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ORIGINAL PAPER

Trade-associated pathways of alien forest insect entries in Canada

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Abstract Long-distance introductions of new invasive species have often been driven by socioeconomic factors, such that traditional "biological" invasion models may not be capable of estimating spread fully and reliably. In this study we present a new methodology to characterize and predict pathways of human-assisted entries of alien forest insects. We have developed a stochastic quantitative model of how these species may be moved with commodity flow through a network of international marine ports and major transportation corridors in Canada. The study makes use of a Canadian roadside survey database and data on Canadian marine imports, complemented with geo-referenced information on ports of entry, populated places and empirical observations of historical spread rates for invasive pests. The model is formulated as a probabilistic pathway matrix, and allows for quantitative characterization of likelihoods and vectors of new pest introductions from already or likely-to-be infested locations. We applied the pathway model to estimate the rates of human-assisted entry of alien forest insect species across Canada as well as cross-border transport to locations in the US. Results suggest a relatively low nationwide entry rate for Canada when compared to the US (0.338 new forest insect species per year vs. 1.89). Among Canadian urban areas, Greater Toronto and Greater Vancouver appear to have the highest alien forest insect entry potential, exhibiting species entry rates that are comparable with estimated rates at mid-size US urban metropolises.

Keywords Pathway analysis · Invasive species · International trade · Freight transport · Human-assisted entry · Long-distance spread

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Introduction

Global trade has been widely acknowledged as playing a crucial role in successful establishment of invasive organisms in new geographic areas (Costello and McAusland 2003; Jenkins 1996; Levine and D'Antonio 2003; Perrings et al. 2005). Indeed, it has been demonstrated that a country's level of international imports (Levine and D'Antonio 2003; Westphal et al. 2008)—either in total or specifically within the agricultural sector (Hlasny and Livingston 2008)—is a reasonable predictor of the number of alien species that can be expected to be introduced. However, while gross trade volumes may serve as a good proxy for estimating the anticipated number of new invasions in a region of interest, determining the finer-scale geographic distribution of these new entries requires detailed knowledge on the movement of specific commodities (i.e., potential carriers of invasive species) through the region's network of freight shipment corridors (Hulme et al. 2008; Hulme 2009; Kenis et al. 2009). Indeed, the increasing proportion of overseas shipments that are containerized or crated (i.e., do not have to be opened or reloaded at a port of entry, but instead at their final destination) emphasize a need to consider the domestic (i.e., intercity) flow of pest-associated commodities via major transportation arteries (De Jong et al. 2004; LeSage and Polasek 2006; Porojan 2001). Moreover, it is critical to analyze international and domestic commodity transportation networks as an integrated system, thus providing a means to fully characterize the pathways of invasion from overseas regions of origin to local markets in the destination region of interest (Ding et al. 2008; Hulme 2009). Notably, this perspective is reflected by a recent shift in the focus of plant biosecurity programs away from control at international borders and towards pathways-based pest risk assessment for identifying potential geographic "hot spots" of invasion (Cook et al. 2010; Hulme 2009).

To better understand this issue, a new class of decision support tools is required that can look beyond biological spread and, instead, estimate the likelihood that new invasive organisms will be entering uninvaded regions through human activities such as trade (Jenkins 1996). For instance, Koch et al. (2011) outlined procedures to combine broad- and fine-scale data on trade and commodity movement with historical pest records in order to estimate alien forest insect species establishment rates at >3,000 individual urban areas across the US. A key input for the study was the US Freight Analysis Framework (FAF), a robust database that describes patterns of commodity imports to US ports of entry as well as domestic commodity shipments between various regions of the country; separately, the FAF also describes freight truck traffic volumes along segments of the nation's road network. Unfortunately, the analytical, data-driven approach applied by Koch et al. (2011) to the US does not translate well to countries that lack such comprehensive data. Instead, a model-based approach may be necessary to harness the limited data available and subsequently derive similar entry rate estimates.

In this study, we present a methodology to predict prominent pathways of human-assisted entries for alien forest insects at inland locations in Canada. The study can be summarized in two basic steps. The first step estimates a nationwide annual rate of new forest insect species expected to enter Canada through the country's international marine ports. The second step then apportions this nationwide annual rate to a set of inland locations and ports of entry across Canada based on the predicted levels and directions of commercial freight shipments along major road corridors (Fig. 1). We estimate the levels and directions of these freight shipments with a probabilistic pathway model developed from roadside survey data about Canadian freight truck activity, including cross-border truck traffic to and from the US. The results provide probabilistic portrayal of human-assisted entry potential of new alien forest insect species at geographic locations ranging from large urbanized areas to minor rural settlements.

The paper focuses on estimating entry rates of bark and wood boring insects on wood and wood-packaging material (here we have selected the same insect families as presented in Koch et al. (2011), not all insects associated with forests). Instead of focusing on particular biological aspects of species introductions, our objective is to highlight the importance of commercial transportation and international trade as key vectors that cause introductions of invasive forest insects at inland locations across North America. The paper's main contribution is that it presents a new modeling approach that estimates the potential of certain types of commodities and cargoes to serve as entry vectors of invasive forest insects in Canada. To illustrate the methodology, we map the entry potential at major inland locations in Canada for new forest insect species entry that may arrive in Canada from major exporting regions such

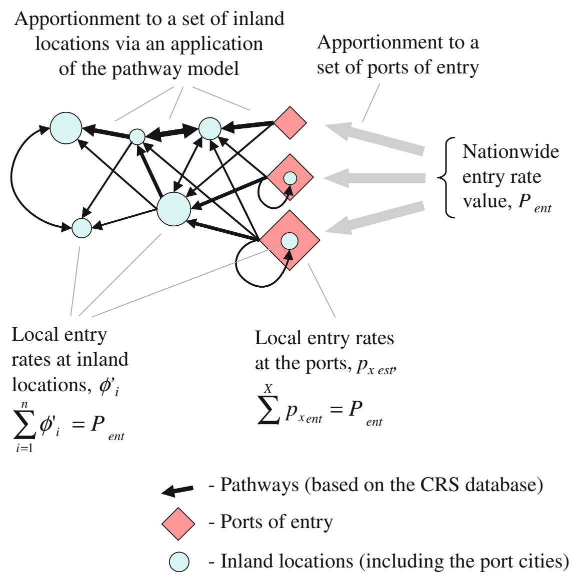

Fig. 1 Analysis summary. Key steps include: (1) estimating the nationwide entry rate for alien forest insects, (2) apportioning the global rate to a set of local rates at the ports of entry based on the volume of pest-specific imports unloaded at each port, and (3) apportioning the ports' entry rates to inland locations across Canada and US using the probabilistic pathway model

as Europe and South/East Asia (i.e., Asia excluding the Middle East region).

Methods

Step 1: estimating the global entry rate of new forest insects with international marine trade for Canada

Our analysis stemmed from the aforementioned study by Koch et al. (2011), who applied a species-accumulation modeling approach (Levine and D'Antonio 2003) to estimate a total annual rate of alien forest insect species establishment in the US as a function of the volume of commodity imports to the country. The study estimated that 1.89 new forest insect species became established in the US each year between 2001 and 2010 based on the total value of imports during this time period (Koch et al. 2011). Given the high degree of integration between the US and Canadian economies and standardized phytosanitary and border control procedures, we expect that the dependency between import volume and entry rate holds similarly for Canada as it does for the US. During the three-year period 2005–2007 (our choice of reporting period was limited by the availability of Canadian trade and transportation data), the total value of imports to Canada was approximately 5.6 times lower than the corresponding value of imports to the US (StatsCan 2011; US Department of Commerce 2009a, b). Given the average rate for the US of 1.89 of new forest insect species per year, a linear rescaling yields a similar entry rate estimate for Canada of $\sim$0.338 species per year, representing approximately 18% of the corresponding US rate. This rate is based on the imports coming directly to the Canadian ports of entry and does not account for re-entries of US imports to Canada via inland land border crossings.

Step 2: estimating the local entry rates at Canadian marine ports

Following Koch et al. (2011), the next stage of our analysis apportioned the nationwide forest insect species entry rate value to approximately $\sim$5,000 Canadian geographic locations (Fig. 1). This apportionment was done in two steps. First, we apportioned the nationwide entry rate to a set of local rates at Canadian ports of entry based on the volume of specific commodity imports (i.e., potential carriers of alien forest pests) unloaded at the ports. These ports' local entry rates were then further apportioned to a set of inland locations using a probabilistic pathway model that estimates the probability of the insects being moved, via commercial freight shipments along major transportation corridors, to various inland urban and rural locations across Canada as well as subsequent entries to the US.

To apportion the nationwide entry rate to individual Canadian ports, we followed the idea described in Yemshanov et al. (2009a) to estimate the local entry potential at 57 major Canadian ports. In short, the apportionment of the nationwide rate was based on the total volumes of certain commodity types (i.e., those that could potentially carry forest insects) unloaded at each individual port annually from specific world regions of interest. The data for individual ports were provided by Statistics Canada for 2005–2007 (StatsCan 2010) and documented the unloaded cargo tonnages (metric tons) by commodity category and by country of origin. For each port, we calculated total tonnages of relevant commodity imports from all world regions and broad geographic regions such as Europe and South/East Asia.

Individual commodity categories are likely to vary in their potential to harbor forest invaders (Haack 2001, 2006; McCullough et al. 2006; Piel et al. 2008; Work et al. 2005). Here we used the list of forest-insect-associated commodity categories from the Koch et al. (2011) study (Table 1) and assumed that 100% of the import tonnages in the categories "logs and other wood in the rough" and "wood products" could harbor forest pests, but that approximately 10% of the import tonnages in other categories of interest represented materials that may harbor these insects (Table 1). Essentially, this weighting scheme increases the importance of logs and raw wood products, and thus increases the local alien forest insect entry potential at those ports which receive higher quantities of these two commodity types.

Similarly, import shipments from different world regions vary in their likelihood of carrying alien forest insects, which may be a result of the level of phytosanitary standards or environmental conditions specific to a particular region (Cook and Fraser 2008; Costello et al. 2007; FAO-IPPC 2006; Margolis et al. 2005). We further rescaled our commodity-type-weighted estimates at the ports of entry using scaling factors developed by Koch et al. (2011) to estimate the varying alien forest insect entry potential of import shipments from particular world origin regions. Briefly, Koch et al. (2011) generated these scaling factors based on the numbers of interception records in the USDA Animal and Plant Health Inspection Service (APHIS) PestID database, which documents ~25 years of interceptions of non-native plant pests at US ports of entry (see Koch et al. (2011) for the exact calculation of the region-specific scaling factors). Canadian interception data were more limited, particularly to three years in the temporal sense, so we felt it best to build upon the more robustly estimated US weights, and only implement any major differences we discovered on the Canadian side. Subsequent verification with Canadian interception data echoed the general geographic trends seen for the US, except that the South/East Asia region accounted for a relatively larger percentage of the interceptions in Canada than in the US. Hence, the scaling factors for imports arriving from South/East Asia were set to 1.0 and, for imports from Europe, Southwestern Asia, South and Central America, Mexico, and the rest of the world, to 1.0, 0.02, 0.36, 0.14 and 0.09, respectively, in keeping with the rates calculated by Koch et al. (2011).

Because we did not have information regarding negative inspections at the ports of entry, we chose to use simple scaling coefficients, based only on the positive interceptions, for the purpose of depicting general trends with respect to the origin regions. Certainly, true approach rates (i.e., involving negatives) would provide more robust scaling coefficients,

Table 1 SCTG (US-Canadian Standard Classification of Transported Goods) commodity categories associated with transport of alien forest insects

SCTG code	Commodity category	Weight, w_l
10	Monumental or building stone	0.1
25	Logs and other wood in the rough	1
26	Wood products	1
31	Nonmetallic mineral products	0.1
32	Base metal in primary or semi-finished forms and in finished basic shapes	0.1
33	Articles of base metal	0.1
34	Machinery	0.1
35	Electronic and other electrical equipment and components and office equipment	0.1
36	Motorized and other vehicles (including parts)	0.1
37	Transportation equipment, not elsewhere classified	0.1
38	Precision instruments and apparatus	0.1
39	Furniture, mattresses and mattress supports, lamps, lighting fittings	0.1
40	Miscellaneous manufactured products	0.1

The weights reflect the estimated potential of a particular commodity category to harbor forest insects but sufficient data to calculate them were unavailable for this study. Alternatively, scaling schemes based on indices of climatic or environmental similarity between import regions and Canada may adjust for the likelihood of biological establishment of organisms of interest, but are not ideal for depicting entry potential because they do not fully reflect the pattern of pest-associated imports that arrive in Canada from particular regions of origin (the latter is rather a function of the regions' economic development and historical pattern of exports). It is also important to note that the origin regions defined in the import trade statistics used this study were quite large (i.e., have sizeable ranges in latitude and latitude), effectively dampening their degree of climatic dissimilarity with each other.

Further examination of the Canadian import data revealed that some ports of entry have very low volumes of relevant imports, which render the calculated local entry rates below 10^{-5} new forest insect species per year. However, historical documentation of alien forest insects in Canada (Langor et al. 2009), as well as interception records in the US PestID database and equivalent interceptions at the Canadian ports, show that ports with low volumes of incoming imports still exhibit a moderate potential for new incursions. Therefore, we transformed the initially estimated port entry rates (i.e., as weighted by commodity type and origin region) to a less variable range using the method described in Yemshanov et al. (2009a). Essentially, this transformation increased the lowest entry rates that were below ~0.0001 to values within the 0.0001–0.0003 range, with little impact on the values originally above ~0.0003. We then rescaled the ports' individual entry rate values, $p_{x\,ent}$, so their sum matched the global entry rate for Canada, P_{ent}:

$$\sum^{X} p_{x\,ent} = P_{ent} \qquad (1)$$

In summary, the apportionment of the global rate P_{ent} to a set of ports of entry provided the potential for each port to be a point of origin for subsequent entry and/or movement of alien forest insect species to other locations in North America.

Table 2 lists the ten marine ports in Canada that receive the largest volumes of imports associated with alien forest insects, from all world regions of origin as well as specifically from Europe and South/East Asia. In addition, Table 2 also shows unweighted import tonnages (i.e., not adjusted for commodity type or world region of origin) of pest-associated commodities as well as each port's allocated share of the nationwide entry rate. Overall, only three Canadian ports receive import volumes that approach the average volumes unloaded at major US ports: Vancouver, Fraser River and Montreal. The rest of the ports receive volumes considerably below the US average (Koch et al. 2011).

Step 3: estimating local entry potential of alien forest insect species at inland locations

For the last step of the analysis, we further apportioned the local alien forest insect species entry potential at Canadian ports to inland locations, such as urban municipalities, rural settlements and border crossings between Canada and the US (Fig. 1). We did this apportionment using a probabilistic pathway model based on the configuration of the road network and the observed flows of relevant commodities along major freight transportation corridors in both countries.

The primary data source for the pathway model was a Canadian roadside survey (CRS) database maintained by Transport Canada. The database stores records of individual freight routes collected during a 2005–2007 survey at truck weigh stations across Canada. Each record summarizes a single freight truck shipment route recorded in the roadside survey, including its origin, destination and (if applicable) border crossing location(s). The records also detail the commodity tonnages associated with each shipment. To make the database spatially explicit, any location mentioned in the database (i.e., any origin, destination, or through-point documented in one or more records) was assigned geographic coordinates based on the Canadian Database of Geographic Names (NRCan 2010) and a corresponding US database of populated places (USGS 2009).

The roadside survey provided a limited sample (i.e., more than 1,2000 individual routes) of the flows of forest-insect-associated commodities between 2005 and 2007, but did not include information about intermediate stops, drops-offs and other events that may cause accidental introductions of insects that may be carried by the freight shipments. For example, insects might escape from a truck that stays overnight

Table 2 Canadian ports with the 10 highest annual levels of forest-insect-associated imports, and their resulting alien forest insect species entry rates

Handling port	Unloaded tonnage of forest-insect-associated commodities, Mt/year**	Annual entry rate, species-year^{-1}***	Rank
Imports from all world regions			
Montréal/Contrecoeur, Quebec	4.02	0.111	1
Vancouver, British Columbia	3.72	0.102	2
Fraser River, British Columbia	1.14	0.031	3
Halifax, Nova Scotia	0.88	0.024	4
Hamilton, Ontario	0.81	0.022	5
Sorel, Quebec	0.37	0.010	6
Windsor, Ontario	0.26	0.007	7
Sault-Ste-Marie, Ontario	0.21	0.006	8
Campbell River, British Columbia	0.20	0.005	9
Oshawa, Ontario	0.17	0.005	10
Imports from Europe			
Montréal/Contrecoeur, Quebec	3.75	0.103	1
Halifax, Nova Scotia	0.72	0.020	2
Hamilton, Ontario	0.30	0.008	3
Sorel, Quebec	0.16	0.004	4
Oshawa, Ontario	0.12	0.003	5
Windsor, Ontario	0.08	0.002	6
Vancouver, British Columbia	0.05	0.001	7
Trois-Rivières, Quebec	0.05	0.001	8
Fraser River, British Columbia	0.05	0.001	9
Québec/Lévis, Quebec	0.03	0.001	10
Imports from South/East Asia			
Vancouver, British Columbia	3.43	0.094	1
Fraser River, British Columbia	0.99	0.027	2
Sorel, Quebec	0.13	0.004	3
Hamilton, Ontario	0.10	0.003	4
Bécancour, Quebec	0.06	0.002	5
Windsor, Ontario	0.06	0.002	6
Port-Alfred, Quebec	0.05	0.001	7
Oshawa, Ontario	0.05	0.001	8
Halifax, Nova Scotia	0.04	0.001	9
Montréal/Contrecoeur, Quebec	0.03	0.001	10

Each port's entry rate (i.e., its portion of the nationwide rate) was subsequently apportioned to individual inland locations with the pathway model

** Unweighted tonnages of 13 SCTG pest-specific groups of imports (see Table 1)

*** The entry rates are based on tonnages adjusted by the origin of imports and the capacity of cargoes to carry an invasive organism

at a rest area. Unfortunately, it is difficult to quantify such risks. We also acknowledge that commercial freight transportation may not be responsible for all human-assisted entries; therefore, we made the simplifying assumption that some introduction potential exists along all parts of a shipment route, and so separately estimated this potential for the individual segments comprising each shipment route (see the subsequent description of the structure of the probabilistic pathway model).

Probabilistic pathway model

The probabilistic pathway model first parsed the CRS records into an aggregated set of unique pathway segments, each connecting two non-adjacent locations, i and j. For each route segment ij, the model estimated a probability, p_{ij}, of an alien forest insect species being transported from i to j over the survey period, t, based on m_{ij}, the total tonnage of freight shipments of forest insect-associated commodities from i to j. The directional tonnage values m_{ij} and m_{ji} ($m_{ij} \neq m_{ji}$) were then used to build a matrix of commodity flows across Canada, **M**. The matrix had a size, Y, equal to the number of unique geographic locations in the roadside survey database (i.e., the nodes of the pathways). The non-diagonal elements of **M** were the m_{ij} and m_{ji} values estimated for the pathway segments defined by each pair of locations $i, j \in [1; Y]$:

$$M = \begin{bmatrix} 0 & m_{12} & \cdots & m_{1n} \\ m_{21} & 0 & \cdots & m_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ m_{n1} & m_{n2} & \cdots & 0 \end{bmatrix} \quad (2)$$

The roadside survey did not provide information about pick-up or drop-off of additional freight at pathway nodes during transit, so the diagonal elements of **M** (i.e., elements where $i = j$) were set to 0.

From **M**, we constructed a subsequent probability matrix, $\mathbf{P}_t$, of a new forest insect species being moved along each pathway segment. To estimate each element of $\mathbf{P}_t$ (i.e., the probability of an insect species being moved along a specific segment ij), we adopted the simple assumption that this probability depends linearly on the total tonnage of forest-insect-associated commodities being transported from location i to location j:

$$p_{ij} = m_{ij}\lambda_t \quad (3)$$

where λ_t is a scaling parameter. Basically, λ_t describes per-unit "flow" in the pathway model (i.e., one metric ton of relevant commodities translates to a λ_t probability of insect movement along a given pathway segment). Unfortunately, we did not have enough empirical data to define this parameter precisely. Model calibration with respect to particular pathway segments is only possible using recent pest records (since the historical configuration of the transportation corridors and the volumes of the commodity flows are not known). Coarse estimation of the value of λ_t was done via using recent evidence of the movement of a significant forest pest, the emerald ash borer (*Agrilus planipennis* Fairmaire) along the highway corridor between Windsor (ON) and Greater Toronto and the corresponding tonnage of relevant commodities moved through this expansion corridor (as reported in the CRS database). However, because the pathway model was only used to apportion the estimated entry rates at the ports to a set of inland locations (so the final probabilities of entry generated with the model were rescaled so their sum matched the global Canadian entry rate)—a precise estimation of λ_t was unnecessary as long as the value was sufficiently small so the sum of the transmission probabilities p_{ij} in each row of $\mathbf{P}_t$ was always much less than 1. As this suggests, $\mathbf{P}_t$ also included one more discrete state to describe the probability that an alien forest insect would not survive transit from i to j, i.e.:

$$p_{i\,term} = 1 - \sum_{j=1}^{n} p_{ij} \quad (4)$$

In turn, terminal segments (i.e., segments with no outgoing routes from endpoint node j) were represented in the matrix by the rows satisfying the conditions:

$$p_{i\,term} = 1 \text{ and } \sum_{j=1}^{n} p_{ij} = 0 \quad (5)$$

Incorporating these elements, the probability matrix $\mathbf{P}_t$ was estimated as follows:

$$P_t = \lambda_t M = \begin{bmatrix} 0 & p_{12} & \cdots & p_{1n} & p_{1term} \\ p_{21} & 0 & \cdots & p_{2n} & p_{2term} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & p_{n2} & \cdots & 0 & p_{nterm} \end{bmatrix}. \quad (6)$$

Essentially, $\mathbf{P}_t$ is a first-order transition matrix (Karlin 1968) that describes, in probabilistic terms, the potential for alien forest insects to be moved with freight shipments along major transportation corridors in Canada. Each row i of the matrix lists all of the possible segments starting at i, while the each column j lists all of the possible segments ending at j. This implies a large size for $\mathbf{P}_t$ (in our case $n \approx 5000$).

We then used $\mathbf{P}_t$ to perform a series of stochastic pathway simulations from the Canadian marine ports of entry. To connect the ports to our pathway network, we assumed a 10-km local neighborhood radius around each port and assigned its entry potential to all locations in $\mathbf{P}_t$ within this distance from the port. The simulations began with a uniform random draw to generate a probabilistic event with the port's entry rate $p_{x\ ent}$ (Eq. 1, Table 2). If this draw was successful at the port, the model then used $\mathbf{P}_t$ to simulate the subsequent movements of the insect from the port of entry through the pathway network to various inland locations. The choice of an outgoing path from the port of entry was based on the transmission probabilities (which essentially were based on the ratios between the tonnages of commodities moved via a particular outgoing route from the port of entry, see Eq. 3). Then, at each pathway node i, the model used the probabilities in $\mathbf{P}_t$ to select the next pathway point. The process continued until the final destination was reached (i.e., no outgoing paths from a node) or a terminal state was selected based on the $p_{i\ \mathrm{term}}$ value. The probability of a new forest insect species entering at a given location i was estimated via multiple randomized simulations of individual pathways:

$$\varphi_i = M_i/M \qquad (7)$$

where M_i is the number of times a pathway travels through a given location i, and M is the total number of simulations from each port of entry including random draws to simulate the port's entry events with $p_{x\ ent}$ ($M = 4 \times 10^6$ in our study). Similarly, for a given directional pathway segment ij, the probability of the species moving from location i to j was estimated as follows:

$$\psi_{ij} = M_{ij}/M \qquad (8)$$

where M_{ij} is the number of times pathway travel from location i to j was simulated to occur. It is important to emphasize that the pathway model's outputs were used only to apportion the national entry rate to a set of inland locations in Canada and the US, hence φ_i and ψ_{ij} values were rescaled linearly to φ'_i and ψ'_{ij} to match their final sum to the nationwide alien forest insect species entry rate:

$$\sum_{i=1}^{n} \varphi'_i = P_{ent}\ and \sum_{\substack{i=1,\\ j=1}}^{n,n} \psi'_{ij} = P_{ent} \qquad (9)$$

In short, this linear rescaling converted the probabilistic φ'_i and ψ'_i values into estimates of the alien forest insect entry rate (i.e., new species per year) for individual locations (φ'_i) and pathways (ψ'_{ij}) of interest.

The use of segment-specific probabilities (instead of specifying probability values for entire shipment routes described in the CRS database) helped reduce the size of the pathway matrix $\mathbf{P}_t$ and the overall computing time. Potentially, this could also lead to circularities in the simulated pathways, where the simulated routes would visit the same locations more than once. This, however, was not the case in our study because the CRS data were already summarized to relatively short directional routes that exhibited no evidence of such circularities.

Geographic portrayal of human-assisted entry rates of new forest insect species

In terms of geographic outputs, we first mapped the primary vectors of potential entries of alien forest insects based on imports from all world regions (Fig. 2) and also based on imports from two specific regions, South/East Asia and Europe (Online Appendix S1, Figs. S1 and S2). In these three maps, each vector has been assigned its rescaled entry rate, ψ'_{ij}. For better identification of the main invasion gateways, we aggregated the multiple parallel pathways starting or ending at the same network node and dropped pathways with very low ψ'_{ij} values.

A certain portion of the modeled freight shipment routes ended in the US. To limit map complexity, we aggregated routes ending at US locations to the level of US Freight Analysis Framework (FAF) region (see US FHA 2006; 114 regions nationwide and one point per FAF region centroid). When appropriate, we also aggregated the Canadian locations to the municipal area level. These transformations reduced the total number of mapped points to less than 5,000 and considerably improved the readability of the pathway maps.

Second, we mapped the rates of alien forest insect species entry at specific locations (i.e., pathway nodes) from all regions of origin (Fig. 3), and created separate maps for forest insects originating specifically from South/East Asia and Europe (Online Appendix S1, Figs. S3 and S4). These maps show the rescaled entry rates, φ'_i, for urban and rural locations in Canada as well as US FAF regions. These maps are complementary to the results presented for the US by Koch et al. (2011). We also ranked the Canadian locations and US FAF regions by these rates to identify those with the highest introduction potential.

Results

Pathways of human-assisted entry of alien forest insects

Figure 2 presents an overview of the main pathways of entry for alien forest insects originating all world

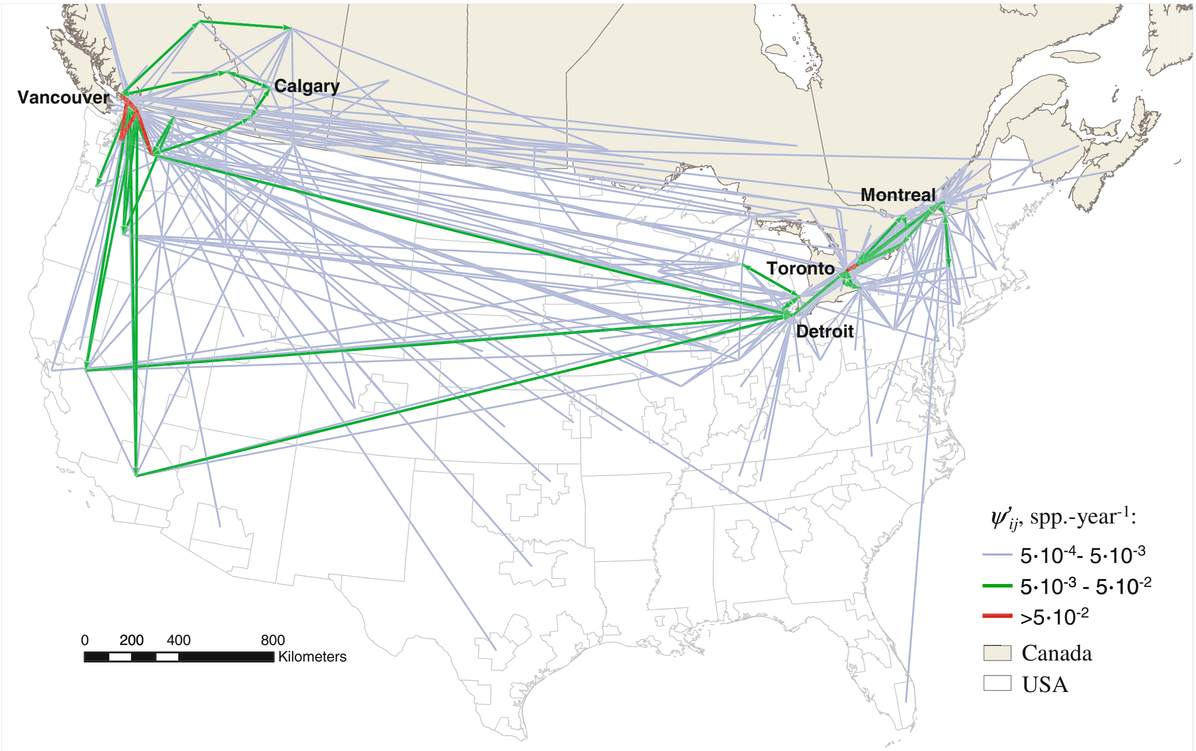

Fig. 2 Map of human-assisted pathways of entry for new forest insects in Canada based on imports from all world regions. *Lines* show the transport pathways defined by freight shipments from Canadian marine ports of entry. The *color* of each *path line* indicates, within a certain range, the probability value associated with the path, where all paths with probability less than 10^{-4} year^{-1} have been filtered out for simplicity. The US *map* shows Freight Analysis Framework (FAF) region boundaries; destination locations in the US were aggregated to the centroids of these regions

regions. The map clearly shows two major pathway corridors. The first corridor initiates from ports in the Greater Vancouver area (including the Fraser River region) that receive significant tonnages of forest-insect-associated commodities from Asia and thus become gateways for the arrival of new species and their subsequent spread to locations in both Canada and the US. The second major corridor includes the shipment routes connecting Detroit (MI), Toronto (ON) and Montreal (QC). Taking these metropolitan areas together, this region has high population density, numerous marine ports along the St. Lawrence River and Lake Ontario, and also several Canada-US border crossings with high traffic volumes. Indeed, this vector demarcates several major gateways where forest insects may enter the eastern US via border crossings from Ontario: at Sarnia, Niagara Falls, Cornwall and Windsor.

Figure S1 (Online Appendix S1) shows the pathways for alien forest insects that are associated with imports from South/East Asia. The map shows major pathways similar to the pathways of entry for alien forest insects originating from all world regions (Fig. 2), except the pathways that originate in Greater Vancouver and cross the US-Canada border to the US Pacific Coast are more articulated. There is also an elevated potential for a species to be transported along the eastbound sections of major Canadian highways that cross the Rocky Mountains, such as Trans-Canada Highway 1 between Golden (BC) and Calgary (AB).

Figure S2 (Online Appendix S1) shows the pathways for alien forest insects that are associated with European imports. As perhaps expected, a majority of imports arrive at eastern ports in the Great Lakes region. Historically, a relatively high percentage (12% overall) of the non-native forest insect species in Canada were first established in the Maritime Provinces (Langor et al. 2009). However, this pattern of invasion has likely shifted in recent years because—as illustrated by Fig. S2—a vast majority of imports to

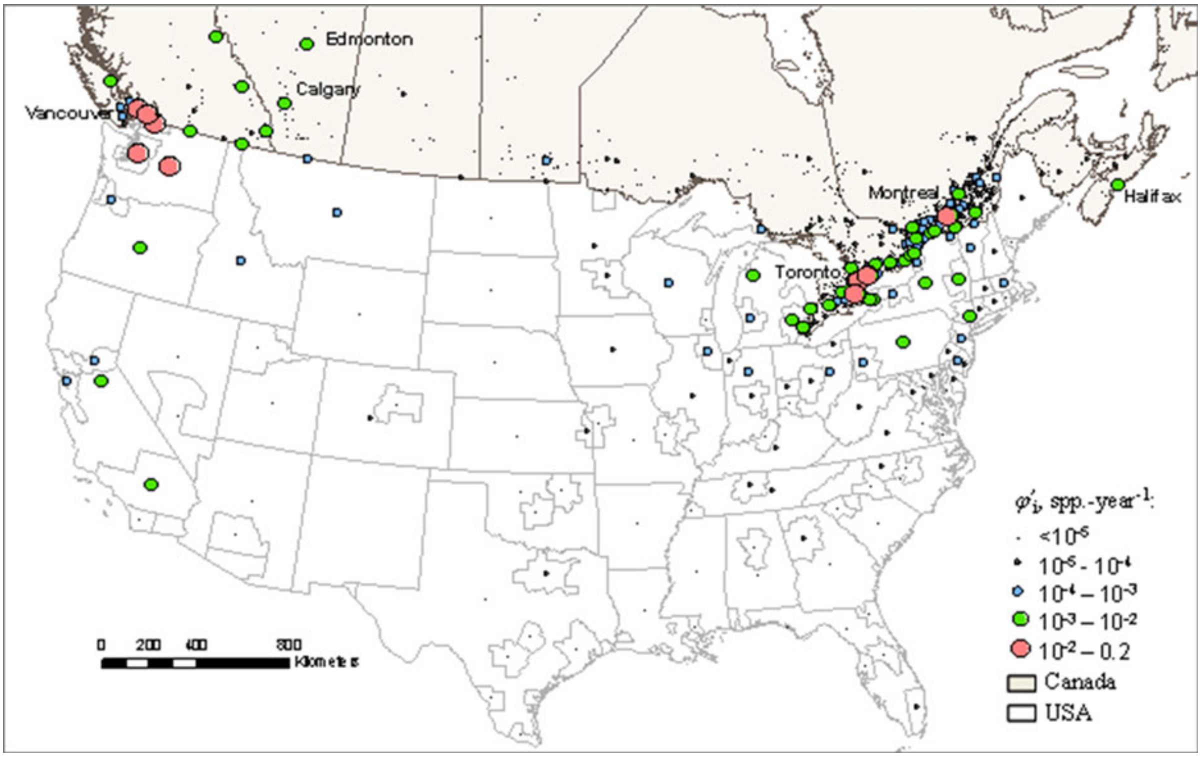

Fig. 3 Alien forest insect species entry rates (species-year^{-1}) at urban and rural locations, based on imports of forest-insect-specific commodities to Canadian ports from all world regions. The US *map* shows Freight Analysis Framework (FAF) region boundaries; destination locations in the US were aggregated to the centroids of these regions

eastern Canada now bypass ports in the Maritimes in favor of Montreal (QC) or Great Lakes ports, which have easier access to major markets and transportation corridors in Ontario, Quebec and the northeastern US. The two most notable spread pathways are the Montreal-Toronto corridor, with numerous routes crossing the Canada-US border near Niagara Falls (ON)—Buffalo (NY), and a second pathway directed from Montreal (QC) toward major urban areas in the state of New York. Indeed, most of the cross-border pathways associated with European imports are directed toward the northeastern US.

Entry rates at major urban areas and other locations

Figure 3 presents a map of the entry rates of alien forest insect species at urban and rural locations based on relevant commodity imports from all world regions. The map indicates that the highest entry rates are found in the Greater Vancouver area and at the nearest border crossing to the US (Blaine, WA). Another high-rate cluster is located near major Canadian ports in the Great Lakes region (Montreal, QC and Oshawa-Toronto-Hamilton area, ON; Table 2). Calgary (AB) and border crossings in southern Alberta have relatively moderate entry potential, which is attributable to the aforementioned eastbound flow of commodities along major Canadian routes such as the Trans-Canada Highway.

Figure S3 (Online Appendix S1) depicts location-specific alien forest insect entry rates associated with imports from South/East Asia. As expected, locations in the Greater Vancouver region exhibit the highest rates of entry, however locations in the US state of Washington (i.e., the Seattle-Tacoma-Olympia and "remainder of Washington" FAF regions) show entry potential equal to the Vancouver-Burnaby urban area. Notably, Calgary (AB) and Golden (BC) show relatively high entry potential associated with imports from South/East Asia. This can be explained by the fact that both cities are located on the Trans-Canada Highway, a major coast-to-coast transportation corridor. Similarly, a moderate entry rate for Winnipeg (MB) can also be attributed to proximity to this corridor.

Figure S4 (Online Appendix S1) shows the location-specific entry rates of alien forest insects that may be brought with European imports. The introduction potential is the highest at locations near major ports along the St. Lawrence River and Lake Ontario (i.e., the Greater Toronto and Montreal regions), where the majority of European imports are unloaded and subsequently transported to inland destinations. Despite being bypassed by most import vessels (see earlier discussion regarding Fig. S2), port cities in the Canadian Maritime Provinces (such as Halifax, NS) still appear to have relatively moderate entry potential.

Table 3 presents a list of the geographic locations with the highest estimated entry rates of alien forest insects based on relevant imports from all world origin regions, while Tables S1 and S2 (Online Appendix S1) show similar lists based only on imports from South/East Asia and Europe, respectively. Clearly, the growth of Asian imports appears to drive the high projected rates of forest insect entry in western Canada and along the US Pacific Coast, while Europe is a more prominent contributor to the entry rates observed in the Great Lakes region (i.e., the listed locations in QC and ON). In fact, Europe typically accounts for approximately 70% of the total rate of entry in urban and rural locations in the Great Lakes region.

Potential transmissions of alien forest insects from Canada to the US

The roadside survey database documented shipments from Canada to each state in the contiguous US, as well as Alaska. The largest cross-border flows of forest-insect-associated commodities from Canadian ports to the US were observed from the Greater Vancouver area toward the state of Washington (Table 3). Overall, the entry rates of alien forest insects in major Canadian urban areas were close to the estimates for major US urban areas reported in Koch et al. (2011). However, only three Canadian urban areas (Greater Vancouver, Greater Toronto, and Montreal) matched major US cities in terms of alien forest insect entry potential.

The results also allowed us to estimate the potential transfer rates of new forest insect species from Canada to the US with cross-border freight transport. Overall the total entry rate allocated to US destinations from Canada (i.e., 0.15 new species per year) constitutes 44% of the nationwide Canadian entry rate, and notably, is approximately 8% of the annual nationwide rate estimated for the US based on its own import and freight shipment data (Koch et al. 2011). Our results also suggest that the US Pacific Coast states (Washington, Oregon and California) have relatively higher potential for receiving new forest insect species from Canada. In large part, this is explained by the fact that these states have the highest likelihoods of receiving new insects from Canada with imports from Asia (Table S1 and Fig. S3, Online Appendix S1). Table S1 also shows that a sizeable share of imports from South/East Asia arrive at Great Lakes ports in Canada, translating to the medium entry rate (i.e., cross-border transmission rate) estimated for the Detroit (MI) area (Fig. S3).

Discussion

Our study provides a practical methodology for assessing the rates and prominent pathways of alien forest insect species entry in Canada and subsequent export of those species to the US. Because there were insufficient data for directly estimating rates of entry at a multitude of individual geographic locations, we instead focused on a novel, model-based approach to apportion an estimated Canada-wide entry potential to these locations. Notably, our approach has demonstrated how stochastic simulation models can be successfully incorporated into "static" analyses of invasive species' introductions (which usually rely only on historical trade and transportation statistics). In particular, the use of a probabilistic pathway model and a network of transportation corridors when estimating long-distance insect spread potential helped leverage the limited trade data that were available.

Conceptually, the approach is similar to gravity models (Bossenbroek et al. 2001; Prasad et al. 2010), however our study uses directional information and helps uncover the pathway "crossroads" and transit hubs (cf. Floerl et al. 2009) through which the movement of alien forest invasive insects is most likely. Because shipping containers, in particular, often contain wood packaging, are infrequently inspected, and may be transported quickly long

Table 3 Top 10 locations in terms of the annual entry rate of alien forest insect species transported from all world regions (individual geographic locations have been aggregated to the level of FAF regions in the US and municipal/urban areas in Canada)

Country	Province/State	Nearest vicinity/urban area/FAF region	Annual entry rate, species-year^{-1}	Rank
Canada	BC	Burnaby (part of Greater Vancouver Area)	0.102	1
USA	WA	Blaine (US border crossing)	0.083	2
Canada	ON	Mississauga (part of Greater Toronto Area)	0.026	3
Canada	QC	Montreal-Anjou	0.026	4
Canada	BC	Abbotsford—Trans-Canada Hwy	0.020	5
Canada	ON	Courtice—Hwy 401 (part of Greater Toronto Area)	0.009	6
Canada	ON	Mount Hope-Hamilton	0.009	7
USA	WA	Seattle-Tacoma-Olympia*	0.008	8
USA	WA	Remainder of Washington (except Blaine-Seattle-Tacoma-Olympia)*	0.008	9
Canada	BC	Aldergrove-Trans-Canada Hwy	0.005	10

* Delineated as a separate FAF region (see US FHA (2006) for delineation of FAF boundaries)

distances before being opened (Allen and Humble 2002), the use of transportation data and road surveys may help better direct surveillance efforts to the most probable locations of accidental introductions in the interior.

Our results also suggest recent changes in the geographic pattern of alien forest insect introductions in Canada. As noted previously, the Maritime Provinces were historically considered the second most likely region of Canada for entries of forest insect species from overseas (Langor et al. 2009), but recent estimates indicate that the vast majority of forest-pest-associated imports now arrive at Montreal and major Great Lakes ports via the St. Lawrence Seaway. Limited anecdotal evidence from pest interceptions in the Great Lakes region—such as the recent introductions of the emerald ash borer (*Agrilus planipennis*), the Asian longhorned beetle (*Anoplophora glabripennis*) and the European oak borer (*Agrilus sulcicollis*)—appears to be consistent with our results.

Notably, our "Top 10" lists of the locations with the highest entry potential (Table 3, and Tables S1 and S2 in Online Appendix S1) show relatively few large urban centers. While large cities such as Montreal (QC), Mississauga-Toronto (ON), and Mount Hope-Hamilton (ON) do appear on the lists, a considerable portion of each list is composed of locations near major highways that are positioned in close proximity to ports, major markets and/or major border crossings, but are not densely populated urban areas. Basically, these locations do not represent final destinations, but instead reveal transportation "crossroads" that are most likely to be visited by commercial vehicles that may carry new forest insects. In this regard, these locations can be envisioned as potential points of incidental introductions (i.e., where insects may be accidentally released during transit of commodities to their ultimate destinations). They can also be envisioned as important foci for surveillance efforts and locations where it would be advantageous to have in place some capacity for rapid response to incursions. We acknowledge that the estimated entry rate values at inland locations were derived with a probabilistic model and therefore can be expected to have some errors around their actual values. Nevertheless, the characteristics of the locations with the highest estimated entry rates are quite revealing and, we believe, consistent with anecdotal evidence regarding where the movement of invasive insects with commercial transportation is the most likely. For example, the first infestations of emerald ash borer east of Windsor, ON was observed near a major truck stop along the Highway 401 corridor between Windsor and Toronto; the truck stop is not associated with any urban area or border crossing, but instead can be considered a typical "crossroad" on the corridor.

We made some assumptions in our modeling effort that bear further explanation. First, the forest-pest-specific SCTG commodity categories considered in our analyses did not include a specific category for live plants. For certain groups of invasive species (e.g., plant pathogens), this commodity type may be extremely important, but for alien forest insects this may not be the most dominant vector. While several Canadian pests have been attributed to live plants (Humble and Allen 2004), McCullough et al. (2006) showed that only 7% of pest interception records in the USDA APHIS Port Information Network (PIN) database were associated with plant materials intended for propagation. Furthermore, as can be seen in Table 1, SCTG commodity categories are coarsely defined. Live plants fall under the broader SCTG category of "other agricultural products", which includes all agricultural products except live animals and fish, cereal grains, and animal feed. Identifying what portion of this broad category was related to forest trees was impossible. Our implicit assumption is that the pathway-based allocation of tonnages (and by extension, entry potential) to individual locations for the commodity categories we included in our analysis closely mirrors the allocation pattern we would see if we included additional categories like live plants.

Related to this, we acknowledge that recently implemented rules for treatment of wood materials (i.e., International Standards for Phytosanitary Measures No. 15, or ISPM 15) could ultimately reduce the likelihood of new forest insect introductions into Canada. Yet, there is still some doubt about the effectiveness of ISPM 15 given the potential for fraudulent behavior or treatment failures, and ISPM-15-compliant wood has been shown to harbor some live insects in at least one study. We plan to revisit this issue as additional data on the impact of ISPM 15 become available, but believe the results presented here are realistic given current knowledge. We also recognize that the roadside survey database lacked information on other potential avenues of human-mediated dispersal, such as movement of commodities via other transportation modes like rail, which, by comparison, moves approximately 37% of the goods (in terms of monetary value) shipped via commercial road transportation in Canada (Dunlavy et al. 2006). Moreover, we expect that human-assisted spread of forest insect species with private passenger vehicles may follow slightly different (i.e., more diffuse) spatial patterns due to more diverse traffic flows, although passenger vehicles likely have much lower capacity to carry hitchhiking organisms when compared to commercial vehicles loaded with pest-associated commodities. Resolving this issue would require gathering more detailed data on domestic passenger traffic flows across North America (such as the US Household Travel Survey from the Bureau of Transportation Statistics, or complementary surveys undertaken by Transport Canada). This is a key area of future work.

Pathway modeling issues

The probabilistic pathway model presented in this study provided a computationally tractable and relatively simple way of incorporating trade and transportation data into assessments of human-assisted movement of invasive alien species. The application study also presents the novel approach of using a directional pathway model to estimate how the potential of invasive pests to enter at ports can be translated to a set of local entry rates at inland locations. In general, the behavior of the model is similar to approximating the network of commodity flows with a gravity model (Kaluza et al. 2010). It should be recognized that our study was focused on reconstructing the sequential pathways of movement of alien forest insects with freight transport and did not attempt to recreate the full topological structure of the transportation network (cf. Albert and Barabasi 2002). We believe that our data may not be detailed enough to reveal the associations between multiple locations (such as fine-scale groups and associations commonly found in social and transportation networks; see examples in Gautreau et al. (2009), LeSage and Polasek (2006) and Robins et al. 2007).

From a technical standpoint, our approach to addressing long-distance, human-mediated dispersal offers a more realistic long-distance dispersal mechanism for use in spatial invasion models. The maps of pest entry rates (Fig. 3 and Figs. S3 and S4 in Online Appendix S1) can be used directly to initialize spatial dispersal models such as described in Yemshanov et al. (2009b) and Koch et al. (2009), or other applications that may use dispersal-kernel-based or stratified spread models (Pitt et al. 2009). Melbourne and Hastings (2009) emphasized the issue of severe, irreducible uncertainties when it comes to predicting spatial spread of invasive organisms. Notably, long-distance dispersal does not necessarily present a stochastic (i.e., irreducible) uncertainty problem in our case, but rather an epistemic uncertainty problem (i.e., uncertainty due to poor, incomplete knowledge), which we have attempted to address with this analysis.

Uncertainty thresholds in the pathway model

Estimation of the entry potential of alien forest insects in Canada is sensitive to key parameters that affect the apportionment of the nationwide entry rate to a set of local rates at inland locations. The scaling parameter, λ_t, and the transmission probability values, p_{ij}, are the most critical parameters in our pathway model. Because the model is essentially a stochastic Markovian pathway matrix, λ_t is a simple multiplier of the tonnage value that converts it to a transmission probability value. Therefore, we can expect to see (and as was evident in our preliminary tests) a linear impact of increasing or decreasing λ_t on the final transmission probability values; basically, a higher λ_t will result in higher probability values and vice versa.

Furthermore, the pathway model in our case was not used as a true simulation model but instead to apportion the arrival rates at the ports of entry to the set of inland locations, such that the absolute probability values generated by the model were rescaled so their sum matches the global entry rate. Because of the rescaling, small changes in the p_{ij} or λ_t values will not have much impact on the final entry rate estimates. In addition, altering the λ_t value may not reveal how uncertainty in the actual tonnage values and the configuration of the transportation network affect the final entry rates. This implies that validation should also include some assessment of the meaningfulness of pest entry hotspots identified by the model. As noted earlier, we believe that our predictions are consistent with anecdotal knowledge suggesting major urban areas, US-Canada border crossings and transportation crossroads as pest entry hotspots.

Ultimately, calibrating and testing the sensitivities of the pathway model represent considerable challenges due to a lack of data about how pests can be moved through the transportation network across the continent. Typically, the behavior of spread models has been validated against historical patterns of pests' establishment. However, validating our pathway model by historical patterns is not really feasible. First, the pathway model depicts the present-day configuration of the transportation network and the corresponding levels of commodity flows through major transportation corridors. In order to use a historical pattern, one would need information on the configuration of the network and commodity flow data during the same time period as the historical pattern; this information is currently unavailable (the roadside surveys have not been conducted regularly in the past, and similar data, if any exist, have not been made publicly available). Moreover, it is hard to track the evolution of the transportation network in Canada and US over time (although this is technically possible and could be a study on its own).

Given that most of the information that was used to build the pathway model was to some extent vague, we believe it is more critical and important from a policy point of view to extend our analysis beyond parameter sensitivities and historical calibration to instead focus on the broader notion of the impact of uncertainty on the model outputs. More rigorous testing of the impact of uncertainty on the p_{ij} values can be implemented in at least two alternative scenarios: (1) testing the additive errors (i.e., adding a uniform random error to the p_{ij} values) and (2) testing multiplicative errors, that is, testing for uncertainty associated with particular (individual) measurements of p_{ij} values but keeping the mean of p_{ij} the same. While the first scenario could depict the "lack of knowledge" about p_{ij} (i.e., by gradually replacing the actual probabilities with uniform random variables pulled from a gradually increasing set of bounds), the second scenario preserves the mean p_{ij} values and subsequently tests the impact of uncertainty on the estimates of the entry rates with little impact on the overall pattern of the commodity flows through the network.

Testing the impact of uncertainties associated with the configuration of the transportation network could have many direct policy applications since the results would help quantify the efficacy of the surveillance efforts for specific transportation corridors (i.e., pest entry vectors). We also expect that our "apportionment" scenario will be more sensitive to changes in the topology of the network (such as removal of certain nodes or important crossroads) than to any random changes in the p_{ij} values. A relatively simple first step is to withhold a random portion of the network's nodes and observe changes in the apportionment rates/probabilities. Technically this could be implemented by undertaking multiple randomized simulations of the pathway scenarios with a certain portion of the network's nodes removed randomly. In short, analyzing the impact of uncertainties would require an application of methodologies that are currently beyond the capacity of traditional sensitivity analysis techniques (cf. Swartzman and Kaluzny 1987; Henderson-Sellers and Henderson-Sellers 1996) and will require special techniques to estimate the impacts of topological changes in the network, changes in the connectivity of the network (Krammer and Täubig 2005) and the existence of structurally dense groups (e.g., hubs or transportation crossroads) (Koschützki et al. 2005). This will be another focus of future work.

Finally, the quality of the CRS data used in the study represents another source of uncertainty. The roadside survey was collected on a voluntary basis, making it difficult to estimate sampling irregularities. While the model simulates most likely pathways through the transportation network based on p_{ij} probability values in the $\mathbf{P}_t$ matrix, there are many subjective reasons why track drives may choose (or avoid) the particular route. This knowledge is often based on anecdotal evidence and rarely has been documented. One possible solution is to assume a certain degree of error in the survey records and incorporate this assumption in the form of random probability values in the $\mathbf{P}_t$ matrix. This, however, would also require making assumptions about the degree of geographic and directional variance in the survey records. As an alternative, one might consider convex set approaches (cf. Yemshanov et al. 2010) to evaluate the robustness of risk projections to these kinds of uncertainty.

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