

Thousands introduced annually: the aquarium pathway for non-indigenous plants to the St Lawrence Seaway

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Non-indigenous species are both economically and ecologically costly. Invasions are occurring at an accelerating rate worldwide and therefore present a critical challenge to natural resource managers. The aquarium trade is commonly recognized as a pathway for non-indigenous plants, but few regulations exist to curb such introductions. In addition, very few studies have attempted to quantify the number of propagules introduced through the aquarium trade each year, probably because it is difficult to directly measure the number of propagules introduced. Here, we use a novel approach to quantify propagule numbers by analyzing each step in the path to introduction and synthesizing this information to calculate propagule pressure for each species. We used the aquarium plant trade in Montreal, Quebec, Canada, as our study system and found that thousands of non-indigenous plant propagules are introduced to the St Lawrence Seaway each year through the Montreal aquarium trade alone. Two known invaders are among those species with the highest measured propagule pressure.

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A non-indigenous species (NIS) is one that is introduced to areas beyond its native range and then establishes a self-sustaining population (Kolar and Lodge 2001). The 50 000 NIS in the US are estimated to cause economic losses equal to \$137 billion a year (Pimentel *et al.* 2000). In addition, NIS are a leading cause of population decline among nearly half of species listed as threatened or endangered worldwide (Wilcove *et al.* 1998).

These alien species are introduced to new areas through a variety of anthropogenic vectors, including ballast tanks, airplane cargo, canals, the nursery trade, and the aquarium trade. Policy makers have begun to account for some pathways, for instance by mandating mid-ocean exchanges to reduce NIS in ballast tanks (US Coast Guard 1993). However, areas often receive NIS from a combination of pathways and current legislation has failed to completely prevent new invasions (Ricciardi 2000). Management measures that ignore important pathways are likely to fail at preventing further introductions.

Given that measures for controlling or eradicating alien species are difficult to implement and often costly, preventing establishment is widely regarded as the best management policy (Kolar and Lodge 2001). It is therefore crucial that managers evaluate the risks posed by all pathways as accurately as possible. The aquarium trade has long been cited as a pathway for NIS, bringing thousands of non-native species into North America each year (Welcomme 1984; Figure 1), and is responsible for introducing some of the most widespread plant invaders,

including spiked water-milfoil (*Myriophyllum spicatum*), giant salvinia (*Salvinia molesta*), and Brazilian waterweed (*Egeria densa*; Reichard and White 2001). Plant invaders such as fanwort (*Cabomba caroliniana*), water caltrop (*Trapa natans*), and *M. spicatum* are already established in the Great Lakes as a result of the aquarium trade (Mills *et al.* 1993). Invasive aquatic plants are particularly expensive to deal with. The total cost associated with just three aquatic plants species, purple loosestrife (*Lythrum salicaria*), *M. spicatum*, and *T. natans*, exceeds US\$800 million per year (Pimentel 2005).

In this study, we focus on propagule pressure as a means of predicting invasion. Propagule pressure is a single value that expresses the number of individuals of a species introduced to a given area per unit time. It is a key component required to quantify the risk posed by a particular invasion pathway. Often, species risk assessments focus on species traits or location characteristics (eg Kolar and Lodge 2002). There are many factors important for establishment and these vary between systems; however, propagule pressure is a consistent predictor of invasion success and therefore merits increased attention (Coulautti *et al.* 2006). The higher the propagule pressure, the more likely a NIS is to successfully invade (Williamson 1996; Hutchinson and Vankat 1997; Lonsdale 1999; Kolar and Lodge 2001). In fact, some researchers argue that propagule pressure is the most important factor in determining whether a species will become established (Williamson 1996) and should be used as a null model of invasion success (Coulautti *et al.* 2006). Interestingly, propagule pressure is rarely quantified and, arguably, more studies need to do this. Furthermore, analyses of pathways of introduction, in addition to single-species analyses, may provide broader

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Figure 1. Caption and photo credit to be provided by author.

insight into the mechanisms underlying invasions.

The lack of quantification of propagule pressure is understandable, as it is seldom possible to directly measure the number of propagules entering an environment. However, it should be possible to obtain an indirect measure by considering the steps leading to an introduction, as propagule pressure is often easier to quantify at these intermediate steps.

In this study, we examine each step in the aquarium-trade pathway necessary for the introduction of propagules into a habitat. We used the aquarium plant trade in Montreal, Quebec, as our pathway and the St Lawrence River as our destination. The St Lawrence is an entry point into the Great Lakes Basin, which is highly valuable to both the US and Canada (Northeast–Midwest Institute and NOAA 2001). Not surprisingly, substantial resources are spent each year to control plant invaders in the Great Lakes (US\$29 million; Pimentel 2005).

■ Methods

Study system

The city of Montreal, with a population of more than one million people, sits on the St Lawrence Seaway and is surrounded by its various tributaries. The Seaway is part of a series of man-made canals connecting the Atlantic Ocean to the Great Lakes. Over 30% of exotic species introductions to the Great Lakes have occurred since the Seaway opened in 1956, including new plant invaders (Mills *et al.* 1993). Aquatic plants are known to spread via canal networks (Mills *et al.* 2000).

Analysis

Our approach for measuring propagule pressure involved estimating the total number of propagules of each species

that enter into a given pathway each year, laying out each step in that pathway (Figure 2), determining the transition probability between each step, and, finally, synthesizing this information into a value of propagule pressure for each species using Bayesian statistical analysis. Store owners purchase plants from distributors and then sell them to customers (Steps 1 and 2 in Figure 2). We assumed that all plants ordered from the distributor are sold, and that the amount of each species sold per year is therefore equal to the amount purchased per year. We estimated the number of customers disposing of their plants in various ways (Steps 3 and 4 in Figure 2). In the final step, we assigned probabilities of plant propagules reaching the St Lawrence Seaway for each of those disposal methods (Step 5 in Figure 2).

In order to estimate the total number of each species of plant that is sold in the Montreal aquarium trade, we asked storeowners to provide copies of invoices from distributors. We were able to sample every aquarium store in Montreal, for a total of 16 stores. Twelve stores, representing over 80% of total plant sales in Montreal, were able to provide quantities for each species (henceforth referred to as “quantified stores”), while the others were only able to disclose the total number of plants they sold that year. We used information from quantified stores to estimate the proportion of each individual species sold in Montreal each year (Step 1 in Figure 3). We used all data to estimate total plants sold each year in Montreal, and integrated this with proportions calculated from quantified stores to determine species-specific propagule pressures (Step 2 in Figure 3).

Next, we determined the proportion of plants entering each disposal sub-pathway by surveying Montreal aquarium customers (Step 3 in Figure 3). Customer surveys were left at the cash register of each store for at least a week. The question we used in our final analysis asked respondents to choose from a list of possible disposal methods for aquarium plants. Among the 75 respondents, there were eight kinds of disposal methods chosen, including “throw in the garbage”, “put out on the street”, “return to the store”, “flush down the toilet”, “flush down the sink”, “put directly in a watershed”, and “other”. For the “other” sub-pathway, respondents described their disposal method, and none of these responses was deemed to risk introduction (eg “bury plant in backyard”).

We used our survey results to estimate probabilities for the behavior of all aquarium plant owners in Montreal, employing Bayesian statistics to explicitly quantify uncertainty. Bayesian analysis is useful when there are prior expectations and/or when we need to consider the uncertainty distribution to assign probabilities to different true parameter values (Lee 1997). We had no prior expectations and therefore used an improper uniform prior, so that our

results were based solely on the data collected. Bayesian statistics provided a way to quantify the uncertainty associated with our sample and to assign probabilities to alternative parameters.

We chose to use a multinomial distribution to calculate the uncertainty distribution associated with all combinations of disposal pathways. We determined the probability that a single plant propagule would reach the St Lawrence through each disposal sub-pathway (Step 4 in Figure 3). Disposal methods with the same probabilities were grouped together in the multinomial distribution to simplify our calculations. We assigned a probability of 0 to the “garbage”, “street”, “return to store”, and “other” sub-pathways (termed “void” in Figure 3). Toilet and sink sub-pathways were grouped together (termed “waste” in Figure 3), as both enter the Montreal sewage system. Release into storm sewers (termed “storm” in Figure 3) and direct release into the watershed (“direct”) were treated as separate sub-pathways, as a fraction of storm sewer effluent enters the sewage system. Thus, in our multinomial distribution, there were three parameters describing population rates of using disposal pathways: “direct”, “storm”, and “waste”. “Void” was unity minus the other pathways. Based on the observed number of individuals using each disposal pathway, we obtained a posterior probability distribution for each combination of disposal pathway usage rates.

We multiplied the proportion entering each disposal sub-pathway (as indicated by the multinomial distribution) by the probability of introduction associated with that sub-pathway, summed across sub-pathways, and multiplied by the total number sold per year to determine the final propagule pressure in the St Lawrence. We performed this analysis for all species combined and for each species separately.

Results

Species and quantities sold

Based on store-owner estimates, the total number of aquarium plant species sold in Montreal each year was 75 384. A total of 138 species of aquarium plants are available for sale in Montreal (WebTable 1). Relative frequencies range from 8.2% of all plants sold for java fern (*Microsorium pteropus*) to just 0.0005% for *Anubias gracilis*. The top 20 species account for over 70% of the total market share, while the top 50 species account for over 93%.

Disposal methods: probabilities of introduction

The “waste” sub-pathway was assigned an introduction probability of 0.004, based on the fact that, of the 900 million m³ of water sent to the Montreal Sewage

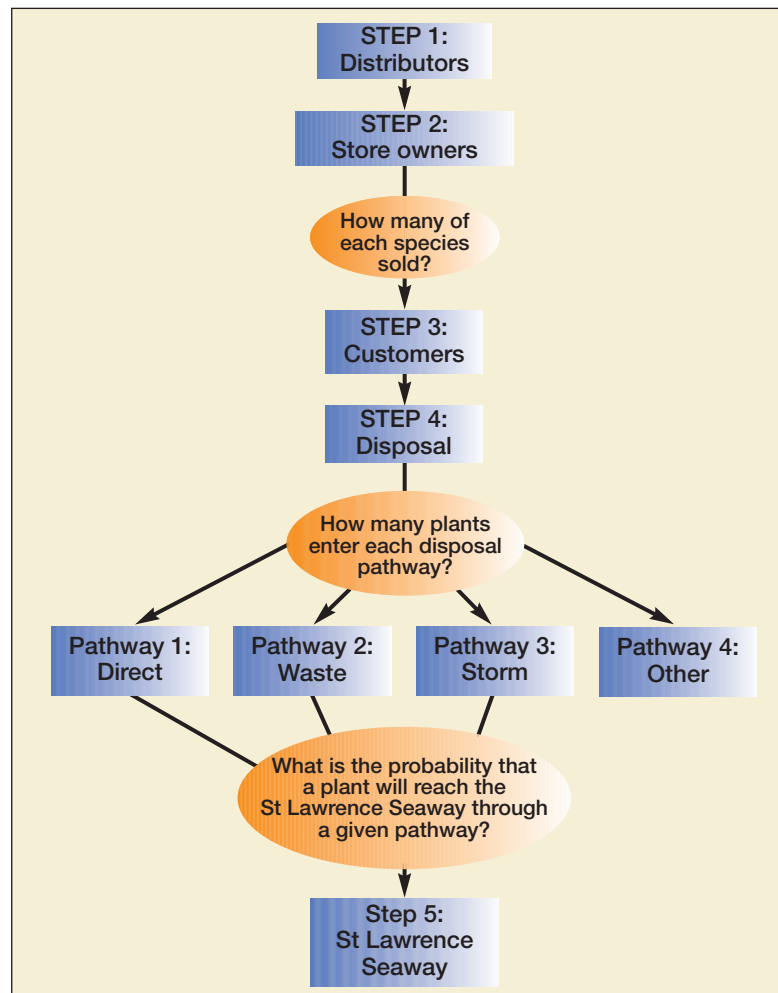


Figure 2. The path of an aquarium plant from distributor to the St Lawrence Seaway. Orange circles denote factors affecting how many plants move from one step to the next.

Treatment Plant each year, 3.88 million m³, or 0.4%, is untreated and directly released to the St Lawrence Seaway (Sierra Legal Defense Fund 2004). A plant disposed through the “storm” sub-pathway had a 0.3426 probability of reaching the Seaway, as 66% of sewage is sent to the treatment plant along with toilet and sink water (multiplied by 0.004 for the proportion of this sewage that is untreated and directly released to the Seaway = 0.0026), while 34% is directly released into the St Lawrence as a result of storm events (Sierra Legal Defense Fund 2004). Plants discarded in watersheds (“direct”) were assigned an introduction probability of 1, whereas “void” plants (eg discarded in garbage) were assigned a probability of 0.

Propagule pressure estimates

We integrated all the information collected to produce final estimates of propagule pressure (Figure 3). Based on our analysis, the most likely propagule pressure for all plants combined is 3015 plants yr⁻¹ (Figure 4a). Figure 4a describes the uncertainty distribution associated with our

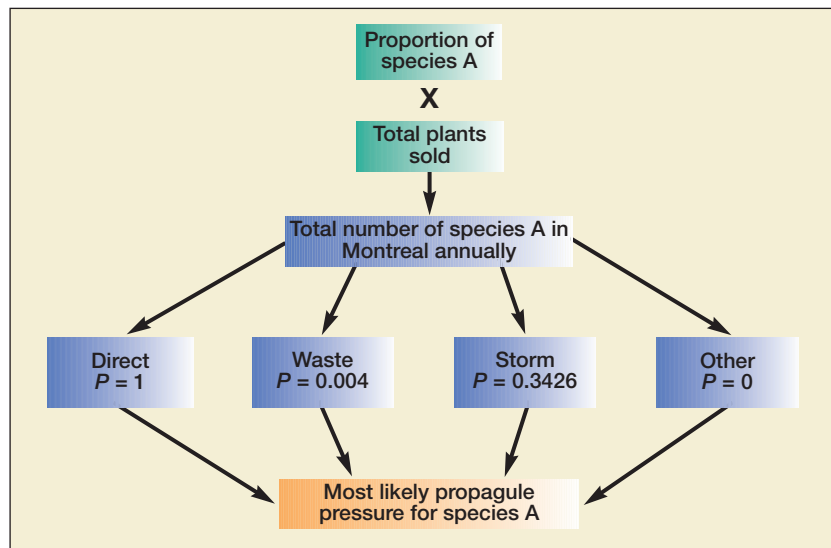


Figure 3. Process of estimating propagule pressures for each species.

estimate. While we found that 3015 plants yr^{-1} is the most likely propagule pressure, using Bayesian analysis we are able to characterize probabilities for other estimates as well. We also determined the distribution of individual propagule pressures for each of the 138 species (Figure 4b). The most likely propagule pressures for the top seven species are (in plants yr^{-1}): 247.21 *M. pteropus*; 201.49 *Cladophora* balls (*Cladophora aegagropila*); 187.65 *E. densa*; 145.24 eelgrass (*Vallisneria spiralis*); 131.25 *Nomophila corymbosa*; 124.81 water hyssop (*Bacopa caroliniana*); and 116.35 *C. caroliniana*.

Discussion

Quantifying propagule pressure from all pathways is an essential step in estimating the actual risk of invasion to a given area, as management efforts that ignore one or more pathways may fail to prevent invasions. In this study, we show that thousands of non-indigenous plant

propagules reach the St Lawrence each year through a known but largely unregulated pathway. Although we focused on the Montreal aquarium trade here, the step-by-step process we outline can be used to ascertain propagule pressures for other areas, other types of organisms, and other pathways.

An important finding of this study is that a plant known to be invasive in other regions of North America, *E. densa*, is also one of the most common species sold in the Montreal aquarium trade. *E. densa* was introduced to lakes in New England through the aquarium trade, where it is now a nuisance species (Bisset 1907; Muenscher 1944; Les and Mehrhoff 1999). This plant should be of special concern, given that it is among the top 10 most popular species in the Montreal aquarium trade and a known invader in a nearby region. In addition, *C. caroliniana* is also one of the top 10 species sold in Montreal, despite the fact that it is already an established nuisance species in the Great Lakes. It is possible that new propagules of this plant continue to be introduced to the Great Lakes via the St Lawrence Seaway, as well as other areas, frustrating attempts to manage or eradicate it in the Great Lakes.

For the purposes of this study, we treated all plant species equally. However, the actual number of plants introduced is likely to depend on characteristics of each species, including growth rate, reproductive rate, and ability to survive in a novel environment. It is also possible that plant disposal methods vary according to the season. For example, most water bodies freeze during the winter in Montreal, limiting aquarium owners' ability to dispose of their plants outside. Future studies could take these and other characteristics into account.

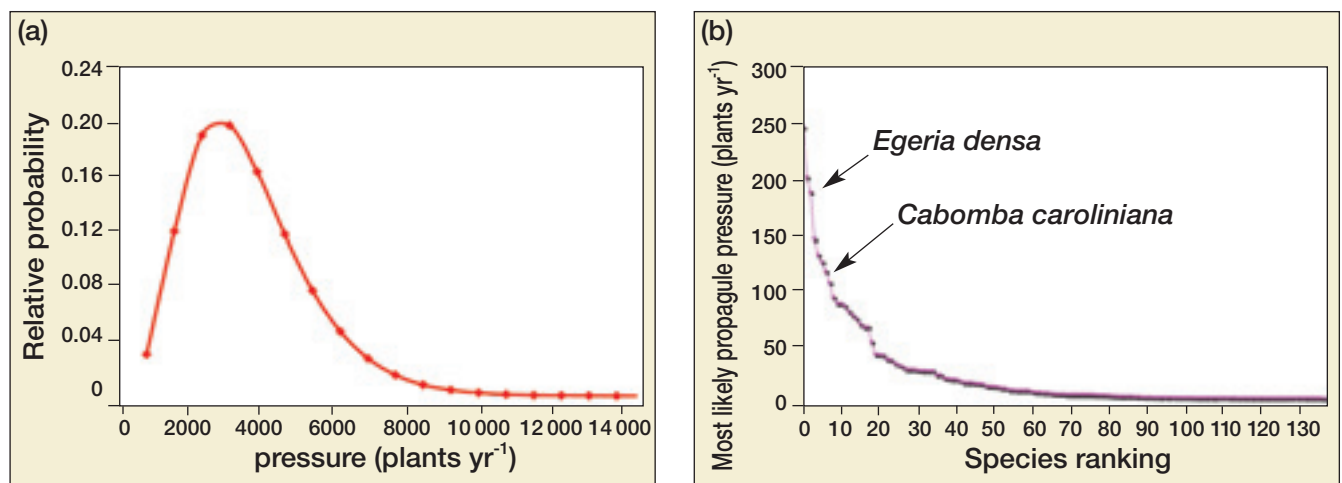


Figure 4. (a) Propagule pressure for aquarium plants reaching the St Lawrence Seaway by way of the Montreal aquarium trade. Bayesian analysis was conducted to determine the relative probability that each propagule pressure was the true one, given the data observed. The most likely propagule pressure was 3015 plants yr^{-1} . (b) Distribution of the most likely propagule pressures across all species. Propagule pressures for two known invaders are identified.

Policy makers are currently focusing on ballast water as the most important pathway of NIS introduction (Ricciardi 2000). Although ballast water is undeniably important, we suggest that pathways such as the aquarium trade contribute significantly to propagule pressure and failure to regulate these pathways could negate other management efforts. The risk posed to the aquarium trade could be reduced by educating the public about the dangers of disposing of their plants improperly. Sale of species that pose a significant invasion risk, such as *E. densa*, could be banned. Other pathways, such as the live food trade and pet trade, merit quantification and could be investigated in future studies.

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