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Risk analysis of the invasion pathway of the Asian gypsy moth: a known forest invader

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Abstract Risk is defined with many minor variations in the biological literature. Common to most definitions are the following elements: the probability of a future event; and the consequences of the event, usually with respect to some predefined human value. Risk analysis includes elements of risk assessment (quantification of risk), uncertainty (of the event and its consequences), risk management (reducing risk to an acceptable level), and development of policy to balance finite resources with uncertainty and risk tolerance. When biological invasion and its risk are jointly examined, it is common that the consequences of invasion are not explicitly quantified, but understood to be sufficiently negative that it must be minimized to the extent possible. Risk analysis then becomes quantification of the probabilities of an introduction (event) and that the introduction leads to establishment, and the uncertainty of those probabilities. I describe a risk analysis framework for the Asian gypsy moth—a known invader—in its pathway. The framework uses the available information regarding the transportation route of the vector (ships), and a phenology model that estimates vector contamination (propagule size), the probability of introduction, and the probability of initial establishment given an introduction. Reducing propagule pressure is arguably the most important factor in reducing biological invasion; propagule pressure can be reduced by inspection and sanitation of the pathway vector (e.g., ships, trucks, humans) at the point(s) of departure and at the point of entry. I demonstrate how the risk analysis framework can be used to more efficiently target incoming ships for inspection and propagule pressure reduction.

Keywords Pathway risk analysis · Phenology · Introduction · Propagule pressure · Asian gypsy moth · International trade

Risk analysis and invasion pathways

Risk is defined with many minor variations in the biological literature. Common to most definitions are the following elements: the probability of a future event; and the consequences of the event, usually with respect to some predefined human value. Risk analysis includes elements of risk assessment (quantification of risk), uncertainty (of the event and its consequences), risk management (e.g., reducing risk to an acceptable level), and the development of policy to balance

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uncertainty and risk tolerance with finite resources to reduce risk. When biological invasion and its risk are jointly examined, it is common that the consequences of invasion are not explicitly quantified, but understood to be sufficiently negative that it must be minimized to the extent possible. Risk assessment then becomes the quantification of two probabilities: of an introduction, and that the introduction leads to establishment. Risk analysis of a pathway is then some combination of the (narrowly defined) risk assessment, the uncertainties, and the policy to manage the risk.

Policies for risk management of biological invasion can be conveniently separated into those that target the risk from known invaders and those that target the invasion pathway as a whole, without specifying which invaders might be in the pathway. In the latter category, the now widely adopted ISPM 15[1] targets wood packaging material as a pathway by which alien organisms are introduced. The ISPM 15 protocol calls for the treatment of all wood packaging material (pallets, crates, dunnage, etc.) to reduce the probability of survival of organisms that may have infested the material (Allen 2017). Ballast discharge is recognized as an important invasion pathway (Steichen et al. 2014; Azmi et al. 2015; Ware et al. 2016), and the Ballast Water Management Convention[2] will require (as of 8 September 2017) ships of the 171 signatory states to implement approved technologies and procedures to reduce the release of alien organisms. In neither of these cases is a specific alien invader the target. In the former category are those policies, each usually restricted to one or a few neighboring countries, that target specific known alien invaders and their known pathways.

The known invader and its invasion pathway

The Global Invasive Species Information Network lists more than 30 pathways, but the Convention on Biological Diversity identifies only two. Hulme et al (2008) argue that policy and regulations (whose intention is the prevention of biological invasion) will be aided by an accepted classification system for pathways; they propose six pathway types. The Asian gypsy moth (AGM) (*Lymantria dispar asiatica* Vnukovskij) is an example of a biological invader in the "stowaway" pathway.

In mid to late summer, mated female AGM are attracted to the artificial lights around Asian ports (Schaefer and Strothkamp 2014) and they lay an egg mass of approx. 400 eggs (Leonard 1981) on the surfaces of ships and containers, some of which are destined for North America (or Australasia, specifically Australia and New Zealand). Introduction of AGM occurs at the destination when larvae emerge from the egg masses while the ship is in port and they are carried by wind to the nearby shore, or when larvae emerge and disperse from the egg masses on offloaded and contaminated containers or cargo. The probability of an AGM stowaway event in Asia, and of a subsequent introduction, is strongly dependent on the timing of the visit to Asian ports where there is a known or suspected AGM population (hereafter "regulated" ports) and the timing of arrival at the North American ports (hereafter "protected" ports). In other words, the probability of an AGM introduction by this stowaway pathway is very strongly seasonally variable. In recognition of this temporal dependence, Canadian and US regulations employ two tactics at two points in the invasion process (Fig. 1):

1. ships that have visited a regulated port during the "risk period" (Table 1) that designates the phenological window of female moth flight and oviposition must undergo a predeparture inspection and cleaning to receive AGM-free certification;
2. these same ships are subject to further inspection[3] at protected ports if they arrive during the "risk period" of the port (Table 2). Ships on which egg masses are detected may be ordered out of national waters for cleaning.

It is not clear if the "risk period" at protected ports (2, above) designates the phenological window of larval emergence from the egg mass (an introduction), or the window in which an introduction would lead to a

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[1] International Standards for Phyosanitary Measures No. 15; International Plant Protection Convention; https://www.ippc.int/en/.

[2] http://www.imo.org/en/OurWork/Environment/BallastWaterManagement/Pages/Default.aspx.

[3] If entering a US port, inspection of these vessels is "mandatory" (USDA APHIS-PPQ 2011); if entering a Canadian port, these vessels are "subject to inspection" (Canadian Food Inspection Agency 2013).

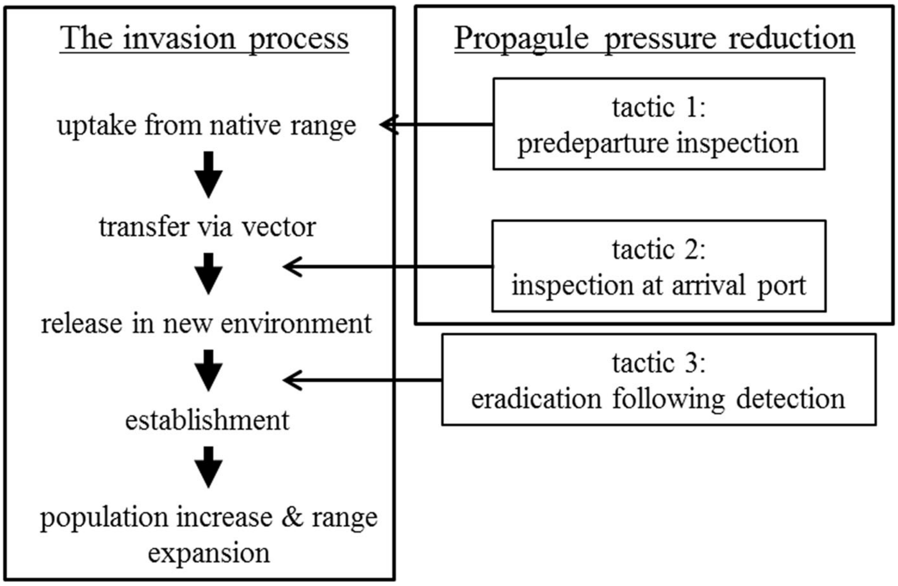

Fig. 1 Cascade of invasion process (adapted from Lockwood et al. 2005; Theoharides and Dukes 2007; Hellmann et al. 2008) showing tactics for reducing propagule pressure and population eradication (in the event of detection)

Table 1 Risk periods in regulated areas (USDA APHIS-PPQ 2011; Canadian Food Inspection Agency 2013)

High-risk area	High-risk period
Japan: Okinawa	25 May–30 June
Japan: south (excluding Okinawa)	1 June–10 August
Japan: east	20 June–20 August
Japan: west	25 June–15 September
Japan: north	1 July–30 September
People's Republic of China	1 June–30 September
Republic of Korea	1 June–30 September
Russia: far east	1 July–30 September

successful completion of the life cycle (initial establishment). I will discuss both, below.

Ships are routinely found with AGM egg masses prior to departure from Asia and undergo cleaning (success of tactic 1); and ships (with and without AGM-free certification) frequently arrive at North American ports with AGM egg masses and are ordered out of national waters for cleaning[4] (success of tactic 2). Nonetheless, AGM populations have been detected onshore by pheromone traps, indicating <100% success of tactics 1 and 2. Given the number of cargo ships travelling between Asia and North America, and the enormous size and complexity of the ships and their cargo, it is not surprising that ship inspections at source and at destination have not prevented introductions. The perceived consequences of an established AGM population are sufficiently high that aerial applications of insecticide have been conducted to eradicate populations that have been detected by onshore pheromone traps. However, the aerial application of insecticides in and around the populated port areas faces severe societal obstacles and should be used as infrequently as possible.

The role of propagule pressure in biological invasion

The invasion process is variously described (Lockwood et al. 2005; Theoharides and Dukes 2007; Hellmann et al. 2008) as a series of steps: uptake from the native range; transfer; release into new environment; establishment; population increase and range expansion (Fig. 1). Each step of the process is a sufficient obstacle that only a small proportion of introductions results in invasion (Mack et al. 2000;

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[4] For example, 20 vessels at western Canada ports with AGM egg masses in 2014. http://www.cosbc.ca/index.php/regulatory-updates/item/686-cfia-and-usda-issue-urgent-asian-gypsy-moth-bulletin.

Table 2 Risk periods (in *red*) in Canadian and US ports for vessels arriving from regulated Asian ports (USDA APHIS-PPQ 2011; Canadian Food Inspection Agency 2013)

Port Location	Month of arrival											
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Western Canada			🟥	🟥	🟥	🟥	🟥	🟥	◧			
Eastern Canada			◨	🟥	🟥	🟥	🟥	🟥	◧			
Alaska				🟥	🟥	🟥	🟥	🟥				
Great Lakes			🟥	🟥	🟥	🟥	🟥	🟥	🟥			
Hawaii												
Oregon			🟥	🟥	🟥	🟥	🟥	🟥	🟥			
Puerto Rico												
Washington State			🟥	🟥	🟥	🟥	🟥	🟥	🟥			
Norfolk, VA and northward			🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥		
South of Norfolk, VA to Jacksonville,			🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	
South of Jacksonville, FL			🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
AL, CA, FL, LA, MS, TX	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥

AL Alabama, *CA* California, *FL* Florida, *LA* Louisiana, *MS* Mississippi, *TX* Texas

Williamson 2006; Brockerhoff et al. 2014). Propagule pressure is probably the single most important determinant of nonindigenous species (NIS) establishment (Williamson 1996; Lockwood et al. 2005; Colautti et al. 2006; Simberloff 2009). Propagule pressure is a composite of the number of discrete events in which individuals are released into the new environment (propagule number) and the number of individuals released in any discrete event (propagule size). Lower propagule pressure reduces the probability that individuals will be introduced into a suitable environment (including seasonal considerations), the genetic variability of the introduced population, and the likelihood that individuals in sexually reproducing species will find a mate. Reducing propagule pressure may be the simplest way of preventing establishment of NIS (Bacon et al. 2012). The two tactics (above) of the USA and Canada that target AGM stowaways are designed to reduce propagule number and propagule size.

Risk analysis for the known invader, Asian gypsy moth

Risk analysis of this alien invader should include:

1. a method to estimate the ship-specific propagule size;
2. a method to estimate the probability that the propagules will be released in the protected port (i.e., larvae will emerge from the egg masses: an introduction);
3. a method to estimate the probability of establishment given an introduction;
4. estimates of uncertainties of 1 and 2; and
5. a policy/protocol to minimize risk by reducing propagule pressure, given finite resources, uncertainty of risk, and an acknowledgement of risk tolerance.

Probabilistically, reducing propagule pressure of this invader in this pathway will be most effective when inspections at protected ports are done on ships: (1) that have the largest propagule size (i.e., ships with the greatest number of undetected egg masses where the probability of finding an egg mass is, therefore, highest); and (2) whose larvae are most likely to emerge while in the protected port; and (3) when the introduction window (timing of emergence of larvae from the egg) is most likely to lead to a successful life cycle. Assessment of these three criteria for multiple ships that are arriving on the same day would distinguish differences in the risks posed by those ships. This would then enable limited surveillance resources to be allocated more effectively than is done now for reducing propagule pressure. I will briefly discuss limitations of the current protocol, as they relate to the three criteria, and then introduce a more biologically based method of assessing the criteria.

Criterion 1: onboard propagule size

The defined "risk period" for Asia ports (Table 1) in the US and Canadian inspection protocol is designed to encompass the phenological window during which oviposition occurs and ships are, therefore, subject to contamination with egg masses. Limitations of the defined risk periods include their excessive duration [c.f. a typical ~14 days oviposition period (Fig. 2)]; the geographic coarseness of the regional divisions (Table 1); and their inability to estimate the varying levels of the onboard oviposition of egg masses that may occur during Asian port visit(s). The larvae that will emerge from the onboard egg masses constitute the propagule size of that ship. A ship's typical 4–5 days visit to a regulated Asian port within the 1–3 months defined risk period (Table 1) may coincide with a large proportion of a typical ~14 days oviposition period (Fig. 2), or with none of it. Visits to multiple regulated ports within the staggered risk periods of Asian ports will result in an increase in propagule size in each port in which the visit coincides with a portion of the oviposition period, and with no increase in the ports in which the visit coincides with none of it. Predeparture inspection is <100% effective. Thus, multiple ships arriving at North American ports on the same day that have visited regulated Asian ports during the risk period may have variable—including zero—propagule size, but the Canadian and US protocol for inspection, and prevention of propagule introduction, treats all such ships equally.

Criterion 2: an introduction when larvae emerge in the protected port

Embryos within the egg masses that escape detection before departure from an Asian port develop

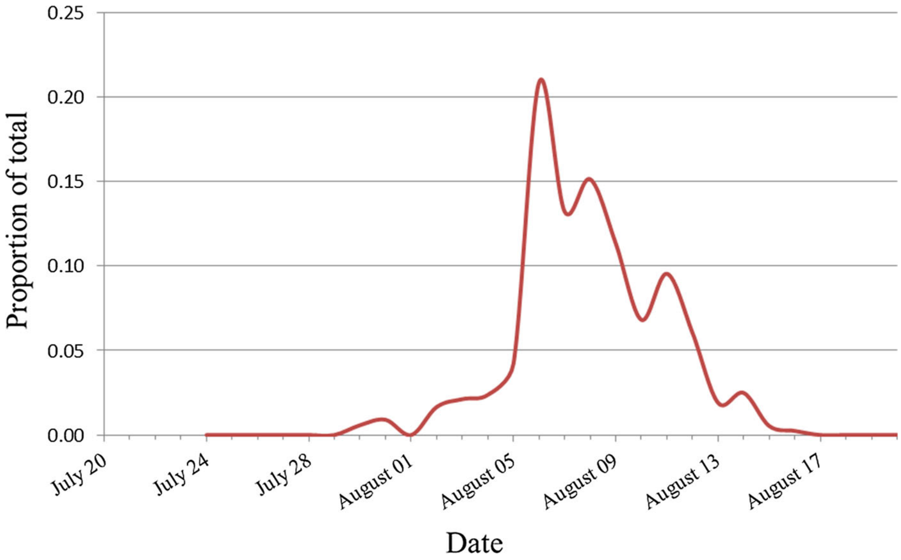

Fig. 2 A typical AGM oviposition pattern simulated by the *GLS-2d* phenology model for an Asian port that has a defined risk period (USDA APHIS-PPQ 2011; Canadian Food Inspection Agency 2013) of 20 June–20 August

according to the temperatures to which they are exposed en route to the protected port. Introduction occurs if larvae emerge from the egg masses while the ship is in port and they are carried by wind to the nearby shore, or if larvae emerge and disperse from egg masses on offloaded containers and cargo. Ships that arrive at a protected port after larvae have emerged from onboard egg masses pose no threat. Likewise, ships that will depart a protected port before larvae emerge from onboard egg masses pose no threat to that port. (However, contaminated and off-loaded containers and cargo may pose a threat. See Criteria 3, below.) The designated phenological window for larval emergence (Table 2) makes no consideration of the effect of en route temperatures on the phenological development of embryos and emergence of larvae from an onboard population of egg masses at the protected port. Thus, multiple ships arriving at a North American port on the same day [within the designated phenological window (Table 2)] are treated as equal threats for introduction despite potential differences in larval emergence times.

Criterion 3: an introduction leads to establishment

Propagules that are transported between a regulated and a protected port will experience a temperature regime unlike any that exists in a single location. Consequently, larval emergence of the introduced generation (including from off-loaded containers and cargo) in the protected port may occur at virtually any time of the year. Early emerging larvae may be exposed to lethal sub-freezing temperatures. Late-emerging larvae may not achieve reproductive status in time for the embryos of the next generation to reach the cold-tolerant diapause phase (Leonard 1968) before the first lethal sub-freezing temperatures occur. Winter in the regulated port must be long enough, with enough low temperatures to satisfy diapause requirements (Gray et al. 2001). In summary, initial establishment depends on an introduction "window" that leads to a suitable temperature regime (Logan et al. 2007; Theoharides and Dukes 2007). Introduction dates can be assessed for the likelihood that they lead to a suitable temperature regime for life-cycle success—the risks that an introduction on those dates will lead to establishment.

Application of a phenology model to assess pathway risk

The pathway for invasion of AGM is via transport on international ships [stowaway (Hulme 2009)]. The specifics of the pathway vector (i.e., dates and routes of ships between the regulated and protected ports) are distinguishing characteristics of the general pathway that have significant effects on the three criteria in the risk analysis: onboard accumulation of propagules in Asia; the probability that propagules will be released while in port (introduction); and the fate of propagules at the protected port (survival and establishment). A geographically robust model of gypsy moth phenology can be a tool for more accurate assessment of the pathway vector specifics (dates and routes) for these three criteria. More accurate assessment will enable more targeted inspection when the number of ships arriving exceeds the capacity of inspection resources (a common occurrence), thus reducing propagule pressure and reducing risk.

The phenology model

Phenology is the study of the relationship between climate and cyclic/seasonal biological phenomena (e.g., flowering, insect emergence). Temperature, photoperiod, moisture, and nutrition may all influence phenology, but temperature is the strongest determinant, and in the case of gypsy moth, the only important factor. A phenology model simulates the occurrence of life-cycle events from an input of temperature (often daily minimums and maximums), and insects progress through a life stage at a rate (R) that is dependent on the temperature (T) of that time (t):

$$R(t) = f(T[t]) \tag{1}$$

Developmental rates are calculated for each small time step Δt (usually 1 h), and the life stage is completed at $t = t_c$ when

$$\sum_{t=0}^{t=t_c} f(T[t]) = 1 \tag{2}$$

This generalized model construct assumes that the response to a given temperature (T) is uniform for the duration (developmental age = 0–1) of the life stage. This may be a reasonable enough assumption for the larval–adult life stages. But, as long ago as 1913, it was recognized (Sanderson and Peairs 1913) that the assumption was violated during the overwintering life stage (embryos within eggs) leading to egg hatch, which is, arguably, the most critical life-stage event for establishing seasonal development of the generation. A new technique of rapidly measuring the respiration rate of individual embryos (Gray et al. 1991) separated the egg stage into three distinct phases. The diapause (Gray et al. 2001) and postdiapause (Gray et al. 1995) phases were subsequently shown to each have a developmental response that was both temperature and age dependent (Fig. 3). Details of the phase-specific phenology models of the egg stage can be seen in Gray et al. (1991 (for prediapause)), Gray et al. (2001 (for diapause)) and Gray (2009 (for postdiapause)). A full life-cycle phenology model was constructed (Gray 2004) by combining the models of embryonic development (leading to egg hatch) with the existing models for the post-hatch life stages (Logan et al. 1991; Sheehan 1992). A population is represented in the Gypsy Moth Life Stage (Gray/Logan/Sheehan) (*GLS*) model by a range of slowest to fastest developers in each egg phase and post-hatch life stage as was observed experimentally. The *GLS* model has been used to estimate risk of establishment at point locations, given a successful introduction at the location, based on climatic suitability in British Columbia, Canada (Régnière and Nealis 2002), Utah, USA (Logan et al. 2007), New Zealand (Pitt et al. 2007, but see Gray 2014 for an illustration of the importance of model initiation date), and Canada (Gray 2004; Régnière et al. 2009). *GLS-2d* is an extension of the control code with which the developmental response of embryos (in the egg masses) is simulated as the egg masses are transported by ship between an Asian port and any destination (Gray 2015).

The developmental rate functions (Eq. 1) of the embryonic stages in *GLS* (and, therefore, in *GLS-2d*, also) were developed from experimental studies with the North American sub-species, *L. dispar dispar*, not the *L. dispar asiatica* subspecies modelled here. Keena (2016) compared hatch patterns of 43 populations of *L. dispar* from Asia, Europe and North America and found statistical difference among populations in the day of first larval emergence and mean day of larval emergence following a rearing protocol of 25 °C for 32 days, 5 °C for 60 days, and 25 °C until emergence. Under this same temperature regime, *GLS-2d* predicts the day of first larval emergence and mean day of larval emergence will be 16 and 21.7 days, respectively, after the end of the 5 °C treatment. These simulated estimates are very close to Keena's (2016) observations from the Korean *L. dispar asiatica* population of the day of first emergence (15 days (visually estimated from her Fig. 4)) and mean day of emergence (18.1 ± 1.6 days).

Criteria 1 and 2: simulation protocol and results

Phenology simulations must choose a date on which to begin simulation; the choice can significantly affect predicted dates of developmental events (e.g., oviposition, larval emergence) and of life-cycle success (Gray 2014). In a strategy to make this choice, Gray (2004, 2010) showed that a stable oviposition pattern (date × oviposition frequency) is achieved within 3–7 generations in any desired location after launching 10 equal-sized egg cohorts at equal intervals from 10 January to 21 November. Therefore, using the port temperatures in its database (see below), *GLS-2d* simulates the oviposition pattern of the seventh generation (i.e., the stabilized pattern) in every regulated port that appears on the log of a vessel that is arriving at a protected port.[5] *GLS-2d* assumes an equal oviposition pressure in all ports. At each regulated Asian port on the ship log, *GLS-2d* "places" a cohort of egg masses onboard each day the ship is in port during the estimated oviposition period. The size of each onboard cohort is equal to the proportion of total simulated oviposition that occurred on that day in the port (Fig. 2). Onboard propagule size is the sum of the cohorts.

GLS-2d has a database of estimated daily minimum and maximum near-surface atmospheric temperatures of 6143 maritime locations (2.81° latitude × 2.81° longitude grid) and 66 ports (Asian, North American, Australasian, and other); users can add additional ports to the database. Following the first onboard oviposition, the daily location of a ship is estimated from the ship log (arrival and departure dates for every port) and the port-to-port waypoints retrieved from a web-

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[5] All vessels arriving at a Canadian or American port must provide a list of the dates and names of ports visited in the last two calendar years.

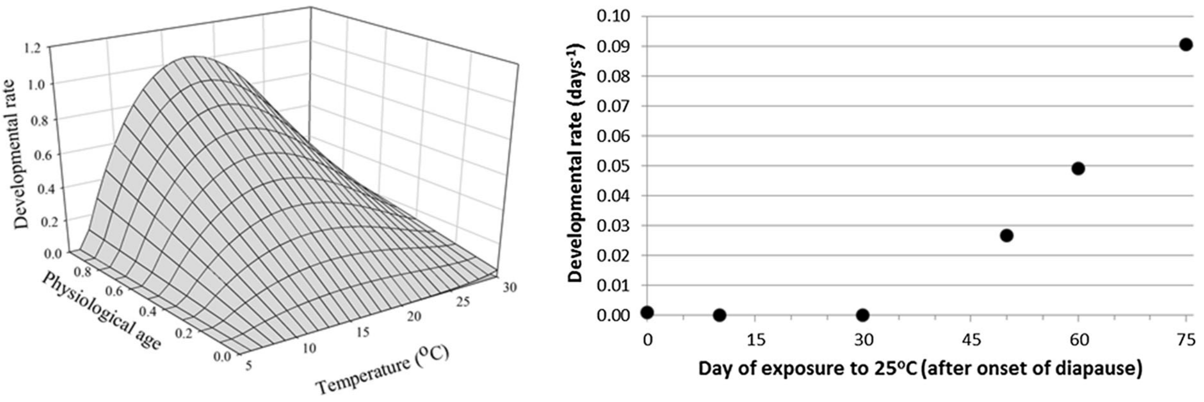

Fig. 3 Age-dependent response to temperature in postdiapause (*left*, Gray 2009, Fig. 8); and in diapause (*right*, Gray et al. 2001, Fig. 3) in the Gypsy Moth Life Stage (*GLS*) model

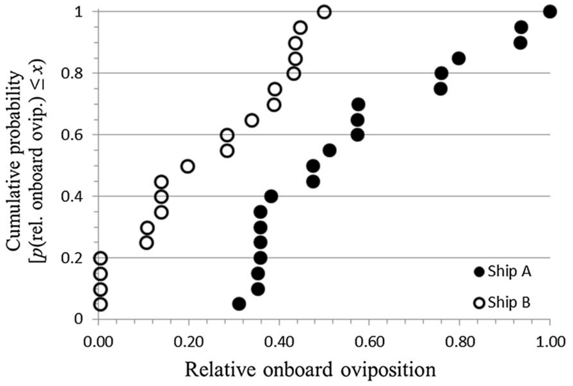

Fig. 4 Preinspection relative onboard AGM oviposition in 20 simulations of two ships. Routes of Ship A and Ship B differed only in the order in which four regulated ports were visited (see Table 3). Absolute sizes of port AGM populations are not known, but are considered to be equal. Preinspection relative oviposition indicates the degree to which ship visits coincided with the period of female oviposition. Cumulative probabilities [p(relative onboard oviposition $\leq x$%)] shows a higher risk posed by Ship A than for Ship B. For example, 50% of the predictions for Ship A are greater than the highest prediction for Ship B; 60% of the predictions for Ship B are less than the lowest prediction for Ship A

based database.[6] The phenological (embryonic) development of each onboard cohort is advanced hourly by a sine wave approximation (Allen 1976) of temperatures from the minimum and maximum temperatures of the daily locations until larval emergence from the egg. The simulated larval emergence pattern can be compared with the dates that the ship will be in the protected port.

GLS-2d simulations of phenology are possible with real-time temperatures. But maintaining an up-to-the-day database of daily temperatures on the spatial scale required for all potential port-to-port routes would be an unmanageable task. Therefore, instead, the *GLS-2d* temperature databases (maritime and ports) are of 20 years, and a *GLS-2d* simulation for each ship is 20 independent iterations of the route. Each iteration is considered an equally likely outcome, and simulation results of onboard propagule size and of larval emergence at the regulated port are presented as cumulative probability distributions [p(survival rate $\leq x$%)] from the 20 iterations in order to illustrate the range and variability of the result.

I will show in the following two examples that very minor differences in the pathway specifics (dates and routes) result in significant differences in the risk factors (criteria 1 and 2). The examples are not meant to be exhaustive, nor are they necessarily representative of identifiable groups of pathway specifics. Rather, the examples illustrate how very minor differences in the pathway specifics can substantially alter the estimated risk.

Example 1: same regulated ports on different days

In this comparison, two hypothetical ships visit the same four regulated ports during the high-risk periods defined for those ports. The durations in each regulated port are the same for both ships, but the order of the

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[6] Netpas Webservice 3.0. (http://netpas.net/products/product_detail_DE_EN.php) lists more than 12,000 ports worldwide and more than 72 million waypoints.

visits to those ports (and therefore, dates) is different for the two ships: Shanghai–Busan–Incheon–Qingdao (Ship A) versus Qingdao–Incheon–Busan–Shanghai (Ship B). Following their visits to the fourth regulated port, both ships follow exactly the same route (ports and dates) before arriving at the protected port of Norfolk, VA, USA on 2 March (Table 3). If we assume (and there is no basis for an alternative assumption) that predeparture inspections of the two ships are equally—but <100%—successful in locating and removing onboard egg masses, then Ship A is predicted to arrive in Norfolk with approx. two times more undetected egg masses than ship B simply by virtue of the order (dates) on which the four regulated ports were visited. Ship B is estimated to have avoided oviposition in the four Asian ports in 40% of the simulations. In 50% of the simulations, the oviposition encountered by Ship A is estimated to be greater than the maximum of all simulations encountered by Ship B (Fig. 4). Under conditions of limited inspection capacity in Norfolk, propagule pressure reduction will be greater by inspecting Ship A than Ship B.

Example 2: same regulated ports and different routes to protected port

In this comparison, two hypothetical ships visit the same regulated ports during the high risk periods defined for those ports. The durations and dates in each regulated port (Shanghai–Busan–Incheon–Qingdao) are the same for both ships, but following the stop in Qingdao the two ships follow slightly different routes before arriving at Norfolk, VA on 2 March (Table 4). If we assume that predeparture inspections of the two ships are equally—but <100%—successful in locating and removing onboard egg masses, then Ship A and ship C are predicted to arrive in Norfolk with the same number of undetected egg masses: the common dates of their visits to the same Asian ports intersected with the identical portions of the female oviposition period.

Table 3 Arrival and departure dates for two ships; both ships visited the same four regulated ports between 20 June and 20 July (but in opposite order), and then followed identical routes to Norfolk, VA

Arrive	Depart	Ship A	Ship B
20 June	24 June	Shanghai, China[a]	Qingdao, China[a]
28 June	2 July	Haiphong, Vietnam	Haiphong, Vietnam
7 July	11 July	Busan, S Korea[a]	Incheon, S Korea[a]
12 July	15 July	Incheon, S Korea[a]	Busan, S Korea[a]
16 July	20 July	Qingdao, China[a]	Shanghai, China[a]
		Ships A and B	
25 July	29 July	Hai Phuong, Vietnam	
7 Aug	12 Aug	Colombo, Sri Lanka	
26 Aug	1 Sept	Yokohama, Japan[a]	
28 Sept	1 Oct	Capetown, South Africa	
11 Oct	15 Oct	Lagos, Nigeria	
25 Oct	29 Oct	Lisboa, Portugal	
2 Nov	7 Nov	Rotterdam, Netherlands	
10 Nov	15 Nov	Trondheim, Norway	
21 Nov	27 Nov	Lulea, Sweden	
29 Nov	4 Dec	Tallinn, Estonia	
8 Dec	23 Dec	Trondheim, Norway	
26 Dec	31 Dec	Gdansk, Poland	
2 Jan	6 Jan	Lulea, Sweden	
11 Jan	16 Jan	Rotterdam, Netherlands	
19 Jan	26 Jan	Trondheim, Norway	
1 Feb	5 Feb	Lulea, Sweden	
16 Feb	19 Feb	Nouakchott, Mauritania	
2 March		Norfolk, USA	

[a] Regulated port in Asia

Table 4 Arrival and departure dates for two ships; both ships visited the same regulated ports on the same days, but then followed different routes to Norfolk, VA

Arrive	Depart	Ships A and C
20 June	24 June	Shanghai, China[a]
28 June	2 July	Haiphong, Vietnam
7 July	11 July	Busan, S. Korea[a]
12 July	15 July	Incheon, S Korea[a]
16 July	20 July	Qingdao, China[a]
25 July	29 July	Hai Phuong, Vietnam
7 Aug	12 Aug	Colombo, Sri Lanka
26 Aug	1 Sept	Yokohama, Japan[a]
28 Sept	1 Oct	Capetown, S. A.

Arrive	Depart	Ship A	Arrive	Depart	Ship C
11 Oct	15 Oct	Lagos, Nigeria	15 Oct	18 Oct	Colombo, Sri Lanka
25 Oct	29 Oct	Lisboa, Portugal	24 Oct	29 Oct	Singapore, Singapore
2 Nov	7 Nov	Rotterdam, NLs	14 Nov	19 Nov	Capetown, S. A.
10 Nov	15 Nov	Trondheim, Norway	5 Dec	9 Dec	Mumbai, India
21 Nov	27 Nov	Lulea, Sweden	17 Dec	23 Dec	Singapore, Singapore
29 Nov	4 Dec	Tallinn, Estonia	28 Dec	2 Jan	Haldia, India
8 Dec	23 Dec	Trondheim, NL	9 Jan	14 Jan	Mumbai, India
26 Dec	31 Dec	Gdansk, Poland	30 Jan	1 Feb	Capetown, S. A.
2 Jan	6 Jan	Lulea, Poland	4 Feb	7 Feb	Durban, S. A.
11 Jan	16 Jan	Rotterdam, NL	2 March		Norfolk, USA
19 Jan	26 Jan	Trondheim, Norway			
1 Feb	5 Feb	Lulea, Sweden			
16 Feb	19 Feb	Nouakchott, Mauritania			
2 March		Norfolk, USA			

[a] Regulated port in Asia

However, larval emergence from egg masses is predicted to be underway when Ship A arrives in Norfolk; larval emergence from egg masses on Ship C is not predicted to begin until 2 months after arrival (and presumably after departure) (Fig. 5).

Criterion 3: simulation protocol and results

Long-term establishment of a population depends on complex ecological interactions over several trophic levels and is difficult to predict (Logan et al. 2007). However, climatic suitability is a minimum requirement. The suitable introduction window can be estimated for each regulated port by initiating an emerged population of first-instar larvae at 52 weekly intervals, and estimating the proportion of each population that successfully completes the life cycle (larval emergence of the next generation). The suitable introduction window was estimated for 13 North American ports (Fig. 6), with five independent iterations in each port.

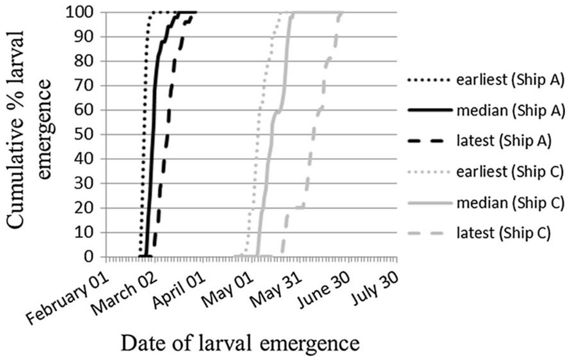


Fig. 5 Larval emergence patterns in Norfolk, VA after the two different routes between the same regulated ports and Norfolk (see Table 4)

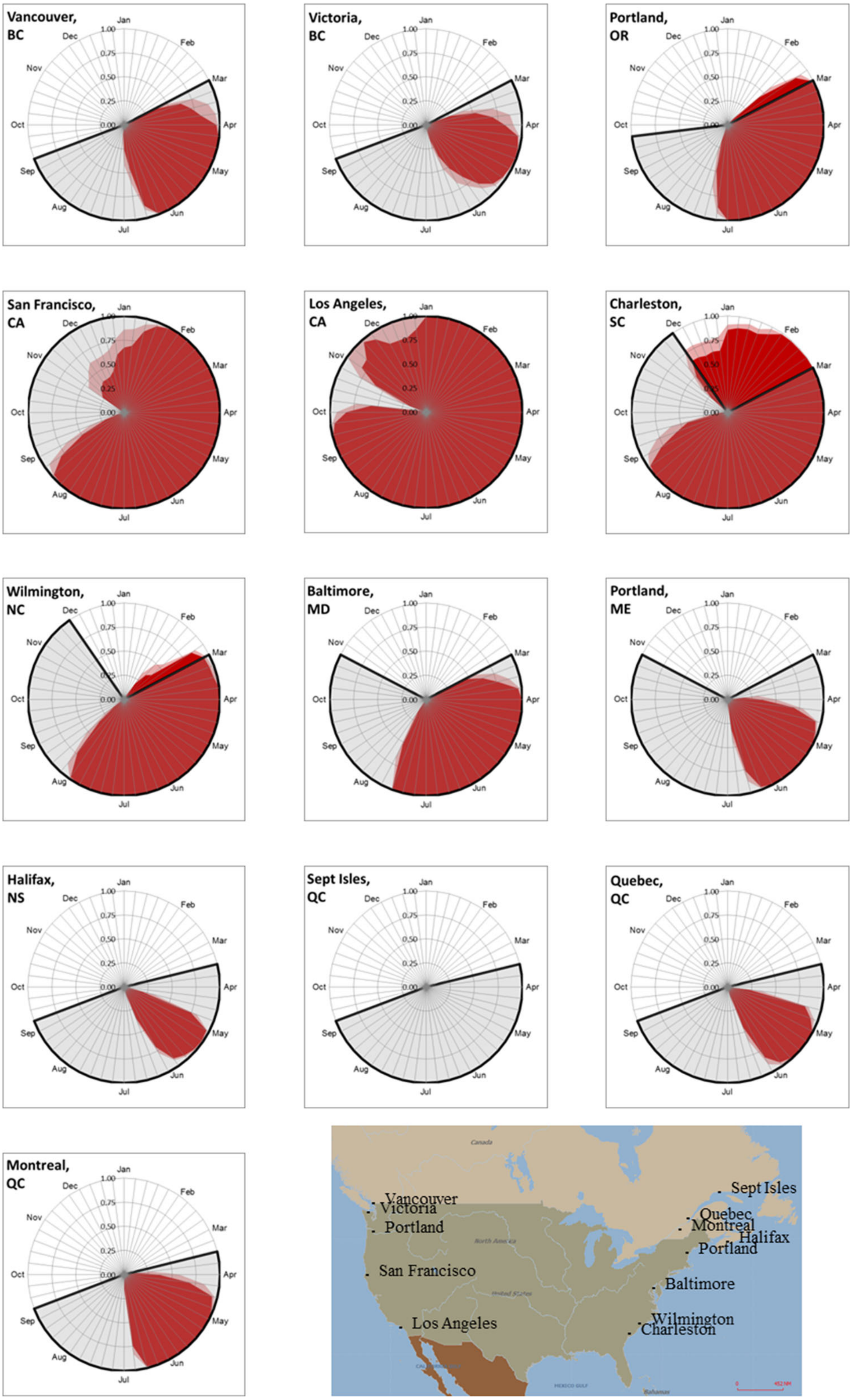
The risk window defined by the US and Canadian regulations (Table 2) is generally longer than that estimated by the phenology simulations. In the North Atlantic ports, the defined risk window of Table 2 reflects a particularly strong aversion to risk. For example, the mean (±SE) simulated generational survival was >0 for populations where larval emergence occurred in Halifax, NS between late April and the end of June (Fig. 6), whereas the defined risk window is from mid-March to mid-September. Simulated populations do not survive in ports on the north shore of the St. Lawrence (e.g., Sept Isles, QC) regardless of the date of larval emergence. On the other hand, the defined window should be shifted to more closely match the simulated window in Charleston, SC. The defined risk window also reflects a strong risk aversion in the North Pacific ports, except in Portland, OR, where the simulated window begins earlier that the defined window. It is also interesting to note that the simulated risk window is substantially shorter in Victoria, BC than in Vancouver, BC, despite those ports being separated by only 100 km.

Concluding remarks

Herborg et al. (2009) constructed an invasion risk map for a benthic pest by combining a vector model of the five principle vectors (aquaculture trade and four categories of sea vessels) and a niche model of the pest. In essence, the vector model assesses the risk of introduction and the niche model assesses the risk of establishment. The work I described here is similar in that it combines specifics of vector traffic (dates of port visits and routes between ports) and spatially explicit en route environmental conditions (temperature) to compare the risks posed by the estimated relative propagule sizes of multiple ships. The comparative estimates can be used to better allocate limited surveillance resources whose purpose is to detect and exclude propagules. The use of climatic suitability to assess the introduction window for establishment is a narrower form of niche modeling (Thuiller et al. 2005) in that it does not include host information, while also being more precise in its formulation of climate requirements.

Biological invasion is often described as a multistep process in which [there is “general agreement that” (Lockwood et al. 2001)] success at each step is quite small (Mack et al. 2000; Theoharides and Dukes 2007; Hellmann et al. 2008). Barriers to invasion include the absence of a transport mechanism, abiotic factors that are fatal during transit, abiotic factors that are fatal in the invasion location, abiotic and biotic factors that prevent/limit population growth, and local landscape factors that prevent spread (Hellmann et al. 2008). Pathway risk analysis should assess the probability (with its uncertainty) that an invader in a pathway can surmount all of these barriers and it should contribute to a policy/protocol that reduces the risk to acceptable levels. However, biotic factors that prevent/limit population growth are complex and multitrophic, and landscape factors that prevent spread will be largely unknown in the invaded area. Therefore, pathway risk analysis is limited to an assessment of the transport mechanism and the abiotic factors during transit and in the invasion location. Fortunately, propagule pressure (the number of introduction events and the size of each event) is the single most important determination of invasion success (Simberloff 2009). Because invasion success occurs only when each of the obstacles has been passed, reducing (but not, necessarily, eliminating) propagule pressure reduces the probability of invasion. Targeted inspection of the vehicles in the invasion pathway is a tactic to reduce propagule pressure.

The volume of seaborne cargo increased 35-fold between 1973 and 2007 (Hulme 2009, citing UN Conference on Trade and Development, 2007, Review of Maritime Transport). A consequence of this increase has been a dramatic increase in the frequency of alien introductions (Meyerson and Mooney 2007; Capinha et al. 2015); the frequency is likely to continue to increase. Many of the most damaging invaders are discovered only after introduction and establishment; the invader was not among the known threats [e.g., Asian long-horned beetle (*Anoplophora glabripennis* (Motschulsky)), emerald ash borer (*Agrilus planipennis* Fairmaire, many others)]. International regulations that target the pathway vector generally, without specific knowledge of what invaders are present (e.g., ISPM 15, and the Ballast Water Management Convention), will help prevent many introductions. Bradie and Leung (2015) advocate the development of risk models for “the suite of species in an introduction pathway”. However, in some other cases, the identity and the vector of an invasive threat are known. In such cases, regulations and prevention


Vancouver, BC
Victoria, BC
Portland, OR
San Francisco, CA
Los Angeles, CA
Charleston, SC
Wilmington, NC
Baltimore, MD
Portland, ME
Halifax, NS
Sept Isles, QC
Quebec, QC
Montreal, QC
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
0.00
0.25
0.50
0.75
1.00
Sept Isles
Vancouver
Victoria
Portland
Quebec
Montreal
Halifax
Portland
San Francisco
Baltimore
Los Angeles
Wilmington
Charleston

◀**Fig. 6** Defined risk window (from US and Canadian regulations) (*black-outlined gray* portion of *circle*), and simulated risk window defined by the generational survival rate (radius of *dark red*) with 95% CI (radius of *light red*) of populations initiated by larval emergence each week in 13 North American ports; $n = 5$

tactics can be improved by using details of the vector and the ecology of the invader in a risk analysis framework, as described here.

The risk analysis framework described here includes four of the five essential components listed above: (1) estimation of propagule size; (2) estimation of introduction probability; (3) estimation of establishment probability given an introduction; (4) estimation of uncertainty of (1) and (2). The framework provides the responsible regulatory agencies a tool with which to develop and institute the fifth component: a policy/protocol to minimize risk. The use of a biologically based risk analysis framework, such as described here, has the benefit that the concepts of uncertainty and of risk tolerance are explicitly acknowledged and can form a part of the risk management policy. A comparison of the estimated propagule sizes of multiple ships (Fig. 4) indicates the uncertainty with the estimate of each ship. The predicted larval emergence times of the example ships (Fig. 5) suggest that only a strongly risk-averse policy would cause Ship C to be inspected—the earliest prediction for larval emergence (24 April) is more than one month after the likely departure of the ship from Norfolk. Jurisdictions should formulate their policy with an acknowledgement of their level of risk tolerance. Lower risk tolerance comes with the costs of more inspections but with the payback of lower probability of introduction. Higher risk tolerance has lower inspection costs, but with higher probability of introduction.

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