing. The biggest challenge in applying pathway models in supporting pest risk assessment is not in model structure but in the parameterization. Prioritization of data collection for important model parameters would improve the utility of pathways models. In addition, making data sources open access will help balancing the interests of international trade with those of nature conservation and protection of agriculture against invasive alien species.

## Author contributions

JCD, WvdW, MP, and RV designed research. JCD collected and analysed data. JCD, MP, WvdW, RCV, CR, LH, MCMM and JS wrote the paper.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.08.009>.

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