Symposium contribution / Contribution à un symposium

Forest biosecurity: alien invasive species and vectored organisms[1]

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Abstract: Alien invasive species pose a serious threat to the ecological and economic sustainability of Canada's forests. Recent establishments of invasive insect pests such as the brown spruce longhorn beetle (*Tetropium fuscum*), Asian longhorned beetle (*Anoplophora glabripennis*), and emerald ash borer (*Agrilus planipennis*) highlight the risk of alien species to natural and urban forests of Canada. An emerging area of phytosanitary concern for scientists and phytosanitary regulators is the relationship between fungi or other organisms (e.g., nematodes, mites) and their insect vectors. Invasive insects may introduce and vector alien fungal pests or may serve as vectors for native fungi. Conversely, native insects can become vectors of introduced fungi. The diversity of fungi vectored by introduced insect species is poorly understood. Canadian and international strategies to prevent the influx of alien invasive species, to monitor their presence, and to control established populations are discussed. Surveys for better understanding risks posed by vectored fungi will require development of novel survey techniques and diagnostic tools.

Key words: alien invasive species, introduced species, quarantine, vectored pathogens, fungi, bluestain, nematode, mites.

Résumé : Les espèces exotiques envahissantes constituent une grave menace pour la durabilité écologique et économique des forêts canadiennes. L'établissement récent d'insectes ravageurs envahissants tels que le longicorne brun de l'épinette (*Tetropium fuscum*), le longicorne asiatique (*Anoplophora glabripennis*) et l'agrile du frêne (*Agrilus planipennis*) met en évidence les dangers que constituent ces espèces exotiques pour les forêts naturelles et urbaines du Canada. Les relations entre les champignons ou d'autres organismes (p. ex. nématodes, acariens) et leurs insectes vecteurs sont un nouveau sujet de préoccupation phytosanitaire pour les scientifiques et les autorités de la réglementation phytosanitaire. Les insectes envahissants peuvent introduire et être vecteurs de champignons nuisibles exotiques ou peuvent servir de vecteurs de champignons indigènes. Inversement, les insectes indigènes peuvent devenir des vecteurs de champignons introduits. La diversité des champignons transportés par les espèces d'insecte introduits est peu connue. Nous examinons des stratégies canadiennes et internationales pour prévenir l'afflux d'espèces exotiques envahissantes, pour surveiller leur présence et pour lutter contre les populations établies. Les relevés qui aideraient à mieux saisir le danger que représentent les champignons transportés nécessiteront le développement de nouvelles techniques et de nouveaux outils diagnostiques.

Mots clés : espèces exotiques envahissantes, espèces introduites, quarantaine, agents pathogènes transportés, champignons, bleuissement, nématode, acariens.

Introduction

Canada has a long history of introductions of alien invasive species that affect forests (3). Pathogens such as those that cause chestnut blight, *Cryphonectria parasitica* (Murrill) Barr, and white pine blister rust, *Cronartium ribicola* J.C. Fisch., have seriously impacted forest resources since their introduction. Chestnut blight first entered Canada in the early 1920s (99) and eliminated the American chestnut (*Castanea dentata* (Marsh.) Borkh.), which was a key component of eastern hardwood forests, while white pine blister rust, introduced to both Europe and North America from Asia in the late 1800s, has seriously restricted the availability of five-needle pines for commercial purposes (88). Dutch elm disease, an insect-vectored pathogen caused by *Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier, first appeared in Canada in 1945 and has since spread throughout the native range of *Ulmus* in North America, as well as to most urban areas beyond the native range of the genus (88). The disease has killed millions of native and introduced elm trees in both natural forest and urban settings (58). Similarly, the insect–

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pathogen complex causing beech bark disease has spread throughout the native range of *Fagus* since it was first detected in Halifax, Nova Scotia, in 1898 (33). These are examples of invasive species that have had significant ecological and economic effects on Canada's forests, and that are now undesirable but permanent components of Canadian forests. This paper discusses recent arrivals of alien invasive species with respect to an emerging area of concern — relationships between alien and native fungi and their insect vectors — and describes how Canada is responding to these threats.

Recent alien invasive introductions

During the past decade, researchers have become aware of an increasing number of alien invasive pests established in Canadian forests. A postentry detection program for invasive bark- and wood-boring beetles in and around the port of Vancouver, British Columbia, documented the recent establishment of five nonindigenous bark and ambrosia beetle species ((Scolytidae), *Trypodendron domesticum* (L.), *Xyleborus pfeili* (Ratzeburg), *Xyleborinus alni* (Niisima), *Xylosandrus germanus* (Blandford), and *Xyloterinus politus* (Say)) and one species of long-horned woodborer ((Cerambycidae), *Phymatodes testaceus* (L.)) in urban parks and adjacent natural forest habitats (59). In addition, three scolytid species that have apparently not yet established in British Columbia, *Cyrtogenius brevior* (Eggers), *Euwallacea validus* (Eichhoff), and *Xylosandrus crassiusculus* (Motschulsky), were detected in traps near warehouses and were likely introduced in association with solid wood packaging. Ongoing studies have demonstrated that four of the recent introductions, *Trypodendron domesticum*, *Xyleborinus alni*, *Xylosandrus germanus*, and *Xyloterinus politus*, have successfully invaded both urban forest habitats and adjacent managed forest lands around Vancouver (L.M. Humble, unpublished data).

Some insect pests recently established in Canada have developed into serious problems with significant ecological and economic impacts. For instance, in 1999, *Tetropium fuscum* (Fabricius), the brown spruce longhorn beetle, was discovered in Halifax (118), where it was recovered from dead and dying red spruce (*Picea rubens* Sarg.). The beetle was later found to be attacking apparently healthy trees. Until this discovery, *Tetropium fuscum* had not been considered of quarantine significance, as it had only been observed as a secondary pest of *Picea* in European forests.

Of note, research studies undertaken to evaluate the biology and ecology of the introduced population of *Tetropium fuscum* isolated a European species of *Ophiostoma*, *Ophiostoma tetropii* Mathiesen, from infested trees and from dead trees previously infested by the beetle (69). Pathogenicity studies suggest that *O. tetropii* has low virulence to living trees (Ken Harrison, Canadian Forest Service, personal communication) and may only be a minor contributing factor to the risk posed by *Tetropium fuscum* to living red spruce. Its discovery in Nova Scotia, however, not only provides a Canadian example of the association between a novel vectored pathogen and a quarantine pest, but emphasizes the potential threat of novel pathogens piggy-backing aboard vectoring insects into new forest habitats.

Not all alien invasives are known to vector pathogens. At least two recent introductions have not been associated with vectored pathogens: the emerald ash borer, *Agrilus planipennis* Fairmaire, first discovered in the Windsor–Detroit region of Canada and the United States (US) in 2002, where it has killed tens of thousands of ash (*Fraxinus*) trees (49, 50), and the Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky), discovered in trees in industrial areas in New York (1996), Chicago (1998), and New Jersey (2002) in the US (47, 48, 50); in Austria (2001) (127, 128); in France (2003) (30); and in Toronto, Ontario (2003) (24).

Alien fungi – insect vector relationships

Scientists and regulators are becoming increasingly concerned about the introduction and spread of alien and native fungi via insect vectors. The relationships between alien and native fungi and their insect vectors are complex and poorly understood. Alien invasive fungi may be introduced and vectored by alien insects. For example, *O. ulmi* and *O. novo-ulmi*, introduced to Canada in 1944 (108) and the 1960s (12), respectively, are both vectored by adults of *Scolytus multistriatus* (Marsham), the European elm bark beetle, also an introduced species. Similarly, *O. tetropii* was likely introduced to Canada in association with *Tetropium fuscum* (69). More recently, an exotic pathogenic blue-stain fungus, caused by *Leptographium wingfieldii* M. Morelet, was found in association with another recent introduction into Canada and the northeastern US, the pine shoot beetle, *Tomicus piniperda* (L.) (70). Elsewhere in the world, *Ophiostoma huntii* (Rob.-Jeffr.) de Hoog & R.J. Scheff is now found in association with *Hylastes ater* (Paykull) in New Zealand (109), and *Amylostereum areolatum* (Chaillet) Boidin has moved with *Sirex noctilio* Fabricius from the northern hemisphere to New Zealand, Australia, South Africa, and South America (115, 139). Introduced insects may also become vectors of native fungi. *Ophiostoma piceae* (Münch) Syd. & P. Syd and *Pesotum fragrans* (Math.-Käärik) G. Okada & Seifert, both native to Canada, were found to be associated with *Tetropium fuscum*, a beetle introduced from Europe (69).

Conversely, native insects can become vectors of introduced fungi. One of the principal vectors of Dutch elm disease fungi, *O. ulmi* and *O. novo-ulmi*, is the native elm bark beetle *Hylurgopinus rufipes* (Eichhoff). Prior to this association, this beetle was considered a nonaggressive secondary species of limited economic importance (13). Similarly, Jacobs et al. (70) documented the recovery of *L. wingfieldii* from two native bark beetle species, *Ips pini* (Say) and *Dendroctonus valens* LeConte, both of which have transcontinental distributions in North America. Native insects have also been identified as potential vectors of the butternut canker fungus, *Sirococcus clavigignenti-juglandacearum* N.B. Nair, Kostichka & J.E. Kuntze (51). Linking to an established native insect vector with existing widespread distribution can lead to rapid dispersal of an alien fungus.

These and other examples of insect-vectored fungi on host species that have not coevolved with the pathogens (33, 43, 57, 86, 110, 123, 134) illustrate a range of interactions between fungi and insect vectors that can contribute to the dynamics of alien-pest establishment and increase risk of ecological and economic impacts in native forests. Clearly, it is not always necessary for an insect or fungus to be introduced with its known associate(s) to negatively affect a new environment. In fact, we must assume novel associations will be established.

The threat posed by vectored fungi is difficult to evaluate, as quarantine agencies lack specific knowledge of and generally do not survey for fungi vectored by intercepted insects. Additionally, the impacts of specific organisms on novel hosts within their introduced range cannot be estimated a priori. However, the magnitude of the risk can be estimated by examining the known geographic distributions and diversity of fungi spread by introduced vectors already established in Canada or by vectors of quarantine concern detected during postentry inspections of imported commodities but not yet established in Canada.

Fungi vectored by established exotics

The diversity of the fungi vectored by introduced and native insect species is poorly understood. At least 18 species of bark- or wood-boring beetles (Scolytidae, Cerambycidae, and Buprestidae) that are not indigenous to North America have established in Canada. More than 43 species of fungi are known to be associated with these species, as well as with an eastern North American ambrosia beetle now established in western North America (Table 1). Fifteen of the associated fungal species, as well as species of Acari and Nematoda (*Proctolaelaps* spp. and *Bursaphelenchus sexdentati* Rühm), have yet to be recorded in North America (Table 1).

Incomplete knowledge of the diversity of fungi associated with native and introduced wood borers contributes to the difficulty of determining which of the fungi associated with these introduced taxa represent introductions to the flora of Canada. For instance, ambrosia beetles (*Trypodendron*, *Xyleborus*, *Xyleborinus*, *Xylosandrus*, and *Xyloterinus* spp.) vector symbiotic ambrosial fungi as food sources for their larvae, but they sometimes also vector other, pathogenic fungi (Table 1). A single fungal species can be associated with multiple beetle vectors, and conversly a single beetle vector can have multiple associated ambrosial fungi (111). Although *Ambrosiella sulphurea* Batra was described from galleries of *Xyleborinus saxeseni* (Ratzeburg) in *Populus deltoides* Bartr. ex Marsh. from Kansas, the fungus is likely of Eurasian origin, as it is known to be vectored only by *Xyleborinus saxeseni*, a species now widely distributed in both northern and southern hemispheres but also of Eurasian origin. Other ambrosial fungi associated with nonindigenous beetles (e.g., *Ambrosiella hartigii* Batra) have also been recovered from native ambrosia beetles (54) long after initial introduction of nonindigenous vectors, which confuses the question of the origin of the fungi. For instance, the origin of the association of *A. hartigii* with the native *Xyleborus sayi* Hopkins has not been determined: the association may be natural or may have originated with the transfer of the ambrosial fungus from a nonindigenous vector to the native vector.

In addition to ambrosial fungi, at least 10 species of ophiostomatoid fungi not known to be present in Canada have been associated with currently established bark- and wood-boring beetle species (Table 1). As neither surveys to evaluate the flora and fauna associated with the introduced vectors nor evaluations of the pathenogenicity of many of these fungi to Canadian tree species are available, the threat posed by the accidental introduction of these fungi cannot always be ascertained.

Fungi vectored by intercepted exotics

The use of green wood to package commodities for international transport represents a significant pathway for introduction of bark- and (or) wood-boring beetles and their associated flora and fauna. Recent audits of pests associated with solid wood packaging by Canada's National Plant Protection Organization (22) documented almost 550 interceptions of bark- or wood-boring beetles in a 3-year period (Table 2), dominated by species of Cerambycidae, Scolytidae, and Bostrichidae. Of these frequently intercepted beetle families, the Scolytidae are commonly associated with wood-staining, pathogenic, and (or) saprophytic fungi (103, 140), with phoretic mites also capable of vectoring fungi (101, 102), and with saprophytic, fungivorous, and (or) pathogenic nematodes (11). This beetle family well represents the potential for introduction of vectored organisms.

Tables 1 and 3 document a significant diversity of vectored pathogens associated with the fully identified Scolytidae species intercepted in Canada during audits of imported wood and wood packaging (22). These fully identified interceptions account for less than 20% of all interceptions made during the audit. While pathogenic fungi are associated most frequently with Scolytidae, multiple other species of vectored pathogens have been associated with species of Anobiidae (56), Buprestidae (41, 126, 131), Cerambycidae (51, 66, 62, 69, 74, 75, 104, 132), Platypodidae (18, 73, 86, 107, 126), and Siricidae (117, 124, 125). Also, the proportion of species-level determinations differs markedly between the dominant families of Coleoptera and Hymenoptera intercepted with wood products during the audits, averaging 56% of all interceptions, and ranging from a low of 8% in the Buprestidae to a high of 80% in the Bostrichidae (Table 2). Because a significant proportion of the intercepted insects associated with wood products are not fully identified, the full diversity of introduced pathogens cannot be ascertained. Thus, pathogens identified in Tables 1 and 3 likely represent only a small proportion of the organisms potentially vectored by the Coleoptera and Hymenoptera transported with such wood products.

Species-level determinations were made for 76% of the Scolytidae intercepted during the audit (22): in total, 42 identified species, including some of the more serious Palaearctic bark-beetle pests (*Ips typographus* (L.) and *Ips cembrae* (Heer)), were recovered. In addition to the 28 species of Scolytidae not known to be established in Canada, intercepted species included Palaearctic conspecifics of native species (*Dryocoetes autographus* (Ratzeburg), *Polygraphus rufipennis* (Kirby), and *Trypodendron lineatum* (Olivier)), as well as nonindigenous species known to be already established in Canada (*Hylastes opacus* Erichson, *Tomicus piniperda*, *Xyleborinus alni*, and *Xyleborinus saxeseni*). Known fungal associates of the Scolytidae species not known to occur in Canada or represented by Holarctic

Table 1. The fungi, mites, and nematodes recorded in the literature as being vectored by nonindigenous bark- or wood-boring beetles currently established in Canada.

Taxon	Date introduced*	Organism vectored[†]	Presence in Canada[‡]	References
Scolytidae				
Crypturgus pusillus (Gyllenhal)	1868	*Atractocolax pulvinatus*		81
		Graphium fimbriisporium		68
		Ophiostoma minutum	+	62
		Ophiostoma neglectum		62, 80
Hylastes opacus Erichson	1987	*Leptographium guttulatum*		63
		Leptographium lundbergii	+	63, 136
		Leptographium procerum	+	63, 136
		Leptographium wingfieldii	+	63, 70, 136
		Proctolaelaps spp.	?	4
Hylastinus obscurus (Marsham)	1878	*Fusarium avenaceum*	+	71
Scolytus mali (Bechstein)	1868	None recorded		
Scolytus multistriatus (Marsham)	1909	*Ophiostoma ulmi*	+	12
		Ophiostoma novo-ulmi	+	12
Scolytus rugulosus (Müller)	1878	None recorded		
Tomicus piniperda (L.)	1991	*Aureobasidium pullulans*	+	42
		Hormonema dematioides	+	121
		Leptographium ?euphyes		63
		Leptographium guttulatum		63, 67
		Leptographium koreanum		78
		Leptographium lundbergii	+	42, 52, 63, 98
		Leptographium pinidensiflorae		63, 96
		Leptographium procerum	+	42, 63
		Leptographium wingfieldii	+	42, 63, 70, 98
		Leptographium yunnanense[‖]		147
		Ophiostoma canum		98
		Ophiostoma clavatum		98
		Ophiostoma huntii	+	42, 63
		Ophiostoma ips	+	76
		Ophiostoma minus	+	98
		Ophiostoma minutum	+	62
		Ophiostoma serpens		52, 63
		Leptographium n. sp.		76
		Ambrosiella sp.		76
		Bursaphelenchus sexdentati		10
Trypodendron domesticum (L.)	1997	*Ambrosiella ferruginea*	+	7, 152
		Bjerkandera adusta	+	152
		Ceratocystis ambrosia	+	6
		Ceratocystis bacillospora		152
		Ceratocystis piceae	+	152
		Ceratocystis torulosa		152
		Gliocladium roseum	+	152
		Trichoderma viride	+	152
Xyleborinus alni (Niisima)	1995	None recorded		
Xyleborinus saxeseni (Ratzeburg)	1919	*Ambrosiella sulphurea*	+	7, 37, 111
Xyleborus dispar (Fabricius)	1817	*Ambrosiella hartigii*	+	38, 39, 111, 152
		Fusarium javanicum		152
		Penicillium citrinum		152
		Trichoderma viride	+	152
Xyleborus pfeili (Ratzeburg)	1992	None recorded		
Xylosandrus germanus (Blandford)	1931	*Ambrosiella hartigii*	+	7
		Fusarium moniliforme var. *subglutinans*	+	135
		Fusarium solani	+	135
		Fusarium sambucinum	+	135
Xyloterinus politus (Say)	1997[§]	*Aspergillus flavus*	+	94

Table 1 (*concluded*).

Taxon	Date introduced*	Organism vectored[†]	Presence in Canada[‡]	References
		Fusarium sp.	+	94
		Penicillium sp.	+	94
		Raffaela sp.	+	1, 94
Buprestidae				
Agrilus planipennis Fairmaire	2003	None recorded		
Buprestis haemorrhoidalis Herbst	1992	None recorded		
Cerambycidae				
Anoplophora glabripennis (Mots.)	2003	None recorded		
Phymatodes testaceus (L.)	?	None recorded		
Tetropium fuscum (Fabricius)	2001	*Ophiostoma piceae*	+	69
		Ophiostoma tetropii	+	69

*The date of first introduction given for the Scolytidae represents the first record of occurrence in North America (45); dates for Buprestidae and Cerambycidae are the first records of occurrence in Canada.

[†]Authorship and synonomy of fungi as designated in Index Fungorum (http://www.indexfungorum.org, accessed October 2004): Fungi: *Ambrosiella ferruginea* (Math.-Käärik) L.R. Batra; *A. hartigii* L.R. Batra; *A. sulphurea* L.R. Batra; *Aspergillus flavus* Link; *Atractocolax pulvinatus* R. Kirschner, R. Bauer & Oberw.; *Aureobasidium pullulans* (de Bary) G. Arnaud; *Bjerkandera adusta* (Willd.) P. Karst.; *Ceratocystis pilifera* (Fr.) C. Moreau [as *C. ambrosia* B.K. Bakshi]; *C. bacillospora* Butin & G. Zimm.; *C. torulosa* Butin & G. Zimm.; *Fusarium moniliforme* f. *subglutinans* (Luc) C. Moreau; *F. avenaceum* (Fr.) Sacc.; *F. javanicum* Koord.; *Gibberella pulicaris* (Fr.) Sacc. [as *Fusarium sambucinum* Fuckel]; *Nectria haematococca* Berk. & Broome [as *Fusarium solani* (Mart.) Sacc.]; *Gliocladium roseum* Bainier; *Graphium fimbriisporum*(Morelet) K. Jacobs, T. Kirisits & M.J. Wingf.; *Sydowia polyspora* (Bref. & Tavel) E. Müll. [as *Hormonema dematioides* Lagerb. & Melin]; *Leptographium ?euphyes* K. Jacobs & M.J. Wingf.; *L. guttulatum* M.J. Wingf. & K. Jacobs; *L. koreanum* J.-J. Kim & G.-H. Kim; *L. lundbergii* Lagerb. & Melin; *L. pinidensiflorae* Masuya & M.J. Wingf.; *L. procerum* (W.B. Kendr.) M.J. Wingf.; *L. wingfieldii* M. Morelet; *L. yunnanense* X.D. Zhou, K. Jacobs, M.J. Wingf. & M. Morelet; *Ophiostoma canum* (Münch) Syd. & P. Syd.; *O. clavatum* Math.-Käärik; *O. huntii* (Rob.-Jeffr.) de Hoog & R.J. Scheff.; *Ceratocystis ips* (Rumbold) C. Moreau [as *O. ips* (Rumbold) Nannf.]; *Ceratocystis minor* (Hedgc.) J. Hunt [as *O. minus* (Hedgc.) Syd. & P. Syd.; *O. neglectum* R. Kirschner & Oberw.; *O. novo-ulmi* Brasier; *O. piceae* (Münch) Syd. & P. Syd.; *O. serpens* (Goid.) Arx; *O. ulmi* (Buisman) Nannf.; *Penicillium citrinum* Thom; *Trichoderma viride* Pers. Acarina: *Proctolaelaps*. Nematoda: *Bursaphelenchus sexdentati* Rühm.

[‡]Species designated "+" are noted as present in North America in Farr et al. (35) or the primary reference cited.

[¶]Ongoing research indicates that the vector of *L. yunnanense* is an undescribed species of *Tomicus* (90).

[§]Although native to eastern North America, *X. politus* was recently introduced into western North America (59).

conspecifics in Canada (*Dryocoetes autographus*) are documented in Table 3.

At least 39 species of fungi, 56% of which have not been recorded in Canada, are associated with the 9 species of scolytid vectors documented in Table 3. Of immediate concern are plant-pathogenic ophiostomatoid taxa such as *Ceratocystis laricicola* Redfern & Minter, which is frequently associated with *I. cembrae*, and *Ceratocystis polonicum* (Siemaszko) C. Moreau, which is frequently associated with *I. typographus*. *Ceratocystis laricicola* has been recorded only in association with *I. cembrae*, but *Ceratocystis polonicum* has been recovered from multiple species of Scolytidae (Table 3). Although *I. typographus* has not yet been reported to have established outside of its native range, its potential for establishment, along with that of its associated fungi, cannot be discounted: other species of *Ips* and their associated fungi have established beyond their native ranges. For instance, the *I. cembrae* – *C. laricicola* insect–pathogen association has been accidentally introduced into Scotland (31, 110), as has *Ips grandicollis* (Eichhoff) and associated blue-stain fungi in Australia (55, 100, 129).

Multiple species of fungi (range varies from 5 to 19 species) are associated with each of the 9 species of bark beetle documented in Table 3, with the greatest number associated with *I. typographus*. With the exception of *Ophiostoma cucullatum* Solheim and two recently described species from Japan, *Ophiostoma aenigmaticum* K. Jacobs, M.J. Wingf. & Yamaoka and *Ophiostoma japonicum* Yamaoka & M.J. Wingf., all fungi associated with *I. typographus* have been associated with other intercepted Scolytidae or Cerambycidae (e.g., *O. tetropii*, with *Tetropium fuscum*). The lack of fidelity between bark-beetle vectors and associated fungi may allow nonindigenous fungi not only to be vectored to coniferous or deciduous hosts by introduced bark- or wood-boring beetles, which themselves fail to establish, but to be transferred subsequently to native species using the same hosts. Such transfers can create novel vector–pathogen relationships (e.g., the introduced pathogens *O. ulmi* and *O. novo-ulmi* vectored in North America by the native bark beetle *Hylurgopinus rufipes* (Eichhoff)). Because knowledge of pathogenicity of nonindigenous fungi to potential tree hosts in Canada is inadequate, consequences of such introductions are difficult to predict. Christiansen and Solheim (28) demonstrated the pathogenicity of *Ceratocystis polonicum* to Sitka spruce (*Picea sitchensis* (Bong.) Carrière), white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and in separate experiments showed that only one of the Scandinavian blue-stain fungi (*Ceratocystis polonicum*) tested was pathogenic to Douglas-fir (29). No mortality was evident in Douglas-fir inoculated with *Ophiostoma bicolor* Davidson & Wells, *Ophiostoma minus* (Hedgcock) H.& P. Sydow, *Ophiostoma pencillatum* (Grosm.) Siemaszko, and

Table 2. Level of identification and numbers of genera and species of wood borers intercepted in Canada, from 1997 to 2000.

Taxon	Level of identification: Family or subfamily	Genus	Species	No. of genera	No. of species	No. of interceptions
Coleoptera						
Anobiidae	11	4	4	4	3	19
Bostrichidae	10	10	92	9	11	112
Buprestidae	9	3	1	4	1	13
Cerambycidae	49	70	101	28	28	220
Lyctidae	0	4	2	1	2	6
Oedemeridae	1	—	—	—	—	1
Platypodidae	4	6	3	2	2	13
Scolytidae	6	26	104	25	42	136
Hymenoptera						
Siricidae	17	2	7	3	4	26
Total	107	125	314	76	92	546

Ophiostoma piceaperdum (Rumbold) Arx (= *Ophiostoma europhioides* (Wright & Cain) Solheim) (65).

Other vectored organisms

Fungal pathogens may be the best-known potential threats to Canada's forests, but they are not the only organisms vectored by nonindigenous bark- and wood-boring beetles. Moser et al. (101, 102) have documented more than 24 species of phoretic mites associated with *I. typographus* in Sweden and Japan. Five mite species were recovered only from Japan, 13 were unique to Swedish populations, and seven were common to both regions. Of the 12 mite species recovered from Japan, all but two were found to carry spores of one or more species of fungi, including *O. bicolor*, *O. piceaperdum* (as *O. europhiodes*), *Ceratocystiopsis minuta* (Siemaszko) Upadhyay and Kendrick, *O. penicillatum*, *O. piceae*, and *Ceratocystis polonicum*.

Because of their small size and cryptic habits, organisms such as phoretic mites and nematodes associated with bark beetles and wood borers are usually overlooked. The diversity, systematics, and ecology of phoretic associates are poorly known, making it difficult to determine either geographic origin of species recovered in association with bark- and wood-boring beetles, or potential impacts of introduction of any mite taxon. At least one of the species recovered from *I. typographus* in Japan, *Trichouropoda hirsutsa* Hirschmann, is a North American species commonly associated with bark beetles and *Monochamus* wood borers and likely represents an introduction to Japan (102). Similarly, Lindquist and Hunter (91) note that *Proctolaelaps ulmi* Hirschmann was likely introduced to British Columbia in association with the European wood-boring weevil *Cryptorhynchus lapathi* (L.) from which it has been recovered. Klepzig et al. (83) and Lombadero et al. (93) document the complex ecological interactions and dependencies between the southern pine beetle and its associated fungi and phoretic mites. At least two of the three species of stain fungi associated with southern pine beetle (*O. minus* and *Ceratocystiopsis ranunculosus* Perry and Bridges) are carried in specialized structures (sporothecae) by phoretic tarsonemid mites (*Tarsonemus ips* Lindquist and *Tarsonemus krantzii* Smiley and Moser) and can be introduced into phloem by mites. Indeed, these phoretic mites are the most important determinant of colonization by *O. minus* (93). As Moser et al. (102) also note, mites that are phoretic on *Ips typographus japonicus* (Niisima) can apparently transmit *Ceratocystis polonicum*. To adequately understand the associated quarantine risks, further evaluations of the ability of phoretic mites to vector plant-pathogenic fungi need to be undertaken.

Knowledge of the diversity, systematics, and ecology of nematodes vectored by introduced bark- and wood-boring beetles is equally limited. Both mites and nematodes may be phoretic on the same individuals. Indeed, the majority of the nematodes species associated with bark beetles are phoretic (95) and can be abundant. Moser et al. (102) reported that all of the *I. typographus japonicus* adults trapped in one sample from Japan contained large numbers of phoretic nematodes under their elytra. Species of the genus *Bursaphelenchus* (Nematoda: Aphelenchoidea) are common associates of bark- and wood-boring beetles and depend on fungal growth for survival (9, 95). Approximately 50 species of *Bursaphelenchus* have been described, with about 60% and 18% of species recorded from coniferous and deciduous trees, respectively. One species, the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickle, is considered to be a serious coniferous forest pest because of its pathogenicity to *Pinus*.

Examples of the development of novel vector relationships with phoretic nematodes can be found. In each region of the world in which the pine wood nematode has established, it is vectored by congeneric counterparts of its North American *Monochamus* vectors (27, 84, 87, 92, 122, 144, 145). The European nematode, *Bursaphelenchus leoni* Baujard, has established in South Africa on a novel host, *Pinus radiata* D. Don (9), in the absence (141, 14, 15) of its only known vector, *Dryocoetes autographus* (10). It is unclear whether *B. leoni* was transferred to *Pinus radiata* by an introduction of *Dryocoetes autographus* that then failed to establish in South Africa or was vectored by other introduced bark-beetle species (e.g., *Hylurgus ligniperda*

Table 3. Fungal associates of the species of Scolytidae intercepted in Canada between 1997 and 2000 (see 22), the region in which the vector–pathogen associations were identified, and the occurrence of the fungi in North America.

Associated fungus*	Species of Scolytidae intercepted†									Region‡	Present in N. America¶	References
	Da	Ha	Hp	Ia	Ic	It	Oe	Pc	Pp			
Ambrosiella macrospora				+						Eu		112
Atractocolax pulvinatus	+		+			+		+		CH, DE		81
Bjerkandera adusta						+				FI	+	133
Ceratocystiopsis minuta					+	+	+			RU(s), JP, **CL**	+	62, 105, 142, 143, 150, 151
Ceratocystis laricicola					+					**UK**, RU(s), JP		53, 110, 112, 143
C. polonicum					+	+		+	+	FI, NO, RU(s), JP		40, 53, 85, 105, 106, 119, 133, 142
Chionosphaera cuniculicola	+		+	+		+		+	+	Eu, CH, DE, IT		82
Dipodascus aggregatus				+						SE	+	36
Graphium fimbriisporum	+		+			+		+	+	AT, DE, FR		68
G. laricis					+					AT, UK		68
G. pseudormiticum							+			AT, DE, ZA		68
Leptographium guttulatum	+	+	+			+				UK, AT, FR		52, 63, 67, 89, 97
L. lundbergii		+	+	+			+			Eu, UK, JP, **ZA**, **NZ**	+	52, 63, 67, 97, 98, 109, 136, 138, 148
L. procerum		+	+							Eu, UK, **NZ**	+	52, 67, 89, 136, 138
L. wingfieldii			+							FR, NO, UK	+	63, 67, 70, 136
Ophiostoma aenigmaticum						+				JP		64
O. aoinoae					+	+				FI, NO, RU(s), JP		85, 105, 119, 133, 142
O. bicolor					+	+		+	+	FI, NO, JP, RU(s)	+	40, 85, 105, 106, 120, 133, 142
O. brunneociliatum				+	+					FR, JP		44, 49, 89, 143
O. clavatum				+						DE,SE		36, 97
O. cucullatum						+				NO, JP		120, 142
O. galeiformis	+	+	+							**CL**		151
O. fusiforme					+					AT, AZ		2
O. huntii		+								**AU, NZ, CL**	+	63, 64, 151
O. ips		+		+	+		+			FR, **NZ**, RU(s), **ZA**, **CL**	+	89, 97, 98, 105, 109, 148, 149, 150, 151
O. japonicum						+				JP		142
O. laricis					+					JP		63, 130, 133, 143
O. lunatum					+					AT		2
O. minus		+			+					Eu, RU(s)	+	62, 98, 105
O. minutum	+		+	+		+		+	+	Eu, JP, ZA	+	62
O. neglectum	+	+	+			+		+	+	DE		62, 80
O. pencillatum		+	+			+		+	+	DE, FI, NO, SE, RU(s), JP	+	40, 52, 62, 63, 80, 85, 97, 98, 106, 133, 142
O. piceae		+	+		+	+		+		FI, NO, RU(s), JP	+	68, 85, 97, 98, 105, 133, 142, 143, 149
O. piceaperdum			+			+		+	+	NO, DE, FI, RU(s), JP	+	52, 63, 85, 106, 120, 133, 142
O. piliferum					+					SE, RU(s)	+	105, 151
O. quercus		+								**CL**	+	151
O. serpens		+					+			Eu, **ZA**		52, 63, 85, 136, 137
O. tetropii						+				AT, FI, SE	+	120, 133
Phialocephala trigonospora	+		+			+				DE		79

*Fungal authorities: *Ambrosiella macrospora* (Francke-Grosm.) L.R. Batra; *Bjerkandera adusta* (Willd.) P. Karst.; *Ceratocystiopsis minuta* (Siemaszko) Upadhyay & Kendrick; *Ceratocystis laricicola* Redfern & Minter; *C. polonicum* (Siemaszko) C. Moreau; *Chionosphaera cuniculicola* R. Kirschner, Begerow & Oberw.; *Dipodascus aggregatus* Francke-Grosm.; *G. laricis* K. Jacobs, T. Kirisits & M.J. Wingf.; *G. pseudormiticum* M. Mouton & M.J. Wingf.; *Leptographium guttulatum* M.J. Wingf. & K. Jacobs; *L. lundbergii* Lagerb. & Melin; *L. procerum* (W.B. Kendr.) M.J. Wingf.; *L. wingfieldii* M. Morelet; *Ophiostoma aenigmaticum* K. Jacobs, M.J. Wingf. & Yamaoka; *O. aoinoae* Solheim; *O. bicolor* Davidson & Wells; *O. brunneo-ciliatum* Mathiesen-Käärik ; *O. clavatum* Mathiesen; *O. cucullatum* Solheim; *O. fusiforme* Aghayeva & M.J. Wingf.; *O. galeiformis* (B.K. Bakshi) Math.-Käärik; *O. huntii* (R.C. Rob.) de Hoog & R.J. Scheff.; *O. ips* (Rumbold) Nannf.; *O. japonicum* Yamaoka & M.J. Wingf.; *O. laricis* K. van der Westh., Yamaoka & M.J. Wingf.; *O. lunatum* Aghayeva & M.J. Wingf.; *O. minus* (Hedgcock) H.& P. Sydow; *O. neglectum* Kirschner & Oberwinkler; *O. pencillatum* (Grosm.) Siemaszko; *O. piceae* (Münch) H. & P. Sydow; *O. piceaperdum* (Rumbold) Arx; *O. piliferum* (Fries) H. & P. Sydow; *O. quercus* (Georgev.) Nannf.; *O. tetropii* Mathiesen.

†Da, *Dryocoetes autographus* (Ratzeburg); Ha, *Hylastes ater* (Paykull); Hp, *Hylurgops palliatus* (Gyllenhal); Ia, *Ips acuminatus* (Gyllenhal); Ic, *Ips cembrae* (Heer); It, *Ips typographus* (L.); Oe, *Orthotomicus erosus* (Wollaston); Pc, *Pityogenes chalcographus* (L.); Pp, *Polygraphus poligraphus* (L.).

‡AT, Austria; AZ, Azerbaijan; CBS, unknown; CH, Switzerland; CL, Chile; DE, Germany; Eu, Europe; FI, Finland; FR, France; JP, Japan; NO, Norway; RU(s), Russia (Siberia); RU(w), Russia (western); SE, Sweden; UK, United Kingdom; ZA, South Africa. Where the identified pathogen is known to be an introduction in a country, the country abbreviation is boldface.

¶Based on Farr et al. (35) and primary references cited.

(Fabricius) or *Hylastes angustatus* (Herbst)) with which it has not yet been found in association in Europe.

With other nematode species, the origin of the nematode–vector association cannot be ascertained. Massey (95) described *Bursaphelenchus scolyti* Massey among nematodes recovered from the lesser European elm bark beetle, *S. multistriatus*, attacking *Ulmus americana* (L.) in the US. *Bursaphelenchus scolyti* is known to occur only in the US and has not been found in association with *S. multistriatus* or other *Scolytus* species vectoring Dutch elm disease in Europe (60, 61, 72, 113). Because recent research has demonstrated that as with the pine wood nematode, other species of *Bursaphelenchus* can be also be pathogenic to conifers (8, 11, 114), more attention needs to paid to organisms vectored by intercepted and introduced bark beetles and wood borers.

Enhancing the biosecurity of Canada's forests

Recent establishments of pine shoot beetle, brown spruce longhorn beetle, emerald ash borer, and Asian longhorned beetle in eastern North America have focussed attention on the role of untreated wood packaging in the dissemination of insect pests around the world. Although considerable regulatory effort has been directed at determining the beetle fauna associated with wood packaging materials, little attention has been paid to their associated microfauna and flora. For instance, although the presence of *Tomicus piniperda* (pine shoot beetle) was first recognized in the US in 1992 and in Ontario in 1993 (21, 46), the first evaluations of its associated fungal complex were not available until 2004. Not surprisingly, a pathogenic European bluestain fungus, *L. wingfieldii*, was discovered in Vermont and Michigan in the US, and in southern Ontario in Canada in both native and introduced pines and has already transferred to transcontinental native vectors (70). The ability of *Tomicus piniperda* to develop in pine species that are widespread in western and southern North America was assessed by Eager et al. (32); however, no assessment of the impacts of *L. wingfieldii* has been conducted. The association of this introduced pathogen with native vectors provides a mechanism for the transfer of the fungus to native pine species, which, in themselves, may be less suitable as hosts for *Tomicus piniperda*. Thus, native pines that are less likely to be directly impacted by *Tomicus piniperda* (32) may still be affected by the introduced pathogen vectored by native bark beetles. Without a clear understanding of the pathogenicity of *L. wingfieldii* to pine species native to North America and of the efficiency of native and exotic bark beetle species in vectoring the fungus, development of regulatory policies to prevent the expansion of *Tomicus piniperda* and *L. wingfieldii* to uninfested regions of Canada and the US will be hampered.

The genetic relatedness of *Tomicus piniperda* populations was analyzed by Carter et al. (17) soon after the beetle was first discovered in North America. Their data suggest that at least two independent introductions took place, with one population originating in ports along the southern shores of Lake Erie and subsequently spreading east and west, and a second population evident in Illinois likely originating near the southern tip of Lake Michigan. As the fungal associates of *Tomicus piniperda* have not yet been evaluated across the beetle's introduced range in the US and Canada (no evaluations were conducted in Illinois, see 70), additional fungal pathogens may already be established. Additionally, no evaluations have as yet been completed for pathogenic nematodes associated with this or any other introduced scolytid. The single nematode species associated with *Tomicus piniperda*, *Bursaphelenchus sexdentati*, (Table 1) has been demonstrated to be pathogenic to Mediterranean pine species and is implicated in the development of pine wilt in Greece (114).

A significant diversity of vectored organisms is associated with the nonindigenous bark- and wood-boring beetles that either have established or been intercepted in Canada. However, a much greater diversity of insect species has established or been intercepted in other areas of North America. Fifty species of nonindigenous bark and ambrosia beetles are known to be established in the US: at least 24% of these have arrived since 1990 (5, 45). Similar to the situation in Canada, little research or regulatory effort has been focused on organisms vectored by these introductions. At least one species, the banded elm bark beetle (*Scolytus schevyrewi* Semenov), is highly invasive and has the potential to exacerbate Dutch elm disease management in North America, as it appears to be more aggressive than the disease's primary North American vector, *S. multistriatus* (5). The ability of banded elm bark beetle to vector Dutch elm disease has yet to be evaluated.

Host–vector–pathogen relationships: research opportunities

It is important to understand the diversity and pathogenicity of vectored organisms associated with Holarctic and naturalized nonindigenous species to ensure that appropriate regulatory policies be developed to prevent their establishment and spread. The diversity of potential pathogens vectored by insects associated with the global movement of live plants and solid wood packaging poses a significant challenge to quarantine agencies around the world. Incomplete knowledge of pathogen communities associated with native and exotic vectors, limited evaluations of introduced and intercepted vectors for presence of pathogens, incomplete understanding of the fidelity of vector–pathogen relationships, and inability to predict a priori the impacts of novel vectored organisms each contribute uncertainty in the development of phytosanitary policy. Evaluation of native or exotic fungal communities associated with specific vectors of concern, as well as systematic revisions of fungal taxa of concern using DNA-based identification tools, can provide both increased taxonomic resolution and the sequence data necessary for the development of rapid diagnostic tests for vectored fungi. DNA-based population studies of pathogens (16, 115, 116, 134) and vectors (17) would also provide insight into the origins and movements of pathogens in international trade. Many scolytid vectors have now established at multiple locations beyond their native ranges and are associated with different fungal pathogens in different regions of the world (151). Knowledge of the origins of vector populations, in turn, would help determine potential pathogens associated with novel introductions. However, the risks to our forests by such vectored pathogens will not be adequately understood until evaluations of pathogens associated with incursions and establishments of nonindigenous bark beetles and wood borers are initiated. Ongoing studies of native fungal communities (e.g., 77) and exotic fungi associated with vectors of quarantine concern continue to discover novel species of pathogens (64, 78, 142, 147) and vectors (90), even in well-studied vector–pathogen systems. The diversity of vectored organisms associated with native, naturalized, and exotic insects identified in this review suggests that additional invasive pathogens may be established in Canada, and that further research needs to be directed towards identifying both fungi present and their potential impacts.

Research and the development of regulatory policy

Regulatory approaches for naturalized populations of nonindigenous species often differ significantly from those for species not yet established in the country. In Canada, federal regulatory controls exist to prevent the introduction of additional populations and the spread of existing populations of recent introductions considered to be major forest pests such as *Anoplophora glabripennis* (25), *Agrilus planipennis* (23), *Tetropium fuscum*, and *Tomicus piniperda* (20). Federal controls also exist to prevent additional introductions of species in association with high-risk commodities (26). However, with the exception of regulations in Alberta against *S. multistriatus*, as part of the province's Dutch elm disease exclusion policy (19), interprovincial regulation of movement of long-established nonindigenous species is generally nonexistent. Surveys to better understand the diversity of pathogens vectored by established nonindigenous species must be undertaken before the risk to regions of Canada in which the insects do not yet occur can be assessed and appropriate regulatory policies developed.

The development of appropriate quarantine policies to protect forest resources is inhibited by a paucity of information regarding all aspects of vectored-pathogen biology and ecology. This lack of knowledge can lead to ineffective quarantine regulations or to regulations that are more restrictive than would be necessary if adequate information were available. The presence of a significant introduced fauna of bark and ambrosia beetles in the forests of Canada offers opportunity for the development of studies to evaluate the incidence and importance of novel vector–pathogen relationships and thereby deliver scientific information useful to the development of effective regulatory policies at both national and international levels. Evaluation of pathogens associated with North American insect vectors that have established in other parts of the world (e.g., *Dendroctonus valens* in China (146)) should also be undertaken to assess potential for introduction of novel pathogens in conjunction with such native species that would not be recognized as pests of quarantine concern by regulatory agencies. These and related research needs should be addressed through the development of strong national and international collaborations to assess vector–pathogen relations and their ecological impacts in native and novel forest environments.

Towards a solution: ISPM No. 15

An ongoing challenge lies in developing methods of preventing movement of these organisms, thereby avoiding the need to respond at all. In an effort to control the international movement of invasive pests, the FAO (United Nations Food and Agriculture Organization) based Interim Commission on Phytosanitary Measures adopted a global standard for treating wood packaging material, ISPM No. 15 (Guidelines for regulating wood packaging material in international trade), in 2002 (34). This standard will, when effectively implemented, significantly reduce phytosanitary risks associated with imported wood packaging material.

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