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Exploring critical uncertainties in pathway assessments of human-assisted introductions of alien forest species in Canada

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A B S T R A C T

Long-distance introductions of alien species are often driven by socioeconomic factors, such that conventional “biological” invasion models may not be capable of estimating spread fully and reliably. In this study, we demonstrate a new technique for assessing and reconstructing human-mediated pathways of alien forest species entries to major settlements in Canada via commercial road transportation and domestic trade.

We undertook our analysis in three steps. First, we used existing data on movement of commodities associated with bark- and wood-boring forest pests to build a probabilistic model of how the organisms may be moved from one location to another through a transportation network. We then used this model to generate multiple sets of predictions of species arrival rates at every location in the transportation network, and to identify the locations with the highest likelihood of new incursions. Finally, we evaluated the sensitivity of the species arrival rates to uncertainty in key model assumptions by testing the impact of additive and multiplicative errors (by respectively adding a uniform random variate or symmetric variation bounds to the arrival rate values) on the probabilities of pest transmission from one location to another, as well as the impact of the removal of one or more nodes and all connecting links to other nodes from the underlying transportation network.

Overall, the identification of potential pest arrival hotspots is moderately robust to uncertainties in key modeling assumptions. Large urban areas and major border crossings that have the highest predicted species arrival rates have the lowest sensitivities to uncertainty in the pest transmission potential and to random changes in the structure of the transportation network. The roadside survey data appears to be sufficient to delineate major hubs and hotspots where pests are likely to arrive from other locations in the network via commercial truck transport. However, “pass-through” locations with few incoming and outgoing routes can be identified with lower precision. The arrival rates of alien forest pests appear to be highly sensitive to additive errors. Surprisingly, the impact of random changes in the structure of the transportation network was relatively low.

1. Introduction

Large-scale domestic and international trade, involving the relatively rapid and long-distance transport of immense quantities of raw commodities and finished goods, has become a defining feature of the world economy. In North America and elsewhere, the proportional growth of trade volumes is expected to exceed the rate of economic growth (UNCTD, 2007; WTO, 2008). The transportation corridors that facilitate all of this trade have also become critical gateways for introductions of alien species: non-indigenous insects, pathogens, and other organisms are often inadvertently transported

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to novel territories in shipping containers and commercial transports, where they may become established as ecologically and/or economically harmful pests (Hulme et al., 2008; Hulme, 2009; Kaluza et al., 2010; Lounibos, 2002; Westphal et al., 2008).

Increasing levels of trade and complexity of transportation networks have been recognized as key drivers of ecological invasions (Bain et al., 2010; Pysek et al., 2010; Bradley et al., 2012). Recent studies have linked the long-distance spread of alien species populations to anthropogenic transport (Blakeslee et al., 2010), patterns of historical trade and settlement (Brawley et al., 2009), marine trade (Bain et al., 2010; Kaluza et al., 2010) and recent economic and demographic benchmarks (Pysek et al., 2010). Notably, quantitative assessments of how alien organisms may be carried through a transportation network and subsequently introduced at various locations remain limited in scope. In part, this may be attributed to the growing complexity of modern transportation networks as well as a multitude of potential socioeconomic factors that influence local and global trade flows, and thus, the associated movements of alien species (Pysek et al., 2010). Furthermore, the capacity to realistically assess the invasion potential of any individual species is usually constrained by a lack of reliable data about the organism's biology and behaviour, as well as time pressures faced by decision makers when attempting to craft an appropriate response to new (or anticipated) incursions. In this situation, rapid assessments of the potential origins of new (or anticipated) species introductions can serve as an important starting point in identifying possible pest outbreaks and strategizing immediate response and screening measures.

When planning rapid-response activities after the discovery of a new invader, decision makers often need to identify, at least in approximate terms, the potential of the species to invade the location(s) of interest (Lodge et al., 2006; Muirhead et al., 2008). These assessments can be undertaken with modeling tools that trace the movement pathways of an alien organism to locations of interest from its suspected region(s) of origin (e.g., Carey, 1996; Muirhead et al., 2006; Wang and Wang, 2006; Pitt et al., 2009). Since a pest found at a particular destination may have originated from multiple locations, such estimates of species arrival are rarely precise, and often have a considerable degree of uncertainty.

In this paper we present a new analytical technique that helps quantify the potential of an invasive pest to arrive at the location(s) of interest from elsewhere. We employ a pathway model that traces the arrivals at the location(s) of interest back to multiple origin locations, and thus offers an advantage over typical cellular automata spread models. Compared to common forward-looking models that predict spread rates with a distance-dependent dispersal probabilistic kernel, the pathway model does not have the same distance constraint. The predicted arrival rate at a given destination location accounts for the possibility of spread from all potential origins based on the configuration of the spread pathways, regardless of distance. By being comprehensive with respect to origins, the model has better capacity to address the contribution of long-distance, human-mediated dispersal.

We concentrate on predicting human-assisted movements of bark- and wood-boring insects with commercial freight transportation through the road network in Canada and the U.S. Similar research in the past suggested that volumes of transported commodities and freight that may harbour alien organisms can be used to predict the likelihoods of unintentional introductions of non-native organisms across large geographic regions (Drake and Lodge, 2004; Hlasny and Livingston, 2008; Tatem et al., 2006; Westphal et al., 2008; Yemshanov et al., 2012b). We performed our analysis within the setting of a complex network of transportation corridors and used existing data on shipments of commodities and cargoes that have been historically associated with alien forest insects (Table S1.1, Appendix S1) to characterize the network. With respect to the analytical results, we primarily focused on municipalities and major border crossings in Canada, but given the high degree of integration between the U.S. and Canadian economies, we also traced movements of pest-associated commodities from and to the U.S.

In terms of systematic groups, we used the same insect families of bark- and wood-boring forest insects as presented in Koch et al. (2011) and Yemshanov et al. (2012a). This work relates to our previous geographic analysis of alien species' entry potential from major Canadian ports (Yemshanov et al., 2012a), but instead of focusing on aspects of alien species arrivals associated with international trade, our objective was to identify general patterns and critical uncertainties associated with the potential movement of alien forest insects through the domestic (i.e., intra-continental) transportation network in North America and to identify important pathways, "hubs" (cf. Floerl et al., 2009) and "crossroad" locations in the network.

2. Methods

2.1. The pathway analysis concept

Consider a transportation network that describes the likely movements of a non-native organism within a region of interest based on the shipment patterns of particular cargoes or commodities known to harbour the pest. The network consists of a set of n locations, or nodes. We assume that any node in the network could be either an originating location for the pest or a site where the pest might be detected. The nodes in the network are connected by a system of pathways. Each corridor has an associated volume of pest-associated commodities that are transported through it during a certain time period. In the general case, the movement of a pest with commercial transportation can be described by a system of ij vectors, each of them depicting the flow of pest-associated commodities between a pair of network nodes, i and j.

We conducted the analysis in three major steps. First, we used existing data on movement of commodities associated with forest pests (i.e., wood- and bark-boring insects) to build a probabilistic pathway model of how these organisms may be moved through our transportation network. Next, we used the pathway model to generate multiple sets of estimates of the pests' patterns of movement from each individual network node (i.e., one candidate origin location at a time) to elsewhere in the network. The pathway model output is a list of the estimated transmission rate values for all unique "origin–destination" pairs of nodes. We then rearranged this list so each destination location would have an associated distribution of its potential origin locations and associated transmission rate values. From this vector we then estimated the average rate at which a species of interest could be expected to arrive at a given location from the other nodes in the network. We summarized these location-specific arrival rate estimates by ranking major Canadian settlements and U.S.–Canada border crossings by their potential to receive alien forest species with commercial freight shipments from other regions in Canada and the U.S. through the transportation network. As a last step, we tested the sensitivity of the rankings to uncertainty about key pathway model parameters, such as the basic configuration of the transportation network and the probability of pest transmission between network nodes.

2.2. Step 1: developing a probabilistic pathway model of pest movement through the transportation network

2.2.1. Data on movement of pest-associated commodities

For this study, we made the assumption that the probability of human-assisted spread of forest pests with commercial transportation is related to the volume of pest-associated commodities moved through particular corridors in the transportation network, as well as the network's local configuration (i.e., the number of outgoing routes from a particular location). For simplicity, we assumed that the likelihood of a forest pest being moved from any location *i* to another location *j* depends linearly on the tonnage of pest-associated commodities that are transported along the corridor, *i*–*j*, connecting the two locations. We did not consider biological aspects pertinent to particular species or taxonomic groups during this analysis, but rather focused on a generalized pathway assessment based on the flows of pest-associated commodities and the configuration of the network.

We used a Commercial Vehicle Survey (CVS) database maintained by Transport Canada to build the network of flows of relevant commodities in Canada and the U.S. The CVS database, which was developed from a 2005 to 2007 survey at truck weigh stations across Canada, consists of records that collectively describe truck-based freight shipment patterns in our study region (see Yemshanov et al., 2012a for a description). Each database record summarizes a single freight shipment route and the transported volumes of certain commodity types that are commonly associated with forest insects (Table S1.1, Appendix S1). Notably, the CVS data documented only the primary pickup and destination locations for each route.

Each location specified in the database was assigned geographic coordinates based on the Canadian Database of Geographic Names (NRCan, 2010) or a corresponding U.S. database of populated places (USGS, 2009). Previously, Yemshanov et al. (2012a) used the CVS data to apportion the entry potential of alien forest species with international trade from major Canadian ports, but here we did not consider only the entry potential of the ports. Rather, by treating every location in the network as a possible origin node, we were able to characterize the forest pest movement potential throughout the entire Canada–U.S. road network.

The CVS data were then parsed into a set of unique pathway segments, each connecting two nodes, *i* and *j*, in the network. Subsequently, the cumulative tonnages of pest-associated commodities for each pathway segment *ij* were used to build a pathway matrix where each element defined the probability, p_{ij}, of a pest being moved with commercial truck transport from location *i* to location *j* (Appendix S1). The pathway matrix stored 4380 nodes and 29,900 non-zero p_{ij} probability values for all possible pairs of (i,j) locations in the transportation network:

$$\mathbf{P}_t = \begin{bmatrix} 0 & p_{12} & \cdots & p_{1n} & 1-\sum\limits_{j=1}^{n} p_{1j} \\ p_{21} & 0 & \cdots & p_{2n} & 1-\sum\limits_{j=1}^{n} p_{2j} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & p_{n2} & \cdots & 0 & 1-\sum\limits_{j=1}^{n} p_{nj} \end{bmatrix} \quad (1)$$

where the elements $1-\sum_{j=1}^{n} p_{ij}$ describe the probability of mortality of an alien species leaving node *i* (see Appendix S1). The time transition was recalculated for a one-year period, reflecting a relatively short-term assessment timeframe. All pathway simulations were assumed to occur within a single year.

We used $\mathbf{P}_t$ to generate stochastic realizations of potential movements of a pest from a given location of interest *i* throughout the transportation network. With *i* set as the point of "origin", the model simulated subsequent movements of the pest from *i* to other network locations *j* by extracting the transmission probabilities from $\mathbf{P}_t$ associated with location *i*. The process continued until a selected node had no outgoing paths or a terminal state was chosen based on the elements $1-\sum_{j=1}^{n} p_{ij}$ in $\mathbf{P}_t$. Finally, for each location pair (i,j), an "arrival rate", φ_{ij}, was estimated from the number of the times the pest arrived at *j* from origin location *i* over *K* multiple stochastic model realizations:

$$\varphi_{ij} = J_{ij}/K \quad (2)$$

where J_{ij} is the number of individual pathway simulations where a pest originated at location *i* and ultimately arrived at location *j*, and *K* is the total number of individual simulations of pathway spread from *i* (for this study, $K = 2 \times 10^6$ for each location pair (i,j)).

In theory, the identification of nodes with the highest potential to receive a non-native pest could be done directly from the CVS data without undertaking stochastic pathway simulations. However, the development and application of the pathway model were necessary for exploring the effects of uncertainty in the underlying traffic flow data and the structure of the transportation network. Moreover, the stochastic model formulation allows us to potentially incorporate other assumptions associated with the organism's survival potential during transit, and to address the possibility of picking up/unloading infested cargoes in intermediate locations.

2.3. Step 2. Analysis of species arrival rates with the probabilistic pathway model

The simulations in Step 1 provided, for each location *i*, a list of the rates, φ_{ij}, at which a pest was moved from that "origin" location to $n-1$ other locations *j* ($j = 1, ..., n, j \neq i$). Because origin and destination locations in the network, and possible connections between them, were fixed, it was possible to recombine the outputs into an assessment of the total species arrival rate at each "destination" location *j* (i.e., based on individual simulations started at other locations $i, i = 1, 2,..., n, i \neq j$, that ended at *j*). Essentially, every node *j* in the transportation network had a corresponding list of its potential *i* source locations, each of which was characterized by the estimated rate of pest arrival from that node *i* to *j*. In practical terms, this step required assembling a table (Table 1) of the φ_{ij} values in dimensions of the *n* origin and *n* destination locations. Each row in Table 1 contains the probabilities (φ_{ij}) of a pest being moved from origin location *i* (marked as "origin" in Table 1) to the other *j* locations in the network. Conversely, each column in Table 1

Table 1

An aggregation of individual pathway simulations into a summary pathway database: (a) The table's rows (the φ_{ij} values in the shaded area) denote the probabilities of a pest being moved from a given origin location (e.g., "Origin location 1") to other nodes in the network (e.g., the destination locations in columns 2, 3, ..., *n*); (b) The columns in the table (the φ_{ij} values in the column outlined in bold) show the probabilities of the pest being moved to a given destination location (i.e., "Destination location 3") from the other network nodes locations (the origin locations in rows 1, 2, ..., *n*).

Locations (nodes) in the transportation network						
"Origin" location (a starting point of pathway simulations)	Destination location 1	Destination location 2	**Destination location 3**	...	Destination location *n*	
Origin location 1	1 (origin)	φ_{12}	$\boldsymbol{\varphi_{13}}$	...	φ_{1n}	<—(a)—>
Origin location 2	φ_{21}	1 (origin)	$\boldsymbol{\varphi_{23}}$	...	φ_{2n}	
Origin location 3	φ_{31}	φ_{32}	**1 (origin)**	...	φ_{3n}	
...	...	...	**...**	...	...	
Origin location *n*	φ_{n1}	φ_{n2}	$\boldsymbol{\varphi_{n3}}$ <—(b)—>	...	1 (origin)	

summarizes the probabilities of a pest arriving at a given "destination" location j (shown in the column's head) from the point of origin i.

Because the arrival rates for each j destination location had to be estimated from each possible i point of origin, this ultimately translated to estimation of $n(n-1)$ arrival rates for all location pairs (i, j). For large n, these $n(n-1)$ rates would be difficult to interpret. However, it was possible to summarize pest movement through the network when the nodes were considered from the destination location perspective. For each location j, we summed the arrival rates φ_{ij} from all other nodes i ($i = 1, ..., n$; $i \neq j$) as a measure of the location's potential to receive a pest from elsewhere:

$$\varphi_j = \sum_{i=1}^{n, j \neq i} \varphi_{ij} \tag{3}$$

We then ranked and mapped the resulting φ_j values in geographical space. The nodes with the highest ranks exhibit the highest potential to receive alien species from elsewhere in the transportation network, and thus may be considered prime candidates for preventive surveillance or other biosecurity activities. Since the CVS data did not include roadside surveys recorded at U.S. weigh stations, we have only reported analysis summaries for Canadian locations and U.S.–Canada border crossings.

2.4. Step 3. Finding uncertainty thresholds in the probabilistic pathway model

2.4.1. Model aspects tested

Errors and knowledge gaps associated with the model structure and key parameters propagate to uncertainty in the model output (Li and Wu, 2006; Walker et al., 2003). In this study, we estimated the impact of uncertainty in key pathway model assumptions on the location-specific φ_j values (i.e., the outputted species arrival rate estimates). We performed the uncertainty analysis in three basic steps: (1) generating a probability distribution associated with a parameter of interest; (2) performing multiple simulations of the pathway model with the parameter values sampled from the distributions; and (3) summarizing the results from repeated realizations of this process (Crosetto and Tarantola, 2001; Crosetto et al., 2000; Li and Wu, 2006; Morgan and Henrion, 1990). Here, we focused on two key model aspects: uncertainty in the transmission probability values, p_{ij} (Eq. (1)), and uncertainty in the configuration of the transportation network (i.e., the presence–absence of a particular node and the paths that connect this node with the other locations).

We evaluated uncertainty in the p_{ij} values from two different perspectives. The first scenario added symmetric variation bounds around the p_{ij} values in the $\mathbf{P}_t$ matrix calculated from the CVS data (see Eq. (1)) but did not change their average values. Each pair of "plus-minus" bounds defined the endpoints for a symmetric uniform distribution $\pm[0; z]$ from which we then sampled the transmission probability values as:

$$p^*_{ij} = p_{ij}(1 \pm \varepsilon), \text{ where } p^*_{ij} \in [0; 1], \varepsilon \in [0; z] \text{ and } z \in [0; 0.6] \tag{4}$$

and then used the p^*_{ij} values in a new set of randomized pathway simulations. This scenario explored the impact of multiplicative errors on the p_{ij} values. In general terms, these errors can be interpreted as uncertainty associated with estimation of the arrival rates, but assuming that the general pattern of the commodity flows within the transportation network is well known (so the mean p_{ij} values across all simulations do not change).

The second scenario estimated the impact of additive errors by adding a uniform random variate ε ($\varepsilon \in [0; z]$) to the p_{ij} values regardless of their expected values and observing the impact on the location-specific species arrival rate, φ_j. This scenario changed the mean values of p_{ij} by adding uniform random variation within gradually increasing sets of bounds, z:

$$p^*_{ij} = p_{ij} + \varepsilon, \quad \text{where } \varepsilon \in [0; z] \text{ and } z \in [0; 0.07] \tag{5}$$

While the first scenario (Eq. (4)) adds uncertainty bounds around the p_{ij} values and does not change the mean values, the additive scenario (Eq. (5)) shifts all p_{ij} values (including the baseline values $p_{ij} = 0$) towards a uniform random distribution and, in turn, changes the patterns of commodity flows across the network.

Our third scenario explored the impact of uncertainty associated with the configuration of the transportation network. This approach goes beyond traditional sensitivity analysis (cf. Henderson-Sellers and Henderson-Sellers, 1996; Swartzman and Kaluzny, 1987) and focuses on changes in the network's topology and connectivity (cf. Krammer and Täubig, 2005; Newman, 2003). To keep the analysis consistent with the abovementioned scenarios, we used a relatively simple simulation technique in which we temporarily removed a uniform random proportion of nodes, ε ($\varepsilon \in [0; z]$ and $z \in [0; 0.6]$), from the network and observed the corresponding changes in the species arrival rates φ_j.

2.4.2. Sensitivity metric

Our primary goals were to identify the locations where uncertainty had the highest relative impact on the species arrival rate φ_j and also to test the stability of the estimated highest φ_j values. For our probabilistic pathway matrix $\mathbf{P}_t$, we generally expected to see greater response to added variation at locations with higher φ_j values. However, instead of comparing locations directly in terms of their φ_j values, we examined the impact of uncertainty on the partial ranks of locations based on these values. We assigned the location with the highest estimated φ_j value an integer rank of 1 and the remaining lower-rated locations with consecutive ranks of 2, 3, ..., n. For each location, we then estimated the difference between its rank given uncertainty and its rank under the baseline scenario (with no uncertainty) as Δr_{jz}:

$$\Delta r_{jz} = (r_{jz} - r_{j0})/n \tag{6}$$

where r_{j0} is the rank of a location j based on its pest arrival rate φ_j in the baseline scenario (i.e., with no uncertainty assumptions); r_{jz} is the rank in the scenario that assumes a level of uncertainty, z (i.e., an upper bound of a uniform distribution $[0; z]$); and n is the total number of ranks equal to the number of nodes in the network.

Since the values r_{j0} and r_{jz} represent ranks rather than the actual transmission rate values, the lowest rank value always denotes the locations with the highest arrival rates, and the highest rank value (which is equivalent to n, the total number of ranks) denotes the lowest-rated locations. Hence, if a location's r_{jz} value increases this indicates a decrease of the arrival rate value, and thus positive values of Δr_{jz} mean a decrease of the species arrival rate (and vice versa). A near-zero Δr_{jz} value suggests that uncertainty has little impact on the corresponding φ_j value. We then identified the nodes with the highest positive and lowest negative values of Δr_{jz} and analyzed their geographical distribution.

2.4.3. Finding uncertainty thresholds

The response of the species arrival rate φ_j to uncertainty also depends on the level of variation in z. For example, a low amount of variation in the p_{ij} values may have little impact on the φ_j values, but this impact could increase abruptly once the value of z exceeds a certain threshold. Therefore, we set a further analytical objective of stratifying the network's locations by their responses to different levels of uncertainty and finding meaningful geographical patterns in this stratification.

For each of the three uncertainty scenarios described above, we performed a series of simulations, starting from the baseline scenario (i.e., with zero uncertainty, $z = 0$) and then increasing the variation bounds for z. Then, for each Canadian location we plotted the average change in rank Δr_{jz} as a function of the uncertainty level z. Since each geographical location had its own unique curve, we further grouped the locations' individual curves into 5–6 compact clusters with distinct shapes. For this analysis, we used hierarchical clustering with a Euclidean distance metric and Ward's agglomeration method (Ward, 1963), an approach that produces compact spheroid groups with the lowest possible variance. We then identified the clusters that exhibited high sensitivity to uncertainty across the broadest range of z and mapped them in geographical space.

3. Results

3.1. Baseline scenario

The distribution of the pest arrival rates in the baseline scenario appears to be highly skewed. The skewness was 11.1, and the median and mean values of φ_j were 0.0056 and 0.027, respectively. The nodes with high predicted arrival rates above 0.5 represented approximately 0.82% of the total population and were predominantly concentrated in densely populated urban areas (which we have termed as "hubs") and at major border crossings (Fig. 1, Table 2, Appendix S2). In eastern Canada, the locations with the highest arrival rates (above 0.5) outlined major transportation corridors between Detroit (MI), Toronto (ON) and Montreal (QC), as well as the U.S. border city of Sault Ste. Marie (ON) (Fig. 1a). Western Canada (Fig. 1b) had fewer hotspot locations, most prominent of which were the U.S.–Canada border crossing near Blaine (WA), White Rock (BC) and Calgary (AB), a major hub city on the TransCanada Highway 1 transportation corridor. The other locations in western Canada with arrival rates above 0.2 were typically urban areas or major border crossings (Fig. 1b, Table 2 and Table S2.1).

3.2. Uncertainty analysis

3.2.1. Sensitivity to multiplicative errors in p_{ij} values

All nodes that showed high sensitivity to multiplicative errors in the p_{ij} values (with the greatest changes in rank, Δr_{jz}) were small towns and rural settlements on primary and secondary highways (Table S3.1). In all cases, the change in rank value was positive, indicating that the arrival rate is predicted to decrease in these locations if accounting for estimation error in the p_{ij} values. Most are in southern Ontario and southern Quebec, with the exception of one location in Nova Scotia. Notably, the average changes in rank for the locations with the highest arrival rates in the baseline scenario (Table 2, Section B) show near-zero sensitivities to uncertainty. This indicates that the arrival rate estimates for large urban areas and major border crossings are fairly robust to multiplicative errors in the p_{ij} values.

3.2.2. Sensitivity to additive errors in p_{ij} values

The locations with the most extreme changes in rank, Δr_{jz}, in response to additive errors in the p_{ij} values (Table S3.2) show both positive and negative extreme changes in rank. This implies that additive uncertainty in the p_{ij} values has the potential to either increase or decrease the species arrival rate φ_j. Significantly, the rank changes for major border crossings and large cities (Table 2, Section C) are at least an order of magnitude lower than the values presented in Table S3.2. This implies that the estimates of the species arrival rates for large cities and major border crossings are moderately robust to additive errors in the p_{ij} values, but to a much lesser degree than in the multiplicative errors scenario.

3.2.3. Sensitivity to uncertainty about the presence/absence of network nodes

The impact of random node removal on the arrival rate values appears to be quite uniform: Table S3.3 shows roughly similar number of locations with positive and negative changes in rank among the locations with the highest changes in rank, Δr_{jz}. This suggests that the impact of random removal of a portion of the network's nodes is fairly symmetric. None of the locations with the

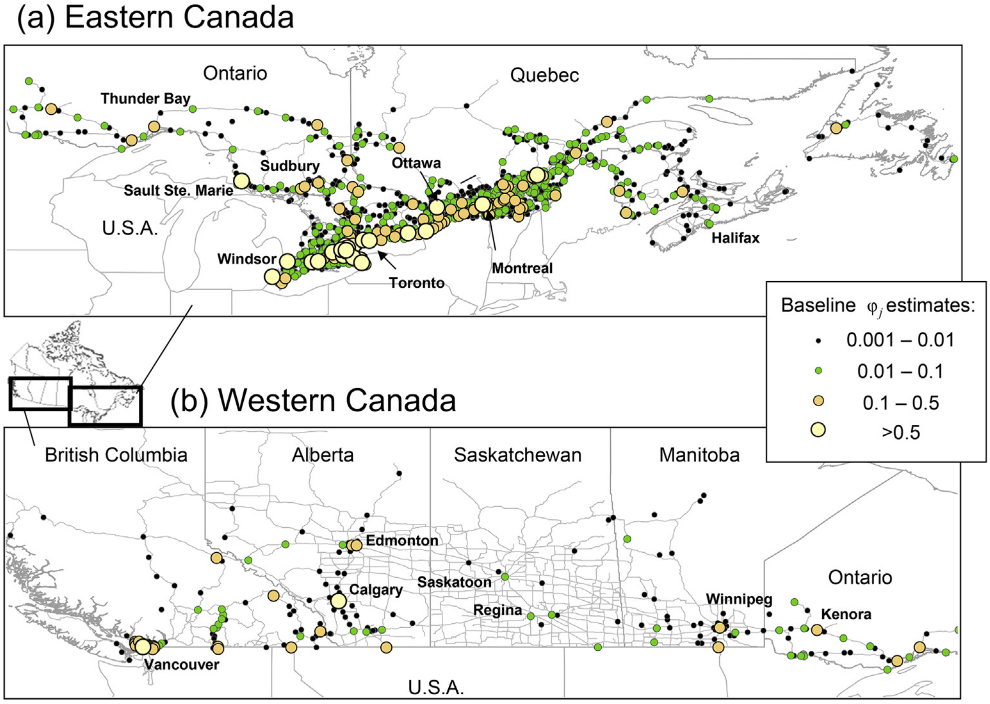

Fig. 1. Location-specific species arrival rates (φ_j) in the baseline scenario: (a) Eastern Canada; (b) Western Canada.

Table 2
Locations with the highest species arrival rates (φ_j) in the baseline scenario (top-20 list).

Location name	Province/ State[a]	Location type[b]	Nearest transportation corridor/border crossing	A. Baseline scenario		Uncertainty analysis					
						B. Multiplicative errors in p_{ij}		C. Additive errors in p_{ij}		D. Random node removal	
				Rank, r_{j0}	φ_j	Δr_{jz}	Cluster no.[c]	Δr_{jz}	Cluster no.[d]	Δr_{jz}	Cluster no.[e]
Toronto	ON	U	Hwy 401 corridor, S[f] ON	1	2.38[g]	–[h]	5	0.004	5	–	5
Mississauga	ON	U	Hwy 401 corridor, S ON	2	1.950	–	5	0.009	5	–	5
Montreal	QC	U	TransCanada Hwy 40/20, S QC	3	1.775	–	5	−0.001	5	–	5
Windsor	ON	UB	Hwy 401, SW ON border w/MI	4	1.628	–	5	−0.001	5	–	5
Trafalgar	ON	U	Hwy 401, S ON near Oakville, ON	5	1.574	–	5	0.052	4	–	5
Oakville	ON	U	Hwy 401 corridor, S ON	6	1.270	–	5	0.022	5	–	5
Whitby	ON	U	Hwy 401 corridor, S ON	7	1.230	–	5	0.034	5	–	5
Brampton	ON	U	Hwy 401 corridor, S ON	8	1.210	–	5	−0.002	5	–	5
Sarnia	ON	UB	Hwy 402, SW ON border w/MI	9	1.200	–	5	0.005	5	–	5
Bowmanville	ON	U	Hwy 401 corridor, S ON	10	1.139	–	5	0.028	5	–	5
Gananoque	ON	UB	Hwy 401, S ON border w/NY	11	1.043	–	5	0.037	5	–	5
Fort Erie	ON	UB	Queen Elizabeth Way, S ON border w/NY	12	0.971	–	5	0.048	4	–	5
Quebec	QC	U	TransCanada Hwy 40/20 corridor, S QC	13	0.881	–	5	−0.007	5	–	5
London	ON	U	Hwy 401 corridor, S ON	14	0.799	–	5	0.022	5	–	5
Vineland	ON	U	Hwy 401 corridor, near Mississauga, ON	15	0.752	–	5	0.056	4	–	5
Blaine (US)	WA	UB	I-5, NW WA border w/White Rock, BC	16	0.673	0.001	5	0.065	4	–	5
Niagara Falls	ON	UB	Queen Elizabeth Way, S ON border w/NY	17	0.672	−0.001	5	0.018	5	–	5
Calgary	AB	U	TransCanada Hwy 1/2, S-central AB	18	0.638	0.002	5	0.051	4	–	5
Cambridge	ON	U	Hwy 401 corridor, SW ON	19	0.633	−0.001	5	−0.003	5	0.001	5
Ottawa	ON	UB	Hwy 417 corridor, SE ON border w/QC	20	0.632	−0.001	5	0.003	5	−0.001	5

[a] Canadian provinces: AB – Alberta; BC – British Columbia; ON – Ontario; QC – Quebec; SK – Saskatchewan; U.S. States: MI – Michigan; NY – New York; WA – Washington.

[b] Location type: U – urban area; B – border crossing.

[c] Cluster profiles (i.e., the average change in rank, Δr_{jz}, as a function of the uncertainty level, z) are shown in Fig. 2c.

[d] Cluster profiles (i.e., the average change in rank, Δr_{jz}, as a function of the uncertainty level, z) are shown in Fig. 3c.

[e] Cluster profiles (i.e., the average change in rank, Δr_{jz}, as a function of the uncertainty level, z) are shown in Fig. 4c.

[f] Directions: S – southern; W – western; E – eastern; N – northern.

[g] Species arrival rate, φ_j is a sum of the arrival rates from individual locations, φ_{ij}, $\varphi_{ij} \in [0; 1]$. Its highest values can exceed 1.0.

[h] The difference in rank, Δr_{jz} is between −0.001 and 0.001.

highest arrival rates in the baseline scenario (Table 2) appear in Table S3.3. Indeed, all of these locations have extremely low changes in rank due to uncertainty in the network configuration (Table 2, Section D). In short, big cities and high-traffic border crossings with high φ_j values have multiple incoming and outgoing routes, therefore a removal of a random portion of nodes (and thus linked routes) appears to have less impact on the arrival rates in these locations compared to more remote locations with low traffic volumes and very few (or no) alternative connecting routes. The low sensitivity to random removal of links connecting the network nodes also suggests that the transportation network may be a scale-free type (Albert et al., 2000; Jeger et al., 2007; Pautasso and Jeger, 2008). A scale-free network has a subset of super-connected hubs that increases the chance of faster-spreading events, while local connectivity is de-emphasized. Analyses to better understand the transportation network's connectivity and topology at multiple scales will be the focus of future work.

3.2.4. *Geographical distribution of critical uncertainty thresholds*

We plotted the geographical distribution of point clusters with the highest sensitivity to uncertainty for each of our uncertainty scenarios in Figs. 2–4, where each cluster groups the locations with similar sensitivity profiles (shown in Figs. 2c, 3c and 4c, as the change in rank, Δr_{jz}, vs. the uncertainty level, z). In the multiplicative errors scenario (Fig. 2 and Table S3.3), the response to uncertainty is asymmetric and yields mostly positive changes in rank. Clusters 1 and 2 (Fig. 2c) show the highest response to the uncertainty level z and include mainly locations in southern Ontario. Most of the locations with the highest changes in rank in Table S3.1 belong to cluster 1 (Fig. 2c). Cluster 3 shows sensitivity to multiplicative errors in p_{ij} only when the uncertainty level z exceeds 0.3 (i.e., ±30% uniform random variation around the baseline p_{ij} values). The locations in Cluster 3 are typically found in areas with limited connecting routes or relatively low road density (for example, highways in northern Ontario or western Canada). As noted previously, the locations with the highest φ_j arrival rates exhibited only negligible changes in rank due to multiplicative errors; all of these locations were assigned to cluster 5 (Table 2, Section B).

In the additive errors scenario (Fig. 3), the response to errors in the p_{ij} values is symmetric. Clusters 1 and 2 correspond (Fig. 3c), respectively, to the locations with the greatest positive and negative changes in rank (Table S3.2). In this scenario, cluster 1 includes mainly locations in Ontario and New Brunswick, while cluster 2 largely includes locations across southern and eastern Quebec and Newfoundland (Fig. 3a). These results suggest that the impact of additive errors in the p_{ij} values may depend on the role a particular location plays in the flow of pest-associated commodities. Locations in areas with diverse traffic patterns, such that the locations can serve as both transit hubs and final destinations, show mostly positive changes in rank (i.e., in Δr_{jz}). Locations in areas with more localized traffic, where they are less likely to be transit hubs, typically show negative changes in rank.

In the scenario that tests the impact of random removal of network nodes (Fig. 4 and Table S3.3), the response to uncertainty does not depend much on the uncertainty level z. The absence of obvious geographic clustering of the locations with the most extreme changes (clusters 1 and 3) suggests that uniform random changes in the network's structure do not generally affect locations with the highest φ_j values; indeed, the locations listed in Table 2 (Section D) all belong to cluster 5, which generally exhibits very low sensitivity to uncertainty.

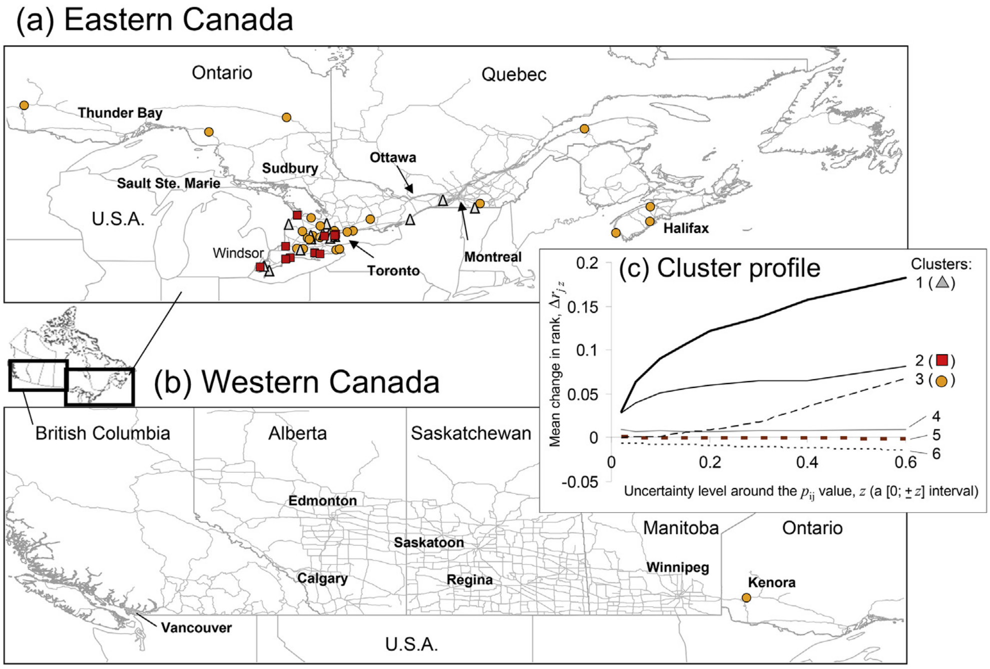

Fig. 2. The locations with the most pronounced responses to multiplicative errors in the p_{ij} values: (a) Eastern Canada; (b) Western Canada; (c) cluster profiles (i.e., curves that summarize, for each cluster, the average change in location rank, Δr_{jz}, versus the level of symmetric random variation z around the p_{ij} values). Clusters 4–6, with low sensitivity to this source of uncertainty, are not shown.

4. Discussion

As implemented in this study, the pathway analysis concept provides a relatively simple way of engaging transportation data in time-critical pest risk assessments and follows approaches commonly used in modeling transportation and trade flows (De Jong et al., 2004; LeSage and Polasek, 2006; Porojan, 2001). General applications of the network-based modeling approach provide sufficient capacity to uncover possible linkages between the spread of non-native organisms and transportation (Blakeslee et al., 2010), trade (Brawley et al., 2009; Bain et al., 2010; Bradley et al., 2012) and other socioeconomic activities (Pysek et al., 2010). Network-based modeling tools also help address more general ecological issues, such as identifying ecological preferences of alien species

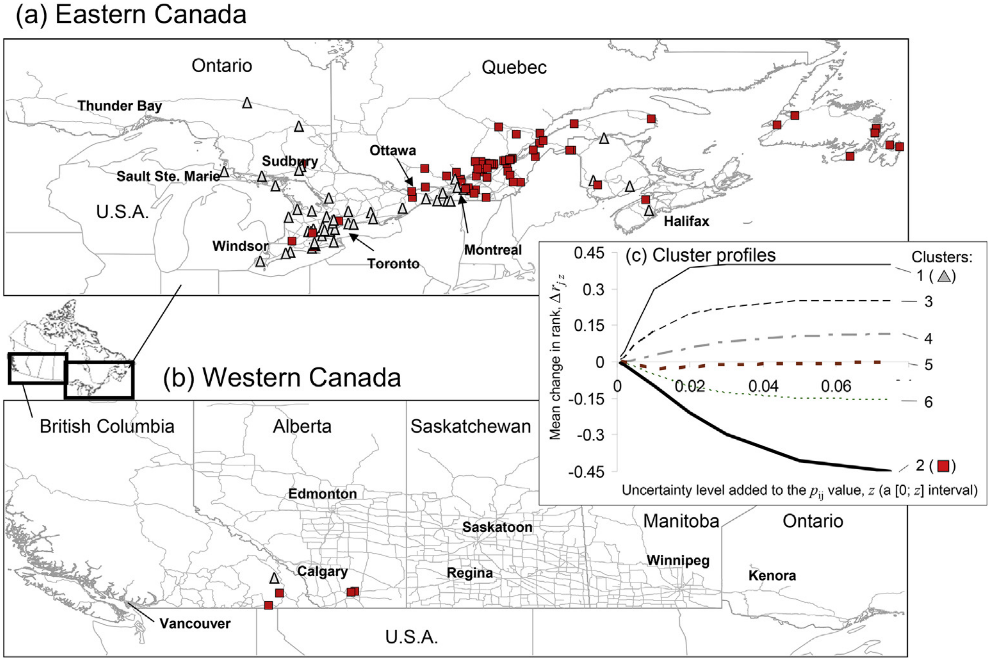

Fig. 3. The locations with the most pronounced responses to additive errors in the p_{ij} values: (a) Eastern Canada; (b) Western Canada; (c) cluster profiles (i.e., for each cluster, the average change in location rank, Δr_{jz}, versus the level of uniform random variation z added to the baseline p_{ij} values). Clusters 3–6, with moderate and low sensitivity to this source of uncertainty, are not shown.

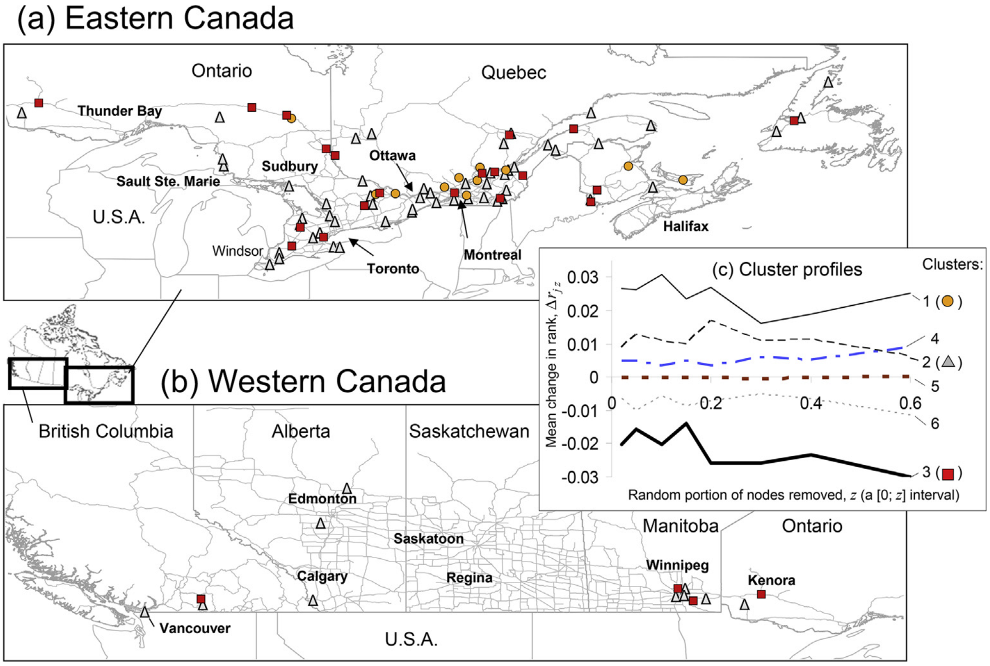

Fig. 4. The locations with the most pronounced responses to uncertainty about the structure of the transportation network: (a) Eastern Canada; (b) Western Canada; (c) clusters' profiles (i.e., for each cluster, the average change in location rank, Δr_{jz}, versus the random percentage of network's nodes z that were removed from the analysis). The geographical locations in clusters 4–6 were insensitive to this type of uncertainty and are not shown.

(Vanderhoeven et al., 2010), persistence of species populations (Bode et al., 2008; Cumming et al., 2010) or the configuration of ecological food webs (Chiu and Westveld, 2011).

The pathway model used in the study had sufficient accuracy to recreate the sequential routes that were recorded in the CVS data (Fig. S1.1). While the current pathway model does not incorporate assumptions about biological or climatic constraints on pest spread and survival, these can easily be added as geographically explicit modifiers of the transmission probabilities p_{ij} in the pathway matrix. For example, geographically explicit environmental niche models (such as presented in Fischer et al., 2011, Herborg et al., 2007 and Thuiller et al., 2005) and climatic suitability assessments (Baker et al. 2000; Elith et al., 2010; Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Peterson, 2006) can be used to adjust the location-specific p_{ij} values. The adoption of geographical modifiers of the p_{ij} values would also make the model performance more similar to the behaviour of gravity models (Haynes and Fotheringham, 1984; Prasad et al., 2010). It is further possible to modify the probabilities of pest survival, or select the locations that are most likely to receive pests based on background information or prior pest surveys.

One noteworthy aspect of our sensitivity analyses is that the individual paths that constitute the network of potential pest movements may intersect or coincide in geographic space, but do not interact with one another, so certain connectivity and interaction aspects that have been described for social and communication networks are not considered here. Potentially, more detailed analyses of the network's connectivity can be performed (cf. Newman, 2003; Barthélemy, 2011; Caschili and De Montis, 2013), however this type of analysis would require data on the configuration of individual transportation routes. Unfortunately, the Canadian CVS data did not provide the actual routes taken by truck drivers, and so could not be matched to individual road network segments. Therefore, instead of using methods developed for analyzing the connectivity of social and communication networks we opted for a more basic solution based on a first-order pathway matrix.

One of the biggest challenges with calibrating pathway-based models of species movement is to find data that document the expansion of individual populations through time or can help to definitively identify the source locations for new infestations so the model can be run from these locations and calibrated to match historic expansion rates. In pathway-based models, the physical distance between nodes in the network is less important than their level of connectivity (Moslonka-Lefebvre et al., 2011), hence a calibration of the model by geographical observations of the historical expansion of species' populations can be problematic. Alternatively, it may be possible to calibrate the pathway model by tracing expanding species populations via genetic analysis (Muirhead et al., 2008). This would help better understand the role of uncertainty in the pathway-driven process of species movement. Furthermore, incorporation of biological models (such as stage-structured population models combined with dispersal models) could provide even more rigorous estimates of the rate of an organism's expansion. However, detailed information about the behaviour of a non-native species in a new environment is often scarce or unavailable. Dispersal models require good quality data to develop the associated dispersal kernel equations and often cannot provide accurate pathway-specific estimates of spread. In these situations, our pathway-centered approach, which mostly focuses on human-assisted long-distance spread, can be considered as a reasonable starting point to identify likely vectors of the species' movement and help prioritize locations for future data collection efforts.

4.1. Critical uncertainty thresholds in the pathway model

The species arrival rates φ_j show different sensitivity to key model assumptions. The overall impact of multiplicative errors in the p_{ij} values appears to be moderate but gradually increases as the level of uncertainty rises (Fig. 2c, clusters 1–3). Notably, the locations with the highest arrival rates have near-zero sensitivity to this type of uncertainty (Fig. 2c, clusters 4–6).

The impact of additive errors on the p_{ij} values was considerably higher in absolute terms, and more symmetric than observed with multiplicative errors (Fig. 3c, clusters 1, 2, 3, and 6). Indeed, adding modest uniform variation within a 0–0.07 range yielded changes in rank of nearly ±45%. Thus, a lack of location-specific knowledge about the p_{ij} values appears to be the most limiting constraint on model performance.

Surprisingly, the scenario that tested the sensitivity to changes in the structure of the transportation network did not reveal serious correlations between change in the species arrival rank and the level of uncertainty z. This suggests that random node removal may only be critical if the removed locations are associated with unique corridors that do not have alternative bypass routes. The low sensitivity to random node removal also indicates that the arrangement of pathways in the landscape represents a scale-free network, where the probability that a given node has m connections follows an inverse power-law distribution (Jeger et al., 2007). Typically, the movement of an invasive organism in a scale-free network is facilitated by super-spreading events (Jeger et al., 2007), in which a few locations (hubs) with high numbers of connections are responsible for the vast majority of infestations (Barthélemy et al., 2004; Duan et al., 2005; James et al., 2007). In our case, the geographical distribution of the nodes with the highest pest arrival rates (Table 2) has helped identify these super-spreading hubs as the biggest cities and major border crossings.

This study used the species arrival rate as a metric of pathway-related risk. While the analyses tested relatively simple assumptions regarding the uncertainty in the arrival rate estimates, the sensitivity analysis concept can be applied to other spatial dispersal models and could potentially help quantify the uncertainty of propagule pressure estimates (i.e., number of dispersing individuals; Lockwood et al., 2005). A lack of empirical data about propagule pressure has been acknowledged as a universal problem for invasion modeling (see Lockwood et al., 2007), and the sensitivity analysis technique presented here could help assess (at least in coarse terms, by testing the arrival rate as a proxy of the propagule pressure) the approximate range of propagule pressure estimates for a species of interest.

5. Conclusions

Decisions about managing alien species incursions frequently occur under circumstances of limited knowledge about a newly detected organism. While acquiring knowledge about the new organism usually takes time, initial assessments typically need to be done quickly, and so must rely upon general knowledge about the species and how it can be moved across the landscape. The pathway analysis concept presented here provides an example of a rapid-response assessment technique that uses transportation-related data to trace back new (or anticipated) incursions to their likely sources and can be considered as a viable starting point for planning further information-gathering efforts or as part of a screening procedure for new non-native organisms (cf. Daehler et al., 2004; Tucker and Richardson, 1995).

Despite the fact that the main data inputs in the pathway model (i.e., the estimates of the commodity flows and the route locations in the Commercial Vehicle Survey) were recorded from written reports completed by truck drivers and hence were considered imprecise, the identification of the arrival hotspots appeared to be moderately robust to uncertainties in key modeling assumptions. The roadside survey data appears to be sufficient to delineate major hubs and hotspots where incursions are likely to arrive from other locations in the network via commercial truck transport. However, “pass-through” locations with few incoming and outgoing routes can be identified with considerably lower precision. Nevertheless, these locations are usually characterized by low-to-moderate arrival rate values. In practical terms, this means they would be lower priority for surveillance or any other proactive biosecurity measures, and would also less likely be the focus of pest response activities.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jenvman.2013.07.013.

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