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

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

Jill Cohen[1], Nicholas Mirotchnick[1], and Brian Leung[1,2*]

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 Eurasian 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 chestnut (*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 plant 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

*[1]McGill School of Environment, McGill University, Montreal, QC, H3A 2A7, Canada; [2]Department of Biology, McGill University, Montreal, QC, H3A 1B1, Canada *(brian.leung2@mcgill.ca)*

Figure 1. *Aquatic plants on display in an aquarium store.*

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, 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, Figure 3).

Next, we determined the proportion of plants entering each disposal sub-pathway by surveying Montreal aquarium customers (Step 3, 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 uncertainty distributions (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, 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 (termed "direct" in Figure 3) 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.

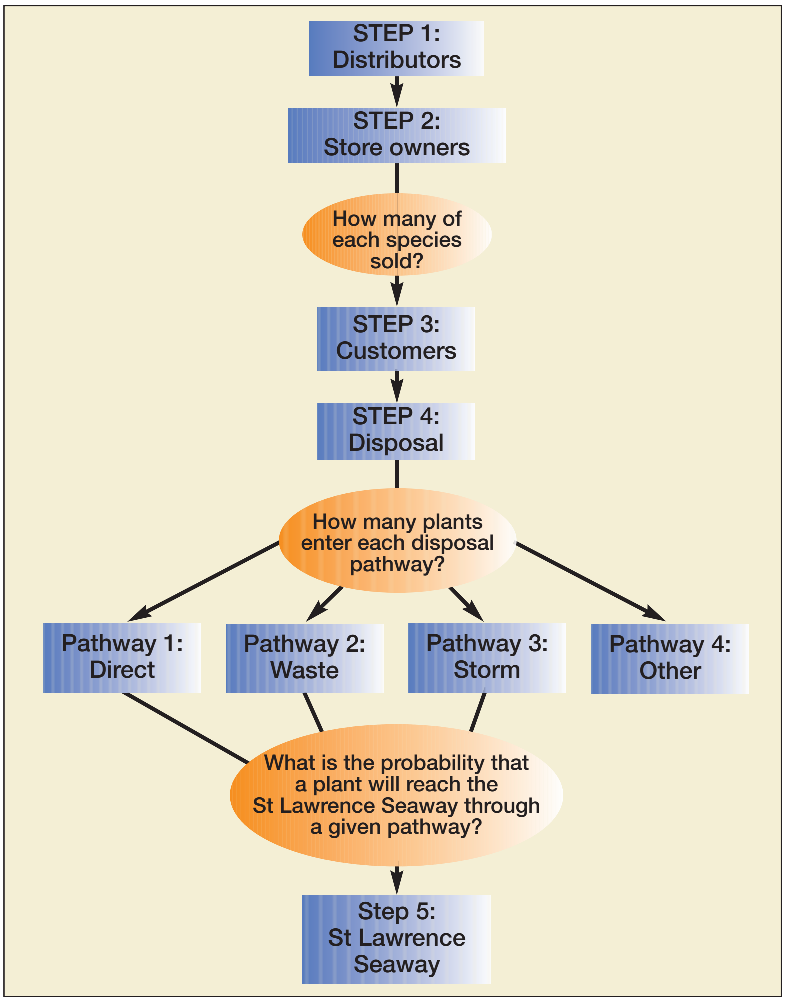

Figure 2. *The path of an aquarium plant from distributor to the St Lawrence Seaway. Orange circles denote factors affecting how many plants move from one step to the next.*

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 (*Microsorum 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 m^3 of water sent to the Montreal Sewage Treatment Plant each year, 3.88 million m^3, 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

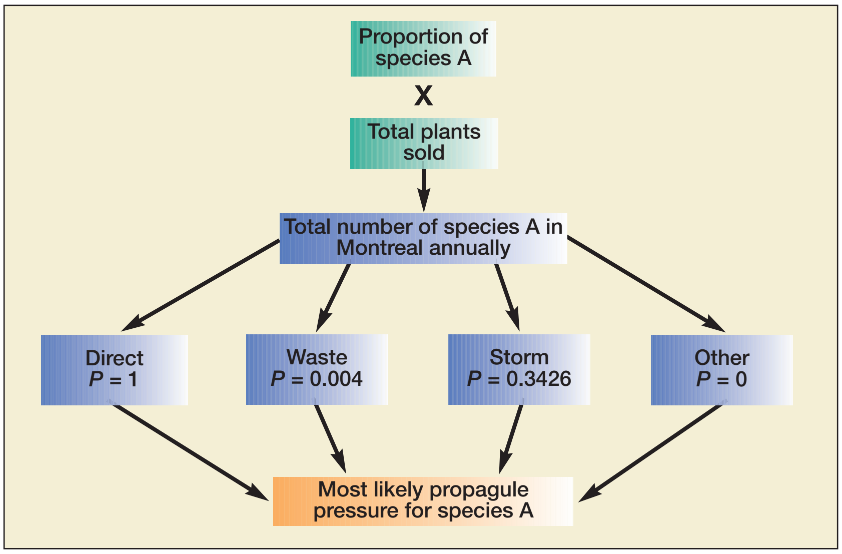

Figure 3*. Process of estimating propagule pressures for each species.*

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 *Microsorum pteropus*; 201.49 *Cladophora aegagropila*; 187.65 *Egeria densa*; 145.24 *Vallisneria gigantean* (eelgrass); 131.25 *Nomaphila coryambosa*; 124.81 *Bacopa caroliniana* (water hyssop); and 116.35 *Cabomba 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.

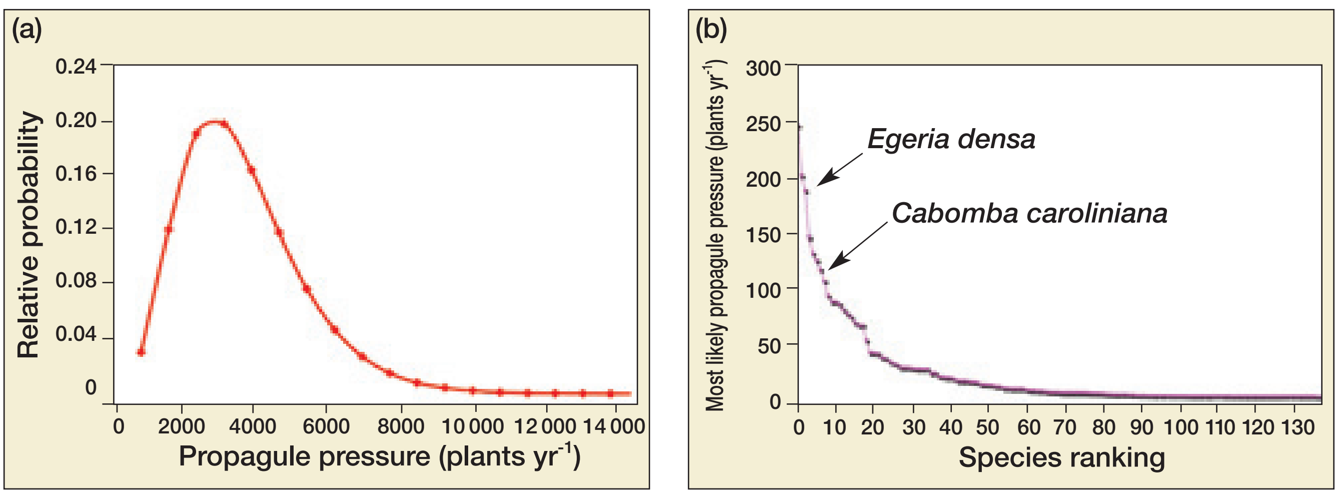

Figure 4*. (a) Propagule pressure for aquarium plants reaching the St Lawrence Seaway by way of the Montreal aquarium trade. Bayesian analysis was conducted to determine the relative probability that each propagule pressure was the true one, given the data observed. The most likely propagule pressure 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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WebTable 1. Rank, relative frequency, and propagule pressure of each species of aquatic plant sold in Montreal, Canada

Species name	*Rank*	*Relative frequency (%)*	*Most likely propagule pressure (plants yr^{-1})*
Microsorum pteropus	1	8.1983	247.2067726
Cladophora aegagropila	2	6.6820	201.485989
Egeria densa	3	6.2230	187.6459367
Vallisneria gigantea	4	4.8165	145.2362458
Nomaphila coryambosa	5	4.3528	131.2531475
Bacopa caroliniana	6	4.1392	124.8126875
Cabomba caroliniana	7	3.8586	116.3507973
Egeria najas	8	3.5107	105.86024
Anubias barteri	9	3.0751	92.72540937
Vallisneria spiralis	10	2.8872	87.06084718
Hygrophila rosanervis	11	2.8811	86.87699681
Ceratophyllum demersum	12	2.8061	84.61351241
Limnophila aquatica	13	2.6432	79.70159727
Rotala wallichii	14	2.5242	76.1138975
Crinium thaianum	15	2.4271	73.1855338
Anubias nana	16	2.2622	68.21387499
Echinodorus schulteri	17	2.1685	65.38756826
Gymnocoronis spilanthoides	18	2.1673	65.35079819
Ceratopteris thalictroides	19	1.7090	51.53199494
Aponogeton madagascariensis	20	1.3356	40.27293078
Aponogeton ulvaceous	21	1.3299	40.10170665
Echinodorus spp	22	1.3082	39.44837574
Cabomba aquatica	23	1.1898	35.8769977
Ludwigia repens	24	1.1673	35.19949216
Bacopa monnieri	25	1.0717	32.31639815
Aponogeton crispus	26	1.0160	30.63649238
Vallisneria asiatica	27	0.9640	29.06929889
Vallisneria torta	28	0.8849	26.68263166
Hygrophila polysperma	29	0.8816	26.58470132
Rotala macrandra	30	0.8762	26.42086816
Echinodorus bleheri	31	0.8512	25.66544949
Mayaca fluviatilis	32	0.8410	25.36026404
Hygrophila difformis	33	0.8408	25.35379694
Alternanthera ficoides	34	0.8357	25.19858658
Mynphaea spp	35	0.8329	25.11389839
Rotala indica	36	0.7139	21.52619862
Blyxa japonica	37	0.7139	21.52619862
Myriophyllum matogrossense	38	0.6132	18.49004995
Vesicularia dubyana	39	0.5918	17.84518786
Hygrophila angustifolia	40	0.5740	17.30780279
Vallisneria americana	41	0.5735	17.29178902
Alternanthera reineckii	42	0.5367	16.1831436
Dracaena sanderiana	43	0.4831	14.56636902
Echinodorus amizonicus	44	0.4759	14.35079908
Dracaena deremensis	45	0.4759	14.35079908
Ludwigia palustris	46	0.4587	13.83158347
Cryptocoryne crispulata	47	0.4407	13.28834722
Hygrophila spp	48	0.4341	13.08817513
Lilaeopsis novae-zelandiae	49	0.3697	11.14712177
Dieffenbachia "exotica variegatus"	50	0.3618	10.9101796
Echinodorus quadricostatus	51	0.3569	10.76309931
Cryptocoryne spp	52	0.3457	10.42434654
Sagittaria platyphylla	53	0.3100	9.346496826
Hydrocotyle leucocephala	54	0.3069	9.254109707
Sagittaria subulata	55	0.2563	7.726950638
Sagittaria natans	56	0.2543	7.668130839
Hygrophila salicifolia	57	0.2380	7.17539954
Limnophila sessiflora	58	0.2380	7.17539954
Lagarosyphon major	59	0.2380	7.17539954
Ceratopteris siliquosa	60	0.2380	7.17539954
Ophiopogon japonica	61	0.2009	6.057084266
Eichhornia azurea	62	0.1843	5.558624965
Acorus variegatus	63	0.1823	5.497033553

Continued

WebTable 1. *Continued*

Species name	*Rank*	*Relative frequency (%)*	*Most likely propagule pressure (plants yr^{-1})*
Alternanthera bettzickiana	64	0.1678	5.058502697
Echinodorus cordifolius	65	0.1634	4.927312989
Syngonium podophyllum	66	0.1445	4.356668553
didiplis diandra	67	0.1338	4.03423751
Cryptocoryne wenditii	68	0.1251	3.771550136
Eustralis stellata	69	0.1251	3.771550136
Echinodorus latifolius	70	0.1190	3.58769977
Myriophyllum hippuroides	71	0.1190	3.58769977
Myriophyllum scabratum	72	0.1190	3.58769977
Cryptocoryne balansae	73	0.1190	3.58769977
Eichornia diversifolia	74	0.1190	3.58769977
Hydrocotyle sibthorpoides	75	0.1190	3.58769977
Micranthemum umbrosum	76	0.1190	3.58769977
Nymphoides aquatica	77	0.1098	3.309614543
Barclaya longifolia	78	0.1041	3.140238159
Acorus gramineus	79	0.0996	3.002581353
Lloydella spp	80	0.0970	2.925592087
Alternanthera rosaefolia	81	0.0868	2.617635025
Hygrophila coryambosa	82	0.0732	2.206204391
Chamaedorea elegans	83	0.0686	2.06836281
Nymphaea stellata	84	0.0608	1.832344518
Rotala spp	85	0.0592	1.786150958
Salvinia natans	86	0.0592	1.786150958
Chlorophytum bichetii	87	0.0587	1.770753105
Nomaphila pussilus	88	0.0480	1.44739819
Liriope muscani	89	0.0480	1.44739819
Echinodorus osiris	90	0.0352	1.062451863
Eleocharis vivpara	91	0.0305	0.919251829
Aponogeton boivianus	92	0.0301	0.908473332
Hemigraphis colorata	93	0.0293	0.882481756
Anubias hastifolia	94	0.0244	0.735401464
Utricularia spp	95	0.0244	0.735401464
Echinodorus parviflorus	96	0.0235	0.708301242
Dracaena compacta	97	0.0235	0.708301242
Glossostigma elatinoides	98	0.0232	0.69863139
Acorus pusillus	99	0.0195	0.588321171
Nymphaea spp	100	0.0194	0.585118417
Echinodorus grandifolius	101	0.0189	0.569720564
Echinodorus martii	102	0.0189	0.569720564
Anubias coffefolia	103	0.0183	0.551551098
Eleocharis spp	104	0.0158	0.477333446
Spathiphyllum cannaefolium	105	0.0134	0.404470805
Vallisneria rubra	106	0.0122	0.367700732
Echinodorus tenellus	107	0.0122	0.367700732
Anubias afzeli	108	0.0122	0.367700732
Cabomba piauhyensis	109	0.0122	0.367700732
Crassula helmsii	110	0.0122	0.367700732
Cryptocoryne becketii	111	0.0122	0.367700732
Selaginella wildenowii	112	0.0122	0.367700732
Ricca fluitans	113	0.0110	0.330930659
Pilea cadierei	114	0.0102	0.307957062
Aponogeton capuroni	115	0.0082	0.246365649
Myriophyllum aquaticum	116	0.0082	0.246365649
Echinodorus rubin	117	0.0081	0.245441778
Cardamine lyrata	118	0.0071	0.215569943
Echinodorus "red flame"	119	0.0061	0.183850366
Cryptocoryne lutea	120	0.0061	0.183850366
Cryptocoryne petchii	121	0.0061	0.183850366
Cryptocoryne undulatus	122	0.0061	0.183850366
Aponogeton natans	123	0.0061	0.183850366
Cyperus alterniflolius	124	0.0061	0.183850366
Heteranthera dubia	125	0.0061	0.183850366
Hydrilla verticillata	126	0.0061	0.183850366
Lilaeopsis brazilensis	127	0.0061	0.183850366
Lobelia cardinalis	128	0.0061	0.183850366

Continued

WebTable 1. *Continued*

Species name	*Rank*	*Relative frequency (%)*	*Most likely propagule pressure (plants yr^{-1})*
Ludwigia sediodes	129	0.0061	0.183850366
Micranthemum micranthemoides	130	0.0061	0.183850366
Potamogeton perfoliatus	131	0.0061	0.183850366
Dracaena godseffiana	132	0.0049	0.147080293
Hemigraphis repanda	133	0.0046	0.138580678
Aponogeton undulatus	134	0.0041	0.123182825
Pistia stratiotes	135	0.0041	0.123182825
Alternanthera spp	136	0.0041	0.123182825
Bolbtis heudelotii	137	0.0012	0.036770073
Anubias gracilis	138	0.0005	0.015397853

