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Characterised and projected costs of nonindigenous species in Canada

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Abstract

Biological invasions by nonindigenous species (NIS) can have adverse effects on economically important goods and services, and sometimes result in an 'invisible tax' on natural resources (e.g. reduced yield). The combined economic costs of NIS may be significant, with implications for environmental policy and resource management; yet economic impact assessments are rare at a national scale. Impacts of nuisance NIS may be direct (e.g. loss of hardwood trees) or indirect (e.g. alteration of ecosystem services provided by growing hardwoods). Moreover, costs associated with these effects may be accrued to resources and services with clear 'market' values (e.g. crop production) and to those with more ambiguous, 'non-market' values (e.g. aesthetic value of intact forest). We characterised and projected economic costs associated with nuisance NIS in Canada, through a combination of case-studies and an empirical model derived from 21 identified effects of 16 NIS. Despite a severe dearth of available data, characterised costs associated with ten NIS in Canadian fisheries, agriculture and forestry totalled $187 million Canadian (CDN) per year. These costs were dwarfed by the 'invisible tax' projected for sixteen nuisance NIS found in Canada, which was estimated at between $13.3 and $34.5 billion CDN per year. Canada remains highly vulnerable to new nuisance NIS, but available manpower and financial resources appear insufficient to deal with this problem.

Introduction

Technological advances in transportation and liberalised international trade allow rapid movement of people and goods throughout the world. An unintended consequence of this unprecedented level of human activity has been intentional and accidental introductions of nonindigenous species (NIS) beyond their native ranges (Mack et al. 2000). Despite increasing public awareness, the number of new invaders continues to increase in freshwater, marine, and terrestrial ecosystems in North America and elsewhere (Sailer 1983; Cohen and Carlton 1998; Ruiz et al. 2000; Ricciardi 2001). This pattern may in part be the result of increased vigilance by scientists, but available evidence suggests that the pattern is real (Ruiz et al. 2000; Ricciardi 2001; Simons 2003). Many NIS positively affect human welfare or appear relatively harmless, while others have effects that are wholly undesirable; it is of course the latter group with which invasion biologists, resource managers and policy makers take interest (Mack et al. 2000; Simberloff 2003).

Numerous definitions have been used to describe NIS that have negative impacts, including 'invasive', 'noxious', 'nuisance', 'pest', and 'weed'. The term 'invasive' in particular has been problematic, as biologists typically use it in reference to species that spread quickly or are widespread in distribution, whereas policy makers use it to imply negative economic, health, or ecological effects (see Richardson et al. 2000). To maintain consistency between uses, we employ the term 'nuisance NIS' herein to describe species introduced beyond their native range that have adverse consequences for economic, environmental or human welfare.

Understanding the magnitude of economic costs associated with nuisance NIS is important for environmental policy and management, yet few studies have evaluated the cost of NIS to national economies. An examination of 79 established NIS in the United States estimated economic losses of about $96.9 billion in United States dollars (USD) between 1906 and 1991 (OTA 1993). More recently, in well-publicised studies, Pimentel et al. (2000, 2001) estimated total damage and control costs of $137 billion USD per year for all NIS in the United States, and collectively more than $314 billion USD per year in the USA, United Kingdom, Australia, South Africa, India and Brazil. Application of Pimentel et al.'s (2000) model to Canada suggested that damage caused by nuisance NIS amounts to $7.5 billion Canadian dollars (CDN) per year (Dawson 2002).

Most assessments of economic costs have been limited to specific NIS within particular localities, and have considered only direct costs associated with control or loss of marketable goods or services. More inclusive models of economic costs of nuisance NIS are difficult to develop owing to a dearth of data pertaining to indirect market costs, as well as both direct and indirect, non-market costs (e.g. reduced aesthetic value). Canada's forests, agricultural systems, and aquatic ecosystems have been invaded by at least 1442 species (MacIsaac et al. 2002), yet no attempts have been made to quantify the economic impacts of these NIS. Here we report the results of a study commissioned by the Office of the Auditor General of Canada to determine the economic impact of nuisance NIS in agriculture, forestry and aquatic sectors in Canada.

Materials and methods

Identifying economic impacts of nuisance NIS is encumbered by a number of challenges. For example, partitioning the effects of synergisms (i.e., non-additive interactions) between NIS and native species, and between species invasions and other environmental stressors (e.g. habitat change, over-harvesting, climate change) can be very difficult (e.g. OTA 1993; Parker et al. 1999; Simberloff and Von Holle 1999; Smith et al. 2000; Harris and Tyrrell 2001; Stachowicz et al. 2002). More importantly, introduction of nuisance NIS may impart externality costs, which are expenses incurred to parties that were not involved with the transaction responsible for the introduction of the species. Externality costs may result from direct activity associated with the nuisance NIS, or as an indirect by-product of its presence. Furthermore, these externalities may impact either market or non-market goods and services. Most costs associated with NIS introductions are external, but deliberate introductions may include internalised costs. For example, numerous game fishes have been introduced deliberately throughout North America (Fuller et al. 1999), but profits gained by recreational fisheries may be partially offset by internal costs associated with displaced native game fishes.

Externality costs, direct/indirect effects, and market/non-market values are exemplified by zebra mussel (*Dreissena polymorpha*) invasions in the Laurentian Great Lakes (Figure 1). Zebra mussels were accidentally introduced by transcontinental, commercial shipping, which generated an externality to the electrical power industry (among others) when waterworks facilities became infested with mussels. Affected companies sustained reduced power generation while pipes were clogged, and subsequently implemented costly antifouling systems (i.e., direct market costs; Figure 1) (LePage 1993). At the same time, some municipalities experienced poor water quality owing to an off-taste generated by presence of geosmin, a compound generated by macrophytes which grew in profusion as a result of zebra mussel-induced increase in water clarity (see MacIsaac et al. 2002). The City of Windsor, Ontario, for example, spent between $400,000–450,000

Zebra Mussel Externalities

Direct		Indirect	
Market	**Non-Market**	**Market**	**Non-Market**
Fouling of industrial water intake lines	Loss of native unionid mussels due to biofouling	Enhanced macrophyte growth requires filtration system for potable water	Loss of turbid water habitat for native fish

Figure 1. Examples of externality costs associated with zebra mussel invasions. Costs may be direct or indirect (i.e. mediated through effects on other species or through ecosystem changes), and may affect either market (e.g. goods or services) or non-market (e.g. ecosystem services, aesthetics) aspects of the invaded ecosystem.

CDN per year for activated charcoal treatment to eliminate taste and odour problems from municipal water supplies after zebra mussels invaded Lake St. Clair, upstream of the city's water intake line (i.e., indirect market cost; Figure 1). More generally, direct costs of nuisance NIS may include enhanced control or management costs, as well as human health effects (Mack et al. 2000). Nuisance NIS also may impose an 'invisible tax' on natural resources and national economies by reducing the production of natural resources (Mack et al. 2000; Perrins et al. 2000). Pimentel et al. (2001) estimated that this 'tax' may exceed $1.4 trillion USD per year worldwide.

Non-market costs associated with nuisance NIS are usually not considered in assessments of economic damage, perhaps because they are much more difficult to quantify (Figure 1). These costs may be related to changes in biodiversity of, or changes to, natural habitats caused by NIS. For example, nonindigenous weed species like cheatgrass (*Bromus tectorum*), leafy spurge (*Euphorbia esula*), spotted knapweed (*Centaurea maculosa*) and purple loosestrife (*Lythrum salicaria*) alter physical and/or chemical attributes of affected habitats, rendering them less suitable to native species (e.g. Bais et al. 2003). Although invasions may have no direct economic consequence, they may nevertheless reduce economically important ecosystem services like the prevention of soil erosion, water detoxification, and consumption of carbon dioxide by growth of native vegetation. For example, non-market costs associated with invasion of zebra mussels in the lower Great Lakes include extirpation of native unionid mussels owing to fouling (direct effect) and loss of preferred turbid-water habitat for some native fish through the biodeposition of particulate matter (indirect effect) (Figure 1; MacIsaac 1996).

To calculate the non-market value of natural ecosystems, researchers may utilise contingent valuations in which an assessment is made of an individual's 'willingness to pay'. This approach enables a financial assessment of environmental non-market goods and services (e.g. aesthetic value, space for recreational activities), but is subjective, likely to vary among interest groups and geographic areas, and is considered controversial in consequence (Turner et al. 1998). Perhaps the largest stumbling block in calculating the costs of habitat degradation is the lack of a generally accepted theory of ecosystem 'value' (Patterson 1998). Without an accepted valuation system it is impossible to develop a model to accurately estimate damages associated with compromised ecosystems. However, by examining the market values of goods and services produced by ecosystem processes, we can explore the possible costs associated with ecosystem disruption caused by nuisance NIS.

No studies exist that systematically assess even the direct costs associated with nuisance NIS in Canada. In a first attempt to gauge the impact of nuisance NIS to Canada's economy, we reviewed available data on the direct and indirect costs reported for thirteen of Canada's most notorious invaders. In some cases, we extrapolated characterised costs for particular regions to other areas in which particular NIS were found, but where no data on economic costs were available. For example, we extrapolated the costs associated with leafy spurge in the provinces of Alberta and Saskatchewan based upon a study of costs in Manitoba and its distribution in each of these provinces. In other cases, we calculated costs based upon reported damage and the value of industries affected in areas infested by nuisance NIS. For example, costs associated with the green alga *Codium fragile* were calculated based on 10% mortality of oysters, and the value of those resources in the area of Prince Edward Island where *Codium* is found. Despite our efforts, characterised costs were a meagre estimate of the total economic impact of nuisance NIS in Canada because only a limited number of effects were available for each species, and because costs were available only for a small fraction of all NIS in the country. Moreover, we were unable to include characterised costs for some of the most potentially damaging species (e.g. green crab *Carcinus maenas*, gypsy moth *Lymantria dispar*) owing to a dearth of data. Consequently, a lack of comprehensive, national data for even the most problematic species precludes an accurate assessment of the total economic impact of nuisance NIS in Canada.

In the absence of comprehensive data, empirical models can provide a useful approximation of the impact of ecological stressors. For example, Ricciardi (2003) utilised a meta-analysis approach to predict the effects of particular NIS. To better estimate the costs associated with nuisance NIS in Canada, we built an empirical model based upon 21 quantified effects for previously identified nuisance NIS from a variety of ecosystems (see Table 1). For each of these studies, we recorded the maximum proportional loss in economic value or experimentally-deduced yield reduction. We used maximum values because they were often the only values reported. We then ranked these losses from least to greatest to build an empirical model from which we projected potential lost production for a set of identified nuisance NIS in Canada (Figure 2). To keep our projection conservative, we selected the median case from this curve as our maximum cost projection (52% loss), and the quartile (25%) and half-quartile (20%) cases for our medium and low projections, respectively.

Table 1. Twenty-one quantified effects of 16 NIS of plant, animal and disease. Proportional loss of resource production or value is given for each effect, along with references.

Common name *(Scientific name)*	Impacted resource	% Loss	Reference
Clubbed tunicate *(Styela clava)*	Shellfish	50	A. Locke, pers. comm.
Ruffe *(Gymnocephalus cernuus)*	Yellow perch, Walleye, whitefish	25–60	Leigh 1998
Leafy spurge *(Euphorbia esula)*	Crop yield, grazing yield	100	Leafy Spurge Stakeholders Group 1999
Spotted knapweed *(Centaurea maculosa)*	Grazing yield	80	Maddox 1979
Horn fly *(Haematobia irritans)*	Cattle	18	Lysyk et al. 2002
Seedpod weevil *(Ceutorhynchus obstrictus)*	Crop yield	20	Dosdall et al. 2001
Stable fly *(Stomoxys calcitrans)*	Cattle, dairy	20–40	Bruce and Dekker 1958; Campbell et al. 1987
Potato late blight *(Phytophthora infestans)*	Crop yield	52	James et al. 1972
Foot and mouth disease *(Aphthovirus sp.)*	Cattle	100	CFIA (2000)
Gypsy moth *(Lymantria dispar)*	Tree mortality, recreation	20–90	Campbell and Schlarbaum 1994
Dutch elm disease *(Ophiostoma ulmi)*	Tree mortality	30	Hubbes 1999
Balsam wooly adelgid *(Adelges peceae)*	Tree mortality	80	Hunt 1983
White pine blister rust *(Cronartium ribicola)*	Tree mortality	94	Hall 1996
Schleroderris canker *(Gremmeniella abietina)*	Tree mortality	62	Campbell and Schlarbaum 1994
Beech bark disease *(Nectria coccinea)*	Tree mortality	50	Campbell and Schlarbaum 1994
Asian longhorn beetle *(Anoplophora glabripennis)*	Tree mortality	68	Nowak et al. 2001

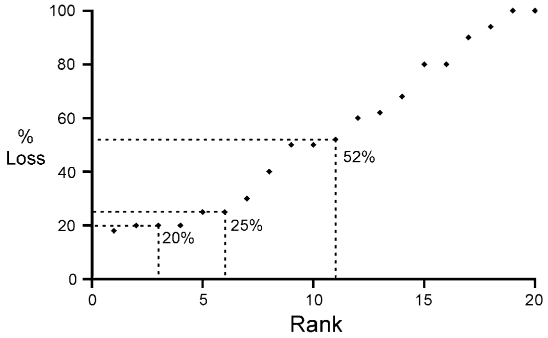

Figure 2. Empirical model of 21 nonindigenous species (NIS) based on their ranked impact. Damage is graphed as reduced yield identified in experimental studies or as proportional, characterised economic loss to particular resources (see Table 1). The median, quartile, and half-quartile cases were used to estimate high, mid and low damage projections, respectively.

For each of the most problematic invaders selected, we identified the resource(s) placed at greatest risk (e.g. lobster fishery, maple timber sales), and then applied our cost function. The value of each affected resource was obtained from Statistics Canada for the most recent year in which data was available, usually 2000. Losses were calculated as a proportion of the national value associated with these resources, and represent a general model for the 'invisible tax' imposed by nuisance NIS upon Canadian fisheries, agriculture and forestry industries.

Assumptions and limitations

Our empirical model is admittedly crude, and there are a number of important caveats that must be considered. Our model was built upon the maximum reported effects of individual species under specific conditions. Scaling up from small-scale, short-term studies to estimate country-wide, annual impacts is fraught with errors (Turner et al. 1998). By scaling up, we assume that resources are distributed and affected in a homogeneous manner, which would likely cause a dramatic over-estimation of the true value. Moreover, these effects are based on uncontrolled impacts of nuisance NIS, but of course control efforts would quickly be implemented to reduce the effects of serious invaders. To counteract these considerable limitations, we made a number of highly conservative assumptions that we believe largely or wholly offset what would otherwise be a sizeable bias. First, our damage projections used conservative numbers from the model (i.e. 52, 25 and 20%), and were applied only to the resources affected by some of the more troublesome NIS found in Canada (Table 1; Figure 2). Thus, the costs incurred by nuisance NIS to a number of other sectors (e.g. tourism, food exports) are not included, nor are losses to most of the secondary industries associated with fisheries, agriculture and forestry (e.g. food processing, packing and distribution). Given that the average farmer loses approximately 13% of his production to reduced yield and control of weeds alone, and that the effects of insects can be much greater, these numbers do not seem unwarranted (Pimentel et al. 2000). Second, while our model was built upon the effects of single species, the 'invisible tax' calculated for these sectors is the net effect of hundreds of NIS (e.g. insects) affecting the same resource (e.g. softwood production). These species may have synergistic or inhibitory effects, and individual effects will vary greatly, but the net result of all nuisance NIS affecting a given resource is surely much greater than the effect of any single species. Third, damage projections were calculated as reduced production, and thus do not include a number of indirect (e.g. human health care costs associated with increased pesticide use, reduced property value) and non-market value (e.g. reduced aesthetic value) costs associated with nuisance NIS. Total ecosystem value may far exceed gross national product (Costanza et al. 1997), but we consider here only the effects of NIS on annual production. Fourth, our projections were applied to the current, reported industry values, which themselves are already deflated by the 'invisible tax' imposed by nuisance NIS. Our damages are therefore calculated from the post-tax value of the industry, rather than the actual, pre-taxed production value, resulting in a further source of underestimation. Fifth, we included only natural resources affected by NIS, thus we excluded other sectors like tourism and health care, that may nonetheless incur costs. Finally, because separate values were not available for hardwood and softwood tree species, we applied softwood values to both, even though hardwoods are much more valuable. All costs reported herein are in Canadian dollars.

Results

The economic cost associated with thirteen species identified in Table 2 include control costs, reduced yield, reduced land value, trade bans on exported goods, compensation paid to farmers, health care costs, and reduced tourism and tourism-related revenues. In total, the annual characterised cost of eleven nuisance NIS is approximately \$187 million per annum. These costs appear quite modest, and in fact pale in comparison to the one-time costs associated with two nonindigenous disease outbreaks that affected Canada during 2003 (SARS, mad cow disease), which posed an additional cost of \$2.5 billion (Table 2). Quantified, annual costs for the eleven identified nuisance species profiled are comparatively low only because comprehensive data were lacking for virtually all of these species. Even for notorious invaders like zebra mussels, we experienced difficulty in assembling direct costs to industry and municipalities. Our empirical model projected costs associated with the 'invisible tax' imposed by all NIS established in Canada. In general, these cost projections were much higher than the characterised costs identified above, totalling \$16.6 billion/year (range: \$13.3 to 34.5 billion/year). Characterised costs were highest for agriculture and related industries, owing to a number of recent economic studies on nuisance NIS of insect and plant. Conversely, the highest projected costs based on our empirical model were in the forestry sector (Table 3) – a pattern reflective of the importance of forest products to the Canadian economy.

Aquatic and marine ecosystems

Characterised impacts were available for four of six identified nuisance NIS in aquatic systems. Zebra mussels (*D. polymorpha)* and quagga mussels (*D. bugensis*), and the sea lamprey (*Petromyzon marinus*), all of which invaded the Great Lakes, made up the bulk of \$32.3 million/year in characterised costs to aquaculture and aquatic-related industries (Table 2). Dreissenid mussels invaded the Great Lakes in the mid-1980s (Hebert et al. 1989), and have affected primarily industries and municipalities with a variety of direct costs (see Figure 1). Despite the prominence given to these mussels in the scientific and popular press, obtaining accurate cost estimates proved challenging. Indirect costs, including possible shifts in commercial and sport fisheries, were not quantifiable.

The sea lamprey, which attacks salmonids and other valuable fishes, likely entered the Great Lakes some time in the 1830s *via* a shipping canal system connected to the Atlantic Ocean (Mills 1993). The Great Lakes Fishery Commission – a joint agency administered by the USA and Canadian federal governments – spends ~\$22 million/year on control and research for the lamprey, \$6 million of which is paid by the Canadian federal government (Table 2). However, costs incurred through reductions in harvest of commercial and sports fishes would likely be much higher without this expenditure.

Purple loosestrife is a common plant in wetlands throughout much of North America. It was likely introduced to the continent more than a century ago by ship, or in livestock feed or bedding (Thompson et al. 1987). Most costs associated with loosestrife pertain to its control (Table 2).

Three invasions of coastal habitats in Atlantic Canada are particularly concerning because they affect the emerging aquaculture industry in the region. *Codium fragile* is a green alga that was first found along the Nova Scotia coast by the early 1990s (see Levin et al. 2002). This species is displacing kelp through competition for substrate, and is possibly facilitated by an introduced bryozoan (*Membranipora membranacea*) that fouls and reduces survival of kelp (Levin et al. 2002). Loss of kelp could hinder sea urchin, oyster, marine plant, and lobster industries. Another recent invader, the clubbed tunicate *Styela clava*, was introduced to the Gulf of St. Lawrence in the late 1990s, likely by a ship vector (Dr Andrea Locke, personal commmunication). It may adversely affect natural and aquaculture oyster and mussel industries through competition for space, although these costs may be offset by sales of *Styela*. Finally, the European green crab *Carcinus maenas* invaded coastal

Table 2. Characterised economic impact of eleven nuisance NIS to fisheries, agriculture and forestry resources. Characterised costs are in Canadian dollars, per annum. Numbers not included in calculation of total annual cost (i.e., one time events) are indicated (*).

Common name *(Scientific name)*	Impacted area and/or industry	Characterised cost (× $1,000)
Oyster thief *(Codium fragile)*	Prince Edward Island: oyster mortality[1]	1500
Purple loosestrife *(Lythrum salicaria)*	Alberta control costs[2]	20
	Saskatchewan eradication project[3]	100
	Ontario biological control program[4]	90
Zebra mussel *(Dreissena polymorpha)*	Ontario power plants: control/operating[5]	6400
	Ontario power plants: research[6]	1092
Quagga mussel (*Dreissena bugensis*)	Ontario cottagers[7]	52,670*
	Great Lakes' municipalities[8]	282
	City of Windsor intakes[9]	450
Sea lamprey *(Petromyzon marinus)*	Lamprey management and research[10]	6000
Leafy spurge *(Euphorbia esula)*	Manitoba: reduced yield and recreation revenues, and control costs[11]	18,870
	Manitoba: reduced land value[11]	30,000*
	Alberta and Saskatchewan: reduced yield and recreation revenues, and control costs[12]	18,870
	Alberta and Saskatchewan: reduced land value[12]	30,000*
Knapweed *(Centaurea maculosa)*	British Columbia: hay production[13]	400
	British Columbia: grazing livestock[14]	79
Horn fly *(Haematobia irritans)*	Canada: cattle production[15]	69,533
Stable fly *(Stomoxys calcitrans)*	Canada: cattle and dairy production[16]	26,780
Seedpod weevil *(Ceutorhynchus obstrictus)*	Alberta: canola production[17]	5000
Potato wart fungus *(Synchytrium endobioticum)*	Prince Edward Island: export ban[18]	30,000*
	Prince Edward Island: lost yield	Neglible
	Prince Edward Island: farmer aid[18]	15,000*
	Canada: federal farmer aid[18]	19,400*
	Canada: reduced export revenue [19]	8940*
Dutch elm disease *(Ophiostoma ulmi)*	Manitoba: control costs[20]	1500
Emerald ash borer *(Agrilus planipennis)*	Essex County[21]: control costs	14,000–16,000*
Severe acute respiratory Syndrome (SARS)	Canada: health care costs[22]	945,000*
	Canada: revenue losses to accommodation industry[23]	500,000*
Bovine Spongiform Encephalitis (BSE)	Canada: beef exports for < 1 year[24]	1,000,000*
Total characterised cost		186,965

[1] Novaczek I (2002) Pers. Comm. Earth Action, Prince Edward Island; [2] Ali S (2002) Pers. Comm. Alberta Purple Loosestrife Project, Alberta; [3] Salzl A (2002) Pers. Comm. Saskatchewan purple loosestrife and invasive species project, Saskatchewan; [4] Corrigan J (2002) Pers. Comm. Department of Environmental Biology, University of Guelph, Ontario; [5] Average expenses $800,000 multiplied by 8 stations, actual costs vary from $500,000 to $1,500,000 per station, per year; Wiancko P (2000) Management and costs of zebra mussels at Ontario Power Generation. 11th International Conference on Aquatic Invasive Species, Toronto, Ontario; [6] Total cost: $13,100,000 divided by 11 years of mussel infestation; Wiancko P (2000) Management and costs of zebra mussels at Ontario Power Generation. 11th International Conference on Aquatic Invasive Species, Toronto, Ontario; [7] Based on 230,000 cottages installing basic filtration system @ CDN$229 each; Moore W (2002) Pers. Comm. Federation of Ontario Cottagers' Associations; Crosbie B, Sferrazza C, Wiancko P, Claudi R, Birnbaum J, Hulton J, Mackie G, Schatz R and O'Neill C (Georgian Bay Steering Committee). 1999. Zebra mussel biofouling control in cottage and other small volume water systems. Part C: A consumer's guide to evaluating the products tested. The Georgian Bay Association, Ontario; [8] Based on minimum costs incurred by a Chatham-Kent facility (CDN$3,000) multiplied by 94 facilities infested with zebra mussels; Fields K (2002) Pers. Comm. Chatham-Kent Water Filtration Plant, Erie Beach raw water Station, Ontario; Cheung P (2002) Pers. Comm. Ministry of the Environment, Canada; [9] Jasim S (2002) Pers. Comm. Windsor Utilities, City of Windsor, Ontario; [10] Christie G (2002) Pers. Comm. Great Lakes Fishery

Commission; [11]Leafy Spurge Stakeholder's Group (1999) Leafy Spurge Economic Impact Assessment, WESTARC Group, Brandon University, Manitoba; [12]Assumes 50% of Manitoba's cost to each of Alberta and Saskatchewan; [13]Davies S, Gow T and Pidwirny M (1996) Living Landscapes. Knapweed. Royal British Columbia Museum and Okanagan University College, British Columbia; [14]Based on 1.97 USD/ha multiplied by 40,000ha infested in Canada; ref #13; United States Department of Agriculture (2002) Animal and plant Health Inspection Service, Plant Protection and Quarantine website: http://www.aphis.usda.gov/ppq; [15]Lysyk TJ, Floate KD and Lancaster RC (2002) Insects and other arthropod pests: horn fly, Saskatchewan Agriculture, Food, and Rural Revitalization, Saskatchewan; [16]Floate KD, Lysyk TJ, and Lancaster RC (2002) Insects and other arthropod pests: stable fly, Saskatchewan Agriculture, Food, and Rural Revitalization, Saskatchewan; [17]Dosdall LM (2002) Pers. Comm. Alberta Agriculture, Food and Rural Development, Alberta; [18]United States Department of Agriculture (2001) Canada trade policy monitoring: the impact of the potato wart on Canadian potato exports. GAIN Report, Foreign Agricultural Service, USA; [19]Calculated as 6% of $149,000,000 in Canadian potato exports, not including Prince Edward Island; Agriculture and Agri-Food Canada (2001) 2000/20001 Canadian potato situations and trends. Canada; [20]Annual expenditure for Manitoba only; Westwood AR (1991) A cost-benefit analysis of Manitoba's integrated Dutch elm disease management program 1975–1990. Proceedings of the Entomological Society of Manitoba 47: 44–59; [21]$3 million in 2003 and $11–16 million projected for 2004 Ken Marchant Pers. Comm. Canadian Food Inspection Agency, Ontario; [22]Ontario Ministry of Health and Long-Term Care (2003) Ontario reveals the cost of SARS. Healthbeat. Issue 91. Ontario; [23]Canadian Tourism Commission (2003) The Impact of SARS on Canada's Accommodation Industry. Canada; [24]Chase S and Walton D (2003) Canada expects easing of US beef ban. Globe and Mail. Friday, June 13, 2003, Ontario.

Table 3. Projected economic impact of nuisance NIS on selected resources in Canadian fisheries, agriculture and forestry. Projected impacts are in Canadian dollars, per annum. Numbers not included in calculation of total annual cost are (indicated by *).

Common name *(Scientific name)*	Resource at risk	Value	Projected impact		
			Min (20%) (× $1,000)	Max (52%) (× $1,000)	Mid (25%) (× $1,000)
Oyster thief	Sea urchin	7152[1]	1430	3719	1788
(Codium fragile)	Lobster	29,986[1]	5997	15,593	7497
	Oyster (wild)	10,166[1]	2033	5286	2542
	Oyster (cultivated)	9915[2]	1983	5156	2479
	Eel	703[1]	141	366	176
	Marine plants (kelp)	2050[1]	410	1066	513
European green crab *(Carcinus maenas)*	Soft-shell clams, blue mussels, American oysters (Gulf of St. Lawrence)	35,000[3]	7000	18,200	8750
	Lobster and rock crab (southern gulf of Newfoundland)	175,000[3]	35,000	91,000	43,750
	Dungeness crab (British Columbia)	20,000[4]	4000	10,400	5000
Clubbed tunicate *(Styela clava)*	Oyster, scallop, clam and mussel production	170,067[5]	34,013	88,435	42,517
Sea lamprey *(Petromyzon marinus)*	Sport and commercial fishing	550,000[6]	110,000	286,000	137,500
Leafy spurge *(Euphorbia esula)*	Crops and grazing livestock	22,978,000[7]	4,595,600	11,948,560	5,744,500
Horn fly	Cattle production	6,600,000[7]	1,320,000*	3,432,000*	1,650,000*
(Haematobia irritans)	Milk production	3,600,000[7]	720,000*	1,872,000*	900,000*
Stable fly	Cattle production	6,600,000[7]	1,320,000*	3,432,000*	1,650,000*
(Stomoxys calcitrans)	Milk production	3,600,000[7]	720,000*	1,872,000*	900,000*
Seedpod weevil *(Ceutorhynchus obstrictus)*	Canola production	1,200,000[7]	240,000*	624,000*	300,000*
Potato wart fungus	Potato exports	149,000[8]	29,800	77,480	37,250
(Synchytrium endobioticum)	Total potato sales	715,000[7]	143,000*	371,800*	178,750*
Asian longhorn beetle	Annual timber sales: maple	63,900[9]	12,780	33,228	15,975
(Anoplophora glabripennis)	Annual domestic exports	1,200,000[10]	240,000	624,000	300,000
	Maple syrup and sugar products	200,000[11]	40,000	104,000	50,000
Balsam wooly adelgid	Annual timber sales: fir	251,340[9]	50,268	130,697	62,835
(Adelges peceae)	Annual domestic exports pine and	4,720,000[10]	944,000	2,454,400	1,180,000
	Fir Christmas trees:	35,000[12]	7000	18,200	8750

Table 3. Continued.

Common name *(Scientific name)*	Resource at risk	Value	Projected impact		
			Min (20%) (× $1,000)	Max (52%) (× $1,000)	Mid (25%) (× $1,000)
	Annual wholesale				
	Pine and fir Christmas trees: Annual exports	28,100[12]	5620	14,612	7025
Brown spruce longhorn beetle	Annual timber sales: spruce	698,640[9]	139,728	363,293	174,660
(Tetropium fuscum)	Annual domestic exports	13,120,000[10]	2,624,000	6,822,400	3,280,000
	Spruce pulp	1,000,000[13]	200,000	520,000	250,000
Dutch elm disease *(Ophiostoma ulmi)*	Elm: total value	2,500,000[14]	500,000*	1,300,000*	625,000*
Gypsy moth *(Lymantria dispar)*	Annual timber sales: hardwoods	485,640[9]	97,128	252,533	121,410
	Annual domestic exports	9,120,000[10]	1,824,000	4,742,400	2,280,000
Scleroderris canker *(Gremmeniella abietina)*	Annual timber sales: pines, spruce and fir	1,333,380[9]	266,676*	693,358*	333,345*
	Annual domestic exports	25,120,000[10]	5,024,000	13,062,400	6,280,000
	Pine and fir Christmas trees: annual wholesale	35,000[12]	7000*	18,200*	8750*
	Pine and fir Christmas trees: annual exports	28,100[12]	5620*	14,612*	7025*
White pine blister rust	Annual timber sales: pine	387,660[9]	77,532	201,583	96,915
(Cronartium ribicola)	Annual domestic exports	7,280,000[10]	1,456,000	3,785,600	1,820,000
	Pine and fir Christmas trees: annual wholesale	35,000[12]	7000*	18,200*	8750*
	Pine and fir Christmas trees: annual exports	28,100[12]	5620*	14,612*	7,025*
Total value of industries		66,327,319			
Total low projected cost			13,265,464		
Total max projected cost				34,490,206	
Total mid projected cost					16,581,830

[1]Value of Atlantic market; Department of Fisheries and Oceans (2000) 2000 Canadian aquaculture production statistics. Department of Fisheries and Oceans, Canada; [2]Department of Fisheries and Oceans (2000) 2000 value of Atlantic and Pacific coasts commercial landings, by province. Department of Fisheries and Oceans, Canada; [3]Total clam, oyster, scallop and mussel production in Canada, less the values presented above for Atlantic and Gulf of St. Lawrence; Department of Fisheries and Oceans Canada (2000) 2000 value of Atlantic and Pacific coasts commercial landings, by province. Department of Fisheries and Oceans, Canada; [4]Winther I (2000) Crab (*Cancer magister*). PSARC Fishery Update. Department of Fisheries and Oceans, Canada; [5]Gross values from Statistics Canada; [6]Talhelm DR (1980) Benefits and costs of sea lamprey (*Petromyzon marinus*) control in the Great Lakes: some preliminary results. Canadian Journal of Fisheries and Aquatic Science 37: 2169–2174; [7]Canadian farm cash receipts from Statistics Canada; [8]Agriculture and Agri-Food Canada (2001) 2000/20001 Canadian potato situations and trends. Agriculture and Agri-Food Canada; [9]Industry value calculated using sale of timber from crown land multiplied by the percent volume by species of gross merchantable, stocked forest; Canadian Council of Forest Ministers (1997) Compendium of Canadian Forestry Statistics 1996. National Forestry Database Program, Canadian Forest Service, Canada; Statistics Canada (1998) Canadian Forestry Statistics 1995; [10]Industry value calculated from sale of domestic exports multiplied by the percent volume by species of gross merchantable, stocked forest; same references as #10; [11]CANSIM (2002) Canadian Socio-economic Information and Management Database, Canada; [12]Canadian Council of Forest Ministers (2001) National Forestry Database Program, Canada; [13]Ministry of Natural Resources (2000) Ontario's forests: questions and answers about the brown spruce longhorn beetle. Ministry of Natural Resources, Canada.[14]Total value of all elm trees in Canada, not used in calculation of annual costs; Krcmar-Nozic E, Wilson B and Arthur L (2000) The potential impacts of exotic forest pests in North America: a synthesis of research. Natural Resources Canada, Canadian Forest Service.

waters of New Brunswick and Nova Scotia no later than the early 1950s, and British Columbia by 1998 (see MacIsaac et al. 2002). While initial transfer of the species to North America was almost certainly by ship, it has moved between sites in North America possibly by ships, in fishery products, or by accidental or intentional release (Cohen et al. 1995). Economic damage associated with this species results from predation on a variety of marine invertebrates including other crabs, softshell clams, and mussels (Table 3).

In total, our empirical model projected damages associated with six aquatic NIS at over $343 million ($298–776 million) per annum, owing primarily to the high value of the sport and commercial fishing industries.

Agriculture

A comparatively large number of cost categories were identified for the six nuisance NIS that affect Canadian agriculture and related industries, at a total cost of almost $170 million/year. A large portion of this is due to infestations of leafy spurge, whose effects include reduced crop and grazing livestock production, control costs, and reduced revenue associated with recreational activity. An additional one-time cost of $30 million dollars is associated with a reduction in property values of farmland infested with the plant (LSSG 1999). Reduced yield is also the primary cost associated with several other nuisance NIS in agriculture, including knapweed *Centaurea maculosa*, which invades meadows, pastures, roadsides and stream floodplains. Invasions of cropland result in hundreds of thousands of dollars in lost hay production annually, with an additional, characterised loss of almost $80,000 to control knapweed in fields used for grazing livestock (Table 2). Costs associated with reduced yield are also available for the horn fly (*Haematobia irritans*) and stable fly (*Stomoxys calcitrans*), which irritate cattle, resulting in decreased milk and beef production. Likewise, the seedpod weevil (*Ceutorhynchus obstrictus*), which was originally found in British Columbia in 1931, attacks crops like canola, cabbage, broccoli and cauliflower, resulting in significant decreases to production (Table 2).

Reduced yield is but one significant cost for nuisance NIS. A potentially much larger loss may result from reduced international trade associated with embargoes of products from areas infested with NIS. For example, following discovery of potato wart fungus (*Synchytrium endobioticum*) in a single field on the island province of Prince Edward Island (PEI) in 1999, an embargo was placed on potato exports to the United States (Table 2). The provincial industry sustained a $30 million loss in exports to the USA, while similar exports from the rest of Canada declined by an additional $8.9 million (6% loss). Federal and provincial governments helped offset further losses to farmers on PEI through provision of $24.4 million in assistance. Thus, a minimum cost of $73.3 million can be linked to the discovery of a single nonindigenous disease in a single potato field. Beef export losses following discovery of a single cow infected with Bovine Spongiform Encephalitis (mad cow disease) in Alberta during 2003 are at least an order of magnitude greater than those associated with the potato embargo (Table 2). Given the rising concern over NIS globally, costs associated with lost exports could be the most significant impact of future NIS in Canada.

The characterised, annual costs for five nuisance NIS in agriculture and related costs pales in comparison to the ‘invisible tax’ calculated by our model. Effects on agricultural crops and grazing livestock, as well as milk production and potato exports result in a total projected cost of $6.7 billion ($5.3–$13.9 billion) per annum.

Forestry

Average costs for the control of Dutch elm disease (*Ophiostoma ulmi*) in the province of Manitoba is approximately $1.5 million/year (Table 2). This disease is spread primarily by native and nonindigenous bark beetles, resulting in 18–50% mortality of infected trees (see MacIsaac et al. 2002). No data were available for the economic impact of any of the seven other nuisance NIS examined in forestry (in Table 3). Despite this limitation, several NIS are known to have had severe impacts on Canadian forests. For example, white pine blister rust (*Cronartium ribicola*) and Scleroderris canker (*Gremmeniella abietina*), are established diseases in Canada. Infestations of these diseases can result in up to 100% mortality of infected trees. Other NIS, like the brown spruce longhorn beetle (*Tetropium fuscum*) and the Asian longhorn beetle (*Anoplophora glabripennis*) are recent discoveries in Canada with potentially devastating impacts. Larvae of these beetles bore into tree cambium, resulting in up to 100% mortality of infected trees (see MacIsaac et al. 2002).

The lack of characterised costs for nuisance NIS in forestry should not be taken as evidence that Canadian forests are weakly impacted by nuisance NIS. Given the number and severity of the effects of nuisance NIS in Canadian forestry (see MacIsaac et al. 2002), the paucity of characterised costs is more likely a reflection of the lack of attention paid to quantifying economic impacts of these species. Moreover, Canadian forests appear to be particularly at risk from future invasions. Specifically, our model projected potential costs associated with the Asian longhorn beetle, which was not known to be established in Canada when our study was conducted in 2002. During summer 2003, however, the species was discovered at two sites in Toronto, Ontario, likely introduced with contaminated wood products or packaging (CFIA 2003). A second beetle species, the emerald ash borer (*Agrilus planipennis*), likely entered by a similar vector and has recently been found in Windsor, Ontario, and adjacent areas around Detroit, Michigan. If not properly managed, both species are likely to have profound effects on Canadian and American forests. The emerald ash borer alone could destroy most of Canada's ash trees (*Fraxinus* spp.), which make up a large proportion of $1.4 billion in annual production of hardwood products, and an additional $500 million per year in nursery stocks (CFIA 2003).

The seven nuisance NIS profiled in forestry likely impart a 'tax' on maple, fir, spruce, and pine timber sales and exports (e.g. Christmas tree sales, pulp for paper products, and maple syrup products) (Table 3). Given the high value of Canada's forest industry, projected economic impacts are highest for this sector, with a total 'tax' of $9.6 billion ($7.7–$20.1 billion).

Discussion

Nuisance NIS pose serious threats to Canada's economy and the health and welfare of its citizens, in addition to its natural ecosystems. We have employed a case study approach in a first attempt to quantify these effects on a national scale. The economic impacts identified herein reveal a diverse array of sectors affected by nuisance NIS (e.g. tourism, crop exports, property value), and myriad ways that these costs are incurred (e.g. losses stemming from competition with, infection of, or predation on native species; control and management; alteration to ecosystem functioning, release of noxious chemicals). A central problem in deriving accurate and comprehensive assessments of damage wrought by nuisance NIS is the paucity of available data to systematically track direct and indirect, market and non-market costs for even the most problematic species. The result is a highly fragmented picture of the true costs of nuisance NIS, rendering impossible our original task of assessing their economic impact to the welfare of Canadians. Our review has focused on the negative economic impacts of NIS in Canada, but in reality some externalities may be positive. For example, zebra mussel filtering activities clarify lake water, possibly increasing the value of cottages and other lakefront properties. Similarly, the recent invasion of the emerald ash borer has very strong negative externalities, but also some positive ones. At a microeconomic scale, negative externalities are imparted upon homeowners and businesses that pay to remove infested and dying trees. However, this cost yields a benefit to landscape companies involved in tree cutting and disposal, possibly resulting in no net change (or even an increase) in measured gross domestic product (GDP). Even where externalities are positive, the overall welfare of citizens may still decrease. For example, beetle control efforts impart opportunity costs (i.e. costs associated with forgone alternatives) because affected landowners/municipalities reapportion economic capital in opposition to choice. At a macroeconomic scale, government funds diverted to compensation or control might otherwise have been spent on other budget priorities. This reduction in freedom may result in an overall decrease in welfare, despite the offsetting of monetary costs (e.g. no change in GDP).

In contrast to some externalities, the 'invisible tax' imposed by nuisance NIS affects production capability through reduced yield, and thus does not have an obvious, positive counterpart. The projected costs of our empirical model underscores the economic severity associated with invasion by nuisance NIS that impose an 'invisible tax' through reduced production of natural resources. Many of the costs associated with nuisance NIS in this study were projected from damage histories of other nuisance NIS, and appear highly variable depending on the loss rate utilised (20, 22, 52% resource loss).

Another potential criticism of our empirical model stems from the effect of reduced yield on the supply, and therefore the price, of damaged goods. For virtually any of the industries evaluated in our model, a large drop in supply would result in a dramatic increase in price. However, this reasoning, based on the well-known relationship between supply and demand, ignores importation from other countries, which will tend to equilibrate costs. Given the cost of importation, prices are likely to be higher, but should not increase beyond the global market price + import cost. Thus the effects of nuisance NIS to Canadian fisheries, agriculture and forestry are really the effects of nuisance NIS in Canada relative to production of other countries. Fluctuations in global production due to natural disasters, political upheaval, and even nuisance NIS effects in other countries, are all independent of the effects of nuisance NIS on Canadian production. We therefore suggest that such scaling effects of the 'invisible tax' to Canadian producers are minimal, but further investigation is needed to confirm this. Despite these potential criticisms of our approach, our results serve as a starting point for future studies.

Given these costs, should we focus on preventing new NIS or controlling those that are already here? Events of 2003 illustrate that additional species have the potential to establish in Canada (e.g. emerald ash beetles), possibly resulting in hundreds of millions or even billions of dollars in future control costs and resource loss. The current outbreaks of emerald ash boring beetles in southern Ontario and south-eastern Michigan, for example, threaten approximately one billion and 800 million native ash trees in these regions, respectively. Multiple outbreaks of Asian longhorn beetles in North America, including during summer 2003 in Toronto, Ontario, threaten a wide array of native hardwood trees. It is not clear when these species first entered the country, but it cannot be assumed that the vector responsible for their introduction has been severed, or that more forest pests will not invade.

Vectors of nuisance NIS vary among economic sectors, and may differ tremendously in strength. Some vectors appear particularly potent in that they are capable of delivering large numbers of individuals of many different species. Ballast water is recognised as a dominant vector of NIS introduction worldwide and within North America's Great Lakes (Grigorovich et al. 2003). However, similarly potent vectors exist in other sectors. For example, Allen and Humble (2002) reported the accidental import of 40 species of bark beetles, wood borers, parasites, predators, fungi and nematodes, including 3 species of quarantine significance. These species emerged from untreated dunnage associated with granite imported from Norway to eastern Canada after which it was transferred to the Pacific coast by rail. Most national governments strive to increase national wealth, often through increased levels of international trade. Given that the economic activity of a country is correlated with the number of established NIS (Dalmazzone 2000), countries with extensive international trading networks appear particularly vulnerable to new invasions (Levine and D'Antonio 2003). Future introductions of NIS to these countries seem assured – absent new policies and programs to reduce invasions – as liberalised trade laws increase international trade further. Moreover, given that perhaps 20-30% of NIS produce negative economic consequences (Pimentel et al. 2001), an economic trade-off may exist between increasing trade revenue and increasing exposure to the 'invisible tax' imposed by nuisance NIS. Assuming that 20% of the >1442 NIS established in Canada have negative impacts, then our characterised costs represent costs associated with just over 1% of species with impacts. Of course, these are among the most problematic NIS, but it seems reasonable to assume that our characterised cost estimate is significantly undervalued nonetheless.

There exists an immediate need for a comprehensive national program to assess and manage the impact of nuisance NIS in Canada. Given the importance of vectors to the introduction of new invaders (Ruiz and Carlton 2003), a national 'biosecurity' policy has been advocated for the

United States, based on the premise that "an ounce of prevention is worth a pound of cure" (Meyerson and Reaser 2003). We contend that this approach is likely the most cost-effective way to optimise the relationship between international trade and exposure to new NIS. Development of a national strategy is presently underway in Canada, although its success is difficult to envisage without additional resources for federal departments mandated to address NIS issues. We contend that the strategy ought to be implemented in conjunction with continental trade partners to maximise continental security.

How much should the Canadian government spend on the prevention and control of nuisance NIS? Our calculation of $187 million CDN/year in characterised costs likely represent only a small fraction of the true cost, and future invaders will only add to this total. If our characterised and projected costs are correct to an order of magnitude, our demonstrated costs represent only 1% of the actual costs associated with nuisance NIS. Arriving at a justified investment for the prevention of new introductions and the control of established NIS would require a model to estimate of the efficacy of such an approach. For example, what is the relationship between investment size and reduction of future invasions? As a point of reference, the investment in control and prevention by Australia and New Zealand, current world leaders in the control of nuisance NIS, is about $100 million AU/year and $121 million NZ/year, respectively (MacIsaac et al. 2002). However, scaling up to an appropriate Canadian investment should incorporate the higher value of natural resources at risk, as well as the investment required to protect a much larger landmass.

Our study has identified a number of economically important industries that are affected by nuisance NIS and at risk from future biological invasions, yet these compose only a small proportion of the industries potentially affected. Comprehensive programs for the management and prevention of new invasions will undoubtedly require significant national funding. However, these expenditures appear warranted given the existing and potential costs associated with established and new nuisance NIS in Canada.

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References

Allen EA and Humble LM (2002) Nonindigenous species introductions: a threat to Canada's forests and forest economy. Canadian Journal of Plant Pathology 24: 1–8

Bais HP, Vepachedu R, Gilroy S, Callaway RM and Vivanco JM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. Science 301: 1377–1380

Bruce WN and Decker GC (1958) The relationship of stable fly abundance to milk production in dairy cattle. Journal of Economic Entomology 51: 269–274

Campbell FT and Schlarbaum SE (1994) Fading Forests: North American Trees and the Threat of Exotic Pests. Natural Resources Defence Council, New York

Campbell JB, Berry IL, Boxler DJ, Davis RL, Clanton DC and Deutscher GH (1987) Effects of stable flies (Diptera: Muscidae) on weight gain and feed efficiency of feedlot cattle. Journal of Economic Entomology 80: 117–119

Canadian Food Inspection Agency (CFIA) (2000) Foot and Mouth Disease Strategy. CFIA Draft Strategy

Canadian Food Inspection Agency (CFIA) (2003) Phytosanitary Requirements to Prevent the Introduction into and Spread within Canada of the Emerald Ash Borer, *Agrilus planipennis* (Fairmaire), into Canada. CFIA Directive D-03-08

Cohen AN and Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279: 555–558

Cohen AN, Carlton JT and Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Marine Biology 122: 225–237

Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P and van den Belt M (1997). The value of the world's ecosystem services and natural capital. Nature 387: 253–260

Dalmazzone S (2000) Economic factors affecting vulnerability to biological invasions. In: Perrins C, Williamson M and Dalmazzone S (eds) The Economics of Biological Invasions, pp 17–30. Edward Elgar, Cheltenham, UK

Dawson M (2002) Plant quarantine: a tool for preventing the introduction and spread of alien species harmful to plants.

In: Claudi R, Nantel P and Muckle-Jeffs E (eds) Alien Invaders in Canada's Waters, Wetlands and Forests, pp 243–251. Canadian Forest Service, Ottawa, Canada

Dosdall MD, Moisey D, Carcamo H and Dunn R (2001) Cabbage Seedpod Weevil Fact Sheet. Alberta Agriculture, Food and Rural Development Agdex 622-21, Alberta

Fuller PL, Nico LG and Williams JD (1999) Nonindigenous Fishes Introduced into Inland Waters of the United States. US Geological Survey, Bethesda, USA

Grigorovich IA, Colautti RI, Mills EL, Holeck K, Ballert AG and Maclsaac HJ (2003) Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Canadian Journal of Fisheries and Aquatic Sciences 60: 740–756

Hall JP (1996) Forest Insect and Disease Conditions in Canada – 1994. Canadian Forest Service, Natural Resources Canada

Harris LG and Tyrrell MC (2001) Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. Biological Invasions 3: 9–21

Hebert PDN, Muncaster BW and Mackie GL (1989) Ecological and genetic studies on *Dreissena polymorpha* (Pallas) – a new mollusk in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 1587–1591

Hubbes M (1999) The American elm and Dutch elm disease. Forestry Chronicle 75: 265–275.

Hunt RS (1983) White pine blister rust in British Columbia. Forestry Canada, Forest insect and disease survey. Forest Pest Leaflet 26

James WC, Shih CS, Hodgson WA and Callbeck LC (1972) The quantitative relationship between late blight of potato and loss of tuber yield. Phytopathology 62: 92–96

Leafy Spurge Stakeholder's Group (LSSG) (1999) Leafy Spurge Economic Impact Assessment, WESTARC Group, Brandon University, Manitoba

Leigh P (1998) Benefits and costs of the ruffe control program for the Great Lakes fishery. Journal of Great Lakes Research 24: 351–360

LePage WL (1993) The impact of *Dreissena polymorpha* on waterworks operations at Monroe, Michigan: a case history. In: Nalepa TF and Schloesser DW (eds) Zebra Mussels. Biology, Impacts, and Control, pp 333–358. Lewis Publishers, Boca Raton, FL

Levin PS, Coyer JA, Petrik R and Good TP (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83: 3182–3193

Levine JM and D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conservation Biology 17: 322–326

Lysyk TJ, Floate KD and Lancaster RC (2002) Insects and Other Arthropod Posts: Horn Fly. Saskatchewan Agriculture, Food and Rural Revitalization, Saskatchewan

MacIsaac HJ (1996) Potential abiotic and biotic effects of zebra mussels on inland waters of North America. American Zoologist 36: 287–299

MacIsaac HJ, Bandoni SA, Colautti RI, van Overdijk CDA and Admundsen K (2002) Economic Impacts of Invasive Nonindigenous Species in Canada: a Case Study Approach. A report to the Office of the Auditor General of Canada, 185 pp

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710

Maddox DM (1979) The knapweeds: their economics and biological control in the western states, U.S.A. Rangelands 1: 139–141

Meyerson LA and Reaser JK (2003) Bioinvasions, bioterrorism and biosecurity. Frontiers in Ecology and the Environment 6: 307–314

Mills EL, Leach JH, Carlton JT and Secor CL (1993) Exotic species in the Great Lakes – a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19: 1–54

Nowak DJ, Pasek JE, Sequeira RA, Crane DE and Mastro VC (2001) Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. Journal of Economic Entomology 94: 116–122

Office of Technology Assessment (OTA) (1993) Harmful Nonindigenous Species in the United States. Government report, OTA-F-565, Washington, DC, 391 pp

Parker IM, Simberloff D, Lonsdale WM, Goodsell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE and Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19

Patterson M (1998) Commensuration and theories of value in ecological economics. Ecological Economics 25: 105–125

Perrins C, Williamson M and Dalmazzone S (2000) (eds) The Economics of Biological Invasions. Edward Elgar, Cheltenham, UK, 264 pp

Pimentel D, Lach L, Zuniga R and Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50: 53–65

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T and Tsomondo T (2001) Economic and environmental threats of alien plant, animal and microbe invasions. Agriculture, Ecosystems and Environment 84: 1–20

Ricciardi A (2001) Facilitative interactions among aquatic invaders: is an 'invasional meltdown' occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences 58: 2513–2525

Ricciardi A (2003) Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasion. Freshwater Biology 48: 972–981

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD and West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93–107

Ruiz GM and Carlton JT (2003) Invasive Species: Vectors and Management Strategies. Island Press, Washington, DC.

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ and Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annual Review of Ecology and Systematics 31: 481–531

Sailer RI (1983) History of insect introductions. In: Graham C and Wilson C (eds) Exotic Plant Pests in North American Agriculture, pp 15–38. Academic Press, New York, NY

Simberloff D (2003) Confronting introduced species: a form of xenophobia? Biological Invasions 5: 179–192

Simberloff D and Von Holle B (1999) Positive interactions of non-indigenous species: invasional meltdown? Biological Invasions 1: 21–32

Simons AM (2003) Invasive aliens and sampling bias. Ecology Letters 6: 278–280

Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seeman JR and Nowak RS (2000) Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. Nature 408: 79–82

Stachowicz JJ, Terwin JR, Whitlatch RB, and Osman RW (2002) Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences 99: 15497–15500

Thompson DQ, Stuckley RL and Thompson EB (1987) Spread, Impact and Control of Purple Loosestrife (*Lythrum salicaria*) in North American wetlands. United States Fish and Wildlife Service, Fish and Wildlife Research 255 pp

Turner RK, Adger WN and Brouwer R (1998) Ecosystem services value, research needs, and policy relevance: a commentary. Ecological Economics 25: 61–65