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ORIGINAL PAPER

Diversity of non-native terrestrial arthropods on woody plants in Canada

David W. Langor · Laura J. DeHaas · Robert G. Foottit

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Abstract A list of non-native phytophagous insects and mites on woody plants (trees, shrubs, vines) in Canada was compiled using information from literature and input from taxonomists. The 419 recorded species include Hemiptera (53% of species), Lepidoptera (22%), Coleoptera (13%) and Hymenoptera (9%). Almost all species originate from the Palearctic, especially Europe, reflecting historical trade patterns. About 41% of species were directly introduced to Canada from countries of origin, and the remainder spread from the United States of America (USA) after initial establishment there. Major ports on the east and west coasts, on Lake Erie and Lake Ontario are the main points of entry for exotic species directly introduced, and southern British Columbia (BC), Ontario (ON) and Quebec (QC) are the major points of entry for species spreading from the USA. Consequently, BC, ON, QC and Nova Scotia have the highest diversity of non-native species, and the prairie provinces and northern territories have the lowest. The extent of the distribution of individual species is related to length of time in Canada, number of introductions and dispersal abilities. Almost all native woody plant genera in Canada have been invaded by exotic phytophages. The large majority of phytophages occur on angiosperms. Woody plant genera with the largest distribution, highest species diversity and highest local abundances tend to host the greatest number of non-native species, including *Picea*, *Pinus*, *Malus*, *Prunus*, *Salix*, *Betula*, *Quercus*, *Pyrus* and *Populus*. The arrival rate of species in Canada increased from the late nineteenth century until about 1960, and declined rapidly thereafter. Quarantine legislation enacted in the USA in 1912 and in Canada in 1976 seems to have reduced the rate of insect invasion.

Keywords Exotic species · Invasive arthropods · Insects · Mites · Woody plants · Invasion pathways · Exotic species database

Introduction

Since the discovery and colonization of North America by Europeans over 500 years ago, there has been an increasing invasion of the continent by plants, animals and fungi from other regions of the globe (Sailer 1983; Stuckey and Barkley 1993; Hendrickson 2002). However, it is only relatively recently that the scale, extent and impacts of invasion

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D. W. Langor (✉) · L. J. DeHaas
Natural Resources Canada, Canadian Forest Service, 5320-122 Street, Edmonton, AB, Canada T6H 3S5
e-mail: dlangor@nrcan.gc.ca

R. G. Foottit
Agriculture and Agri-Foods, Ottawa, ON, Canada

by alien species have been given full appreciation. Despite the increasing concern about the adverse effects of invasive alien species (Krcmar-Nozic et al. 2000; Pimentel et al. 2000; Colautti et al. 2006), there are large information gaps concerning this significant component of North American biota. For example, the species introduced by modern humans into North America have not been adequately catalogued. The best known groups include the vertebrates and vascular plants. In Canada, about 20–27% of the ca. 5,800 species of vascular plants are alien, and the distribution of most species is well known (Haber 2002). However, there is a relative dearth of information about species-rich, taxonomically challenging and poorly surveyed groups such as terrestrial arthropods, fungi (Yarwood 1983), nematodes and micro-organisms, and among these groups, the arthropods are certainly best known.

Of the estimated 50,000 non-native species that have been introduced to the United States (including Hawaii), only about 4,500 (9%) are arthropods (Pimentel et al. 2000). Of the arthropods, only about 2,000 are estimated to occur in the continental United States (Pimentel et al. 2000). This is likely a large underestimate. Turnbull (1979) stated that he had produced a list of 301 alien insect species in Canada, but this list was never published. Many species lists and taxonomic monographs produced in Canada over the last 25–30 years have provided indications of which species were not native to Canada. For example, Bousquet (1982) tallied 469 non-native Coleoptera species in a total Canadian fauna of 7,447 species (i.e., 6.3% of species introduced), and Maw et al. (2000) tallied 337 non-native species of Hemiptera in a total fauna of ca. 3,900 species (i.e., 8.6% of species introduced). Recent efforts have tallied about 1,900 non-native terrestrial arthropods in Canada (Langor, unpublished data), and this number will likely exceed 2,000 by the time ongoing assessments are completed. Thus, non-native species account for approximately 3.2% of the insect fauna and 4.7% of the spider fauna of Canada (Biological Survey of Canada 2007a; Langor, unpublished data). Other groups such as mites are too poorly known to make a reasonable estimate of the percent of the fauna represented by non-native species.

Among the non-native terrestrial arthropods in Canada, a large proportion feed on woody plants. Some of these are among the most notorious invasive alien species in Canada, as indicated by the amount of recent media coverage, and include the gypsy moth, *Lymantria dispar* (L.), Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky), brown spruce longhorned beetle, *Tetropium fuscum* (Fabricius) and the emerald ash borer, *Agrilus planipennis* Fairmaire. Hendrickson (2002) listed 180 species of alien insects established on woody plants in Canada, and this list was based largely on the data provided by Mattson et al. (1994). However, many species were overlooked by Hendrickson (2002) and several species have been detected in Canada since that time. To provide a foundation for future syntheses of data concerning distribution, spread and impact of alien species in Canada, herein we provide a synopsis of known non-native terrestrial arthropods feeding on woody plants in Canada.

Methods

An initial list of alien species feeding on woody plants (trees, shrubs, vines) in Canada was developed by exhaustive literature searches (covering literature published up to December 2007), and especially by perusal of species lists, catalogues and taxonomic treatments of the Canadian fauna. This list was then vetted widely among arthropod taxonomists, especially those in Canada and the USA, and was modified based on feedback from experts. The species list on which the analyses are based is included as Appendix A—see Electronic supplementary material. We included only species that feed on living plants and excluded species associated exclusively with dead wood.

For each species we sought out the following data through consultation of literature and taxonomic experts: common names; synonyms; current distribution in Canada, and current North American and global distribution; region of origin (Africa, Palearctic-Europe, Palearctic-Asia, Palearctic-Eurasia, South America); location and date of first report of the species in North America and in Canada; pathway of introduction (directly to Canada, indirectly via the USA, or unknown); known and preferred hosts in Canada, in the USA and in its native range; and preliminary notes on pest status, control measures, natural enemies, and life history.

Alien arthropod species were classified as ‘directly introduced to Canada’ if reported in the literature as

such, reported in Canada before being reported in the USA (i.e., dates and locations of first reports are known for both countries), or reported as having been directly introduced into Canada as well as spreading from the USA. Arthropods were classified as 'indirectly introduced' if reported as spreading into Canada from the USA or reported as introduced into the USA (location and date of first report known) and also found in Canada, but the method (and usually date) of introduction into Canada is unknown. Many of these species probably spread into Canada from the USA.

The current provincial and territorial distribution of non-native species was determined based on literature records and by examination of specimens in the six regional collections of the Canadian Forest Service and the Canadian National Collection.

Results

Diversity of non-native species

A total of 419 non-native species (416 insects and three mites) are recorded from woody plants in Canada (Appendix A—see Electronic supplementary material), consisting mainly of Hemiptera (53% of species), Lepidoptera (22%), Coleoptera (13%) and Hymenoptera (9%). Other insect orders with representatives are Diptera and Thysanoptera. Seven of those species present in Canada are not yet recorded from woody plants there; however, they commonly infest woody plants in their native range and are highly likely to occur on woody plants in Canada. These species are included in analyses. As well, 44 non-native species are recorded from woody plants in adjacent parts of the United States but have not yet been recorded from Canada, although some of these likely have already spread into Canada without our knowledge. These species were not considered herein.

Of the 223 species of introduced Hemiptera, most species (65%) are in the suborder Sternorryhncha, dominated by aphids (Aphidoidea) and scales (Coccoidea), but also including Psyllidae and Phylloxeroidea (Fig. 1a). Clypeorrhyncha represent 21% of species, mainly leafhoppers (Cicadellidae), but also spittlebugs (Cercopidae). The 55 species of non-native Coleoptera on woody plants are dominated by weevils (69%), especially bark beetles in the subfamily Scolytinae (27% of total beetle species) (Fig. 1b). All of the 38 species of Hymenoptera feeding on woody plants are Symphyta, dominated by sawflies in the Tenthredinidae (79% of taxa) and Diprionidae (11%) (Fig. 1c). Among the 91 species of Lepidoptera on woody plants, the vast majority of species are micro-Lepidoptera, especially Tortricoidea (34%) and Gelechoidea (19%), and the dominant macro-Lepidoptera are Noctuoidea (12%) (Fig. 1d).

The non-native species are divided into three feeding guilds. The majority (54%) of the non-native fauna are sap feeders, reflecting the dominance of Hemiptera; however, this guild also contains two species of thrips (Thysanoptera) and three species of mites (Acarina). Bark-and wood-feeders (including external feeders on roots and gall makers on twigs) represent 12% of the Canadian fauna, and 84% of the species in this guild are Coleoptera, dominated by weevils and bark beetles (Curculionidae) and long-horned beetles (Cerambycidae). However, this guild also includes two species of Hymenoptera and six species of Lepidoptera. Foliovores (including gall-makers on leaves and bud-feeders) represent 34% of the overall fauna, including Lepidoptera, Hymenoptera, Coleoptera and Diptera.

Sources and geographic patterns of establishment

The vast majority of non-native species on woody plants originated from the Palearctic, especially from Europe (82% of all species). Of the 380 species on woody plants whose origins are known only two originate from a region other than the Palearctic: *Ischnaspis longirostris* (Signoret) (Hemiptera: Diaspididae) from Africa, and *Pinnaspis aspidistrae* Signoret (Hemiptera: Diaspididae) from the Oriental Region.

There are two pathways of entry for non-native species into Canada: direct introduction from the country of origin, and indirect introduction via spread from the USA after being directly introduced there. Of the 372 species of non-native species whose pathway of entry is known or suspected. about 41% (152 species) were directly introduced into Canada. It is thought that the largest proportion of non-native species (220 species) were first introduced to the USA and subsequently spread to Canada. For many

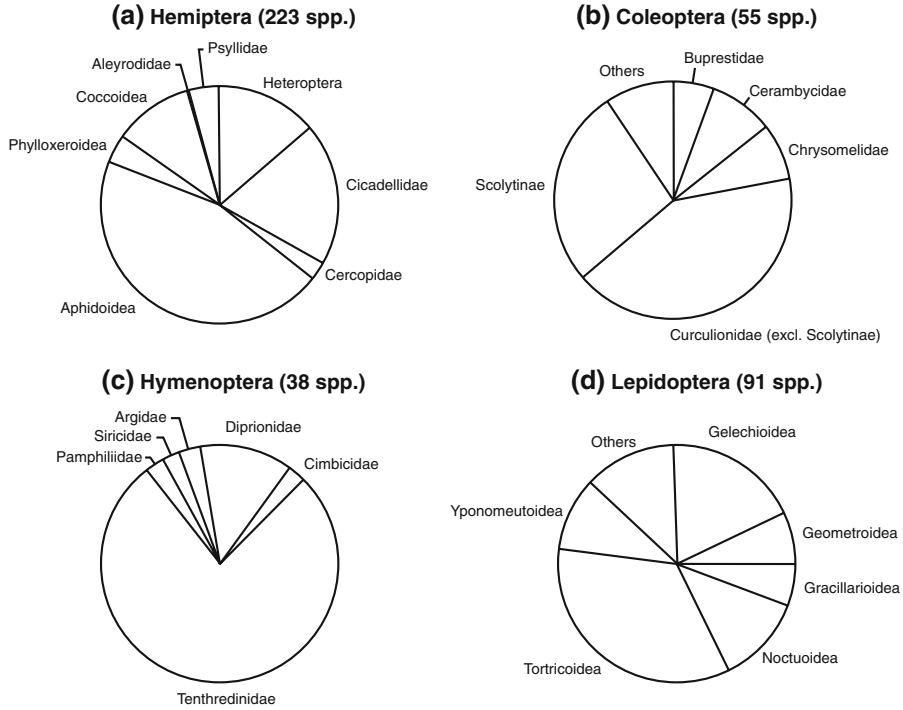

Fig. 1 Taxonomic composition of major orders of non-native insects on woody plants in Canada. (**a**) Hemiptera, (**b**) Coleoptera, (**c**) Hymenoptera, (**d**) Lepidoptera

species it is very difficult to retrace pathways of entry, especially for those introduced a long time ago and that are now present in both countries.

Analysis of the geographic points of entry for non-native species provides an indication of which parts of the country are most susceptible to invasion. Overall, most species were first detected in Ontario (ON, 28%), British Columbia (BC, 25%), the maritime provinces (12%) and Quebec (QC, 9%) (Fig. 2). Very few species were first detected in the prairie provinces and north (1.2%) and Newfoundland and Labrador (NL, 2.9%). Of the 152 species believed to have been directly introduced to Canada, 40% were first recorded in BC, 21% in the maritimes, 19% in ON, 12% in QC, 6% in NL and 2% in the prairie provinces and north (Fig. 2). It is clear from examination of specific locality records that the areas where most direct introductions occur are: the lower Fraser Valley of BC (at least 30 species introduced); the southern portion of Vancouver Island, BC (at least 11 spp.); southern ON, especially the western area of Lake Ontario, north shore of Lake Erie, and Niagara Peninsula (at least 16 spp.); St. John's, NL (at least 7 spp.); and Halifax, Nova Scotia (NS, at least 6 spp.). A substantially different pattern of introduction is discernable for species that were likely indirectly introduced to Canada via spread from the USA; the largest proportion were first detected in ON, especially southern ON (33%), followed by BC, especially the lower Fraser Valley (16%), southern QC (7%), the maritimes (7%), the prairie provinces and north (1%) and NL (1%) (Fig. 2).

Distribution of non-native species in Canada

BC has the highest diversity of non-native insects and mites on woody plants in Canada (270 species), followed by ON (263), QC (217) and NS (181) (Fig. 3). The Canadian north (Yukon [YK], Northwest Territories [NT], Nunavut [NU] and Labrador [LB]) have been colonized by very few species. The three prairie provinces (Alberta [AB], Saskatchewan [SK] and Manitoba [MB]) have the lowest non-native diversity of all the provinces, even lower than that of the tiny province of Prince Edward Island (PE).

A plot of the range (number of occupied provinces and territories) by the number of non-native species best fits a log normal distribution (Fig. 4). About 29% of species have a limited distribution (one jurisdiction), and only 57 species are found in more than half of the political jurisdictions of Canada. The

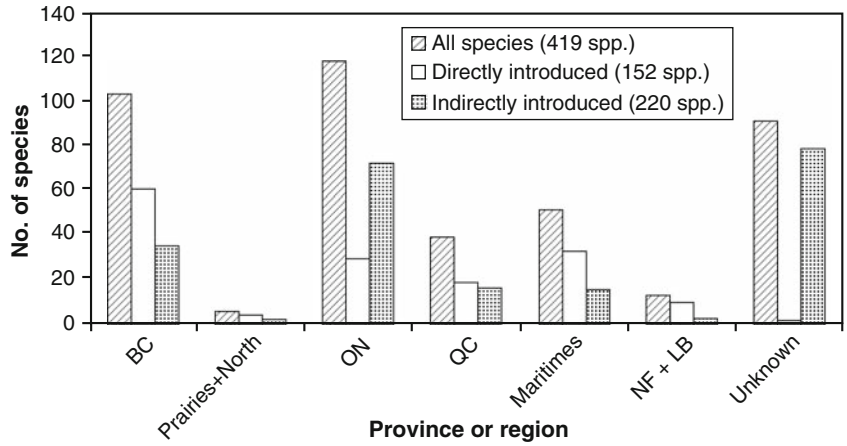

Fig. 2 Points of first entry for non-native insects and mites on woody plants in Canada. Species were either directly introduced from the country of origin, or indirectly introduced via spread from the USA after being directly introduced there. Province abbreviations: BC, British Columbia; ON, Ontario; QC, Quebec; NF + LB, Newfoundland and Labrador

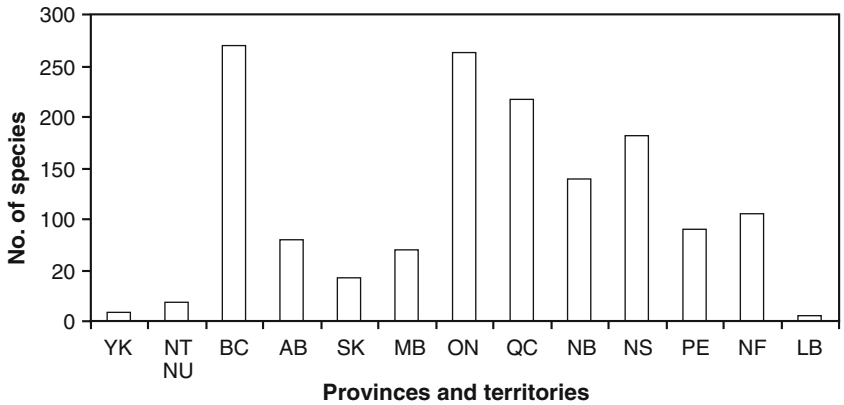

Fig. 3 Number of non-native insects and mites on woody plants in each province and territory of Canada. Province and Territory abbreviations: YK, Yukon; NT, Northwest Territories; NU, Nunavut; BC, British Columbia; AB, Alberta; SK, Saskatchewan; MB, Manitoba; ON, Ontario; QC, Quebec; NB, New Brunswick; NS, Nova Scotia; PE, Prince Edward Island; NF, Newfoundland (insular); LB, Labrador

regression between the length of time that a species was resident in Canada and its geographic range (no. of provinces and territories in which it is present) was significant ($r^2 = 0.246$; $P < 0.0001$) indicating that geographic range is positively influenced by length of time that a species has been in Canada (Fig. 5).

The overall number of non-native species in each major insect order, as well as the proportional representation of each order in provincial and territorial faunas, varies across the country (Fig. 6). Of the 223 species of non-native Hemiptera on woody plants in Canada, 70% are found in BC and 58% in Ontario. In all provinces, Hemiptera represented the highest number of non-native species, and proportional representation of the non-native fauna ranged from 39% in NL to 57% in BC. Hemiptera were uncommon in the north. Of the 55 species of non-native Coleoptera, QC and ON each had 76% of the species followed by NS (60%) and BC (47%). Coleoptera comprised a higher proportion of the faunas in ON, QC and the maritime provinces (16–21%) than elsewhere in Canada. Although there are only 38 species of non-native Hymenoptera feeding on woody plants in Canada, 89% occur in ON and 82% in QC. Proportionate representation of non-native fauna by Hymenoptera is highest in the north (37–44%) and in SK (21%), and lowest in the maritimes (8–9%). Of the 91 species of Lepidoptera, 72% are found in BC and 60% in ON. As a proportion of provincial faunas, Lepidoptera exhibit much less variation across the country (16–30%) than other major orders.

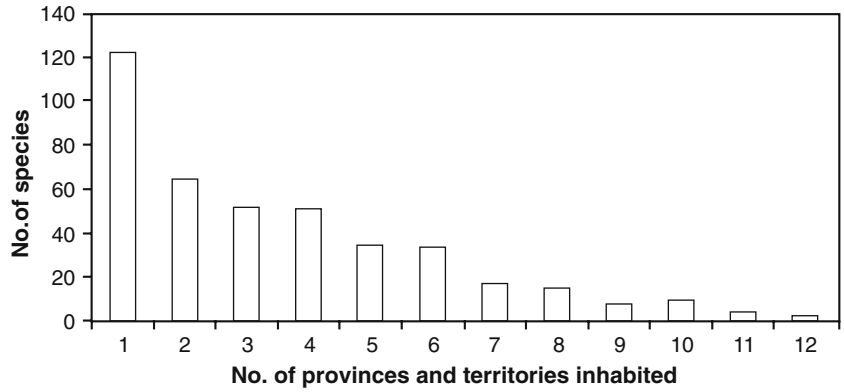

Fig. 4 Number of provinces and territories inhabited by non-native insect and mite species on woody plants in Canada. Records for Nunavut and the Northwest Territories are combined

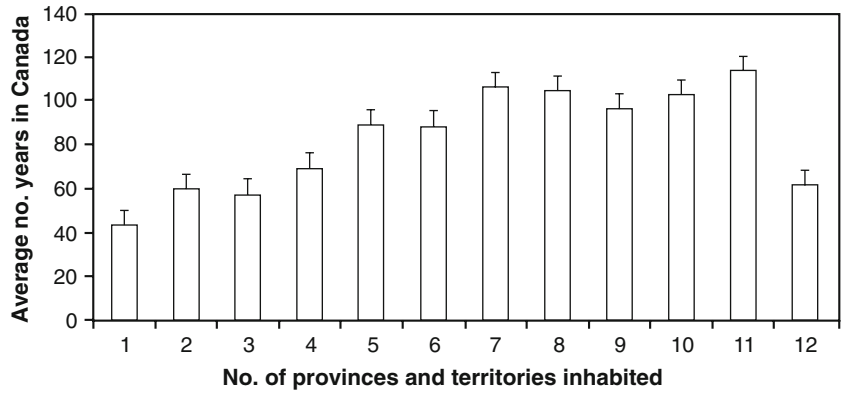

Fig. 5 Mean (SE) number of years of residency for non-native species on woody plants in relation to geographic range in Canada. Records for Nunavut and the Northwest Territories are combined

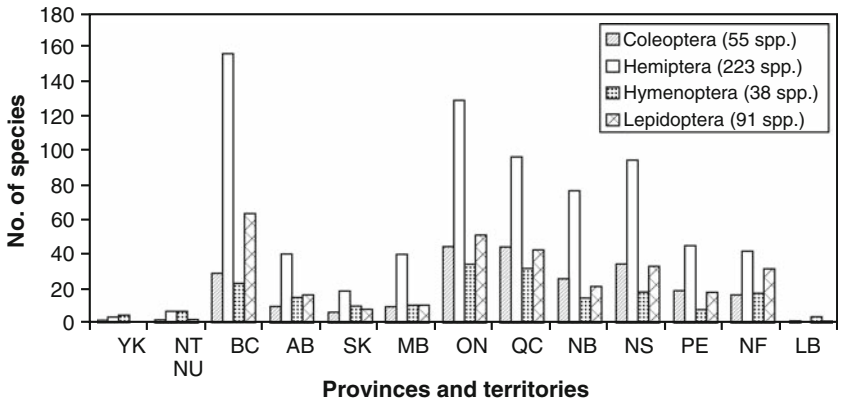

Fig. 6 Distribution of four major orders of non-native insects on woody plants in Canada. For province and territory abbreviations, see caption for Fig. 3

The number of species in each feeding guild also varied among provinces and territories (Fig. 7). Of the 50 species of bark- and wood-feeders, the greatest number of species were in the faunas of ON (38), QC (34), NS (27) and BC (26). Only one species, the strawberry root weevil, *Otiorhynchus ovatus* (L.), was found in the north. The prairie provinces had 4–8 species in their faunas. The proportional representation of provincial and territorial faunas by bark- and wood-feeders varied relatively little, ranging from 5% in the Northwest Territories (NT) and Nunavut (NU) to 16% in QC. Of the 227 species of sap feeders (almost all Hemiptera), BC has the most species (141), followed by ON (132). Only seven species are found in the northern territories, and, among the provinces, the sap-feeding faunas of the prairie provinces are most depauperate. In terms of proportionate representation within provincial and territorial

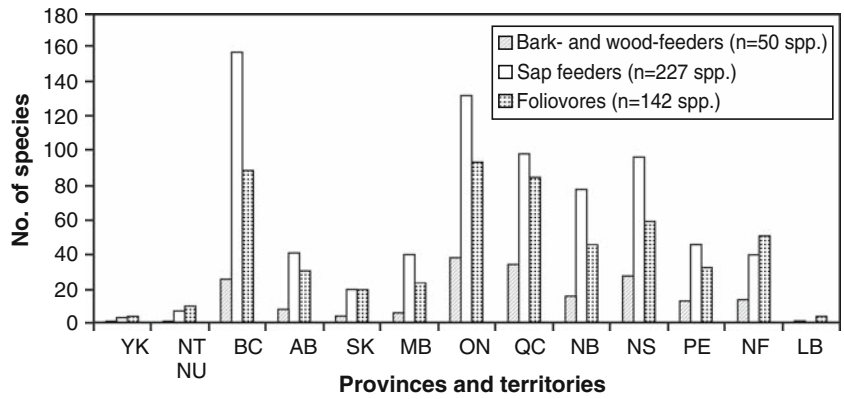

Fig. 7 Distribution of non-native insects and mites on woody plants in Canada by type of feeding damage. For province and territory abbreviations, see caption for Fig. 3

faunas, sap feeders are most dominant in BC (59% of fauna); however, proportional representation is also high in other provinces, ranging from 38% in NL to 57% in MB. There are no non-native sap feeders recorded from LB. Of the 142 species of foliovores, most are found in ON (93), BC (87) and QC (85). Foliovores are the dominant feeding guild in the northern territories and LB, representing 57–80% of the non-native faunas there. Among the provinces, the foliovore faunas of the prairie provinces are most depauperate, and proportional representation ranges from 32% in NS to 49% in NL.

Host range

The majority of non-native species (326 species) are found only on angiosperms, 59 species are found exclusively on gymnosperms and 34 species feed on both gymnosperms and angiosperms (Fig. 8). In terms of breadth of diet, 195 are stenophagous (feed on a single woody plant genus), 85 are oligophagous (on three or fewer genera) and 139 are polyphagous (on more than three genera) (Fig. 8). Stenophagous and oligophagous species are proportionately more abundant on gymnosperms (58 and 27% of species, respectively) than on angiosperms (49 and 20%). A high proportion of angiosperm-feeders are polyphagous (31%), but polyphagy is present in only 15% of gymnosperm-feeding species.

Of the 93 species that feed on gymnosperms, the greatest number of species are found on *Pinus* (54 spp.) and *Picea* (47 spp.) (Appendix B—see Electronic supplementary material). Of the 360 species that feed on angiosperms, the greatest number are found on genera of fruit trees, *Prunus* (85 spp.), *Malus* (79 spp.) and *Pyrus* (63 spp.). Other angiosperms with rich faunas of non-native species are *Salix* (73 spp.), *Betula* (72 spp.), *Quercus* (62 spp.) and *Populus* (59 spp.).

Temporal pattern of colonization

Of the 419 species of non-native insects and mites feeding on woody plants in Canada, approximate

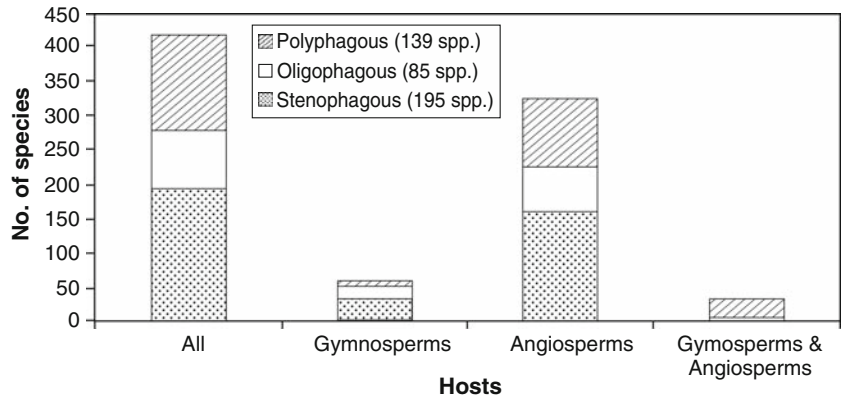

Fig. 8 Host range of non-native insects and mites on woody angiosperms and gymnosperms in Canada

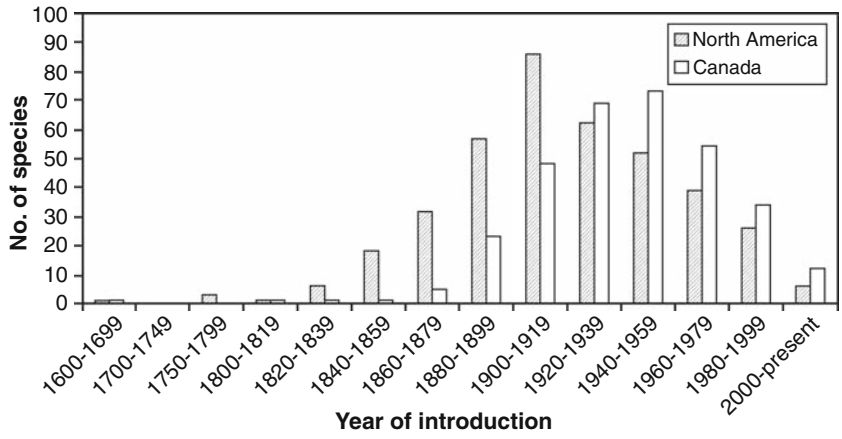

Fig. 9 Year of first introduction into North America and into Canada for non-native insects and mites on woody plants

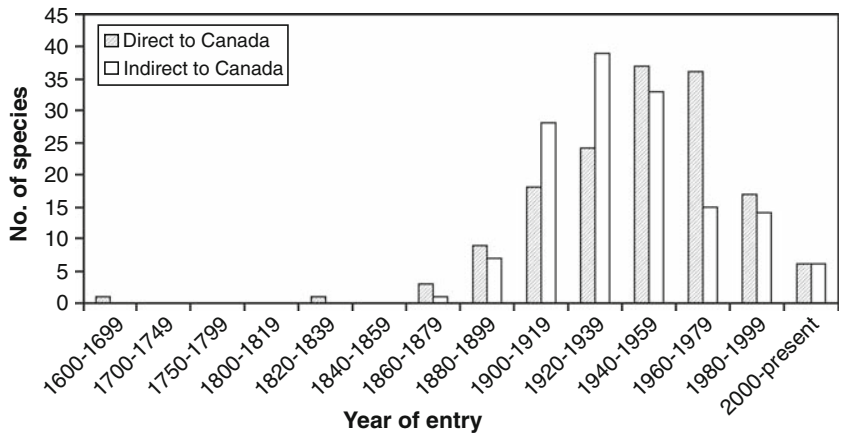

Fig. 10 Year of introduction into Canada for directly and indirectly introduced species of insects and mites on woody plants

times of arrival in North America have been estimated for 389 species. Only 11 of those species are recorded from North America before 1840 (Fig. 9). The earliest record is the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), which was recorded from apple trees in Ontario in 1635. After 1840, the rate of introduction of species into North America increased rapidly, peaking between 1900 and 1919. Thereafter, the rate of introduction declined steadily. A similar temporal pattern of colonization is evident for Canada, although the period of rapid colonization did not commence until later (1880–1899) and peaked later (1940–1959) than for North America as a whole (Fig. 9).

The temporal pattern of introduction also differs for those species directly introduced to Canada from countries of origin compared to those species that were indirectly introduced to Canada via spread from the USA (Fig. 10). The number of species that indirectly reached Canada peaked between 1920 and 1939, and declined rapidly thereafter. The number of species that were directly introduced to Canada peaked in 1940–1979, followed by a rapid decline.

Discussion

Diversity

Clearly the number of established non-native insect and mite species feeding on woody plants in Canada and the United States is much higher than previously recorded. The most recent list of non-native insect species feeding on woody plants in Canada is that of Hendrickson (2002), who tallied 180 species, largely extracted from the list provided by Mattson et al. (1994) for North America. Thirteen species listed in

the current database were introduced into North America (including Canada) since the publication of Mattson et al. (1994), but only one of those was included by Hendrickson (2002). As well, about 40 species listed by Mattson et al. (1994) as present in the USA but not in Canada are, in fact, known from Canada. About 225 species of non-native species in our database were not recorded by Mattson et al. (1994) even though they were present in North America before 1990. About 150 of the new records are Heteroptera and the large majority of those records have recently come to light due to detailed faunistic analyses (Maw et al. 2000; Miller et al. 2002, 2005; Miller and Miller 2003; Foottit et al. 2006; Scudder and Foottit 2006). Finally several species listed by Mattson et al. (1994) and Hendrickson (2002) as phytophagous on woody plants in Canada were not included in our list as they feed on only seasoned wood (five species) or are native (three species). Combining current work with that of Mattson et al. 1994, there are at least 585 species of non-native insects feeding on woody plants in the USA and Canada. As well, we catalogued three species of phytophagous mites on woody plants, and these have not yet been tallied for the USA.

Cataloguing the non-native species in Canada is perpetually a work-in-progress because: species invasion is a dynamic process with new species arriving on a regular basis; there is a dearth of knowledge about the composition of major components of the Canadian fauna (native and introduced species); and our knowledge of the native distribution of species is still evolving (e.g., some species thought to be introduced may be Holarctic). As knowledge of the Canadian and Nearctic fauna improves, there is little doubt that the list of non-native arthropod species on woody plants will grow.

The overwhelming dominance of Hemiptera (53% of species) among the non-native species on woody plants is striking. Overall, Hemiptera is estimated to represent about 6% of the native insect fauna of Canada (Biological Survey of Canada 2007a), but approximately 23.5% of the total non-native insect and arachnid fauna of Canada (Langor, unpublished data) and 24.4% of the non-native insects and arachnid fauna of the 48 contiguous states of the USA (Sailer 1983). More notably, Hemiptera represents 45% of the non-native phytophagous insect species in Canada (Langor, unpublished). There are several possible reasons why the Hemiptera, and especially the Sternorrhyncha (aphids and scales), have been the most successful phytophagous insect invaders. A high percent of aphid and scale species are parthenogenetic (Niemelä and Mattson 1996). Parthenogenetic capacity is a valuable trait for colonizing species and those inhabiting patchy or ephemeral habitats because it allows continual propagation even at low population levels. Parthenogenesis also promotes, more rapidly than sexual species, adaptation through random mutations (Ledig 1992). No wonder that about 40% of the non-native insects on woody plants in North America exhibit parthenogenesis, whereas only about 11% of the native species are parthenogenetic (Niemelä and Mattson 1996). The success of aphids and scales may also be related to their small size (especially their eggs) which may allow them to more easily escape detection than larger, more conspicuous insects. The success of cicadellid leafhoppers and mirid bugs cannot be explained by parthenogenesis; however, these groups generally have endophytic oviposition which may more easily allow eggs to escape detection during inspection. As well, many mirids are both phytophagous and predaceous (Wheeler and Henry 1992), which increases the niche/food options in new environments.

The high diversity of Curculionidae among the non-native Coleoptera on woody plants may also be attributed to the fact that a large number (at least 100 species) of European weevils are parthenogenetic (Lanteri and Normark 1995; Niemelä and Mattson 1996). Also, Curculionidae is the most species-rich family of beetles, so it is not unexpected to see this family well represented in the non-native fauna. Some weevils, especially those, such as *Otiorhynchus* spp., that feed on plant roots and spend much time in the soil, were likely introduced in ships ballast (Lindroth 1957). Root inhabiting insects also easily escape detection because of their cryptic habits. It is notable that a high percentage of the non-native Coleoptera are bark- and wood-feeders, and many of these species were inadvertently brought into North America on solid wood packing material (Allen and Humble 2002; Haack 2006; Humble and Allen 2006).

Among the non-native Hymenoptera (all of which are Symphyta, and can reproduce with only females), tenthredinid sawflies are the dominant family, and this likely just reflects the fact that this is the most diverse family of Symphyta in the northern

hemisphere. Although the diversity of non-native Hymenoptera on woody plants in Canada and the USA is much lower than that of other orders such as Hemiptera, Coleoptera and Lepidoptera, symphytans currently and historically represent many of the most notorious, widespread and destructive invasive species in Canadian forests. The remarkable success of sawflies in North American forests may be related to the fact that there are relatively few other sawfly competitors on Nearctic woody plants. In Europe there is a much higher diversity of sawflies per woody plant species (ca. five) than in North America (ca. one) (Neuvonen and Niemelä 1983; Haack and Mattson 1993). The combination of parthenogenetic abilities, low interspecific competition with native sawflies, the apparent abundance of unexploited or under-exploited niches and the general absence of specialist parasitoids common in their native range, have allowed populations of many sawfly species to quickly explode on reaching North American shores (Haack and Mattson 1993). Species such as the European pine sawfly, *Neodiprion sertifer* (Geoffroy), introduced pine sawfly, *Diprion similis* (Hartig), European spruce sawfly, *Gilpinia hercyniae* (Hartig), pine false webworm, *Acantholyda erythrocephala* (L.), larch sawfly, *Pristiphora erichsonii* (Hartig), European apple sawfly, *Hoplocampa testudinea* (Klug), and five leaf-mining sawflies on birch have been among the most damaging non-native insects on woody plants in Canada (Armstrong and Ives 1995). Fortunately, some of these have been brought under successful control by implementation of classical biological control programs (Mason and Huber 2002).

Lepidoptera is the second largest order among the non-native fauna. The micro-Lepidoptera represents the large majority of introduced species in both Canada and the USA (Mattson et al. 1994), likely because they easily escape detection due to their small size and cryptic habits (many are miners of leaves, buds or twigs). Among the non-native macro-Lepidoptera, the Noctuidae and Geometridae are best represented in the Canadian fauna, likely simply reflecting that fact that these are the most diverse families of macro-moths and the odds of their introduction are simply proportional to their relative composition in the native fauna of the Palearctic (the source of all non-native Lepidoptera in Canada).

The apparent poor representation of Diptera and Acarina among the non-native fauna of Canada is likely somewhat artificial. Of all the major groups of phytophagous arthropods, these two are the most poorly surveyed and studied in North America. There are likely many more non-native species in the Canadian fauna than we realize at this time. As many of these species are small and cryptic in habits (e.g., leaf, stem and twig miners), they are easily able to escape detection during inspection.

Sources of invaders and points of entry

The geographic origins and points of entry of non-native arthropods on woody plants in Canada tend to largely reflect human colonization and trade patterns. All but two species of the 419 species known from Canada originate from Palearctic, 82% of them from Europe. This is not surprising as, historically, the overwhelming source of colonists and trade for Canada, excepting the USA, was Europe. Over the last 20 years, as trade with Asia (particularly China) increased dramatically (Asia Pacific Gateway 2007), the proportion of non-native species originating from Asia increased to at least 19% of newly introduced species compared to 6.7% before this period. As the USA has had a much greater volume of trade and immigrants with the Europe and northern Asia than Canada, it is not surprising that most of the Palearctic arthropods introduced to North America first arrived there. Consequently, about 60% of the non-native insect and mite species in Canada are thought to have arrived (naturally or aided by humans) via the United States. As well, some species directly introduced to Canada have also spread to the USA (Sailer 1983). This inadvertent exchange of non-native species between Canada and the USA clearly argues that both countries need to continue to work together in developing policies concerning invasive alien species.

As a large portion of the historical and current trade between Canada and the Palearctic was via ship, it is the major shipping ports that served as the point of entry for the majority of species: Halifax and St. John's on the east coast; Vancouver and Victoria on the west coast; and the Great Lakes, especially ports on Lake Ontario. The interior areas of Canada, such as the prairie provinces, have not been important entry points for exotic species. However, with the

large increase in source-to-destination container shipping in recent years, it may be expected that increasingly areas of Canada far from ports may be sites of new introductions (Allen and Humble 2002).

Current distribution

Herein we only coarsely describe the distribution of non-native species, i.e., at the provincial and territorial level. Ongoing work to database specimen records in the collections of the Canadian Forest Service, the Canadian National Collection of Insects, and selected university collections (Langor, unpublished) will soon allow more detailed distribution maps to be generated, and permit spatial and temporal analyses of invasion patterns and species spread. Clearly BC, ON, QC, and NS are the areas with the highest diversity of non-native species. To a large extent this pattern is a reflection of the main points of entry (i.e., ports) for many of the species directly introduced to Canada. As well, southern parts of these provinces are where species spreading from the USA most commonly enter Canada. Southern BC, ON and QC also have the highest diversity of woody plants in Canada, which maximizes habitat options for newly introduced species. Unsurprisingly, the most depauperate areas (the prairie provinces and the territories) are those furthest from major points of introduction.

It is expected that the longer the period of time a species has been present in Canada, the wider its distribution should be, and indeed this relationship is evident and significant. As well, current distribution is undoubtedly influenced by the number of independent introduction events and the geographic spread of distribution points. Rate of spread of a species will also be affected by natural dispersal abilities, capacity to establish populations from a small number of immigrants (i.e., parthenogenetic versus sexual reproduction) and presence of suitable hosts. Many introduced species are also inadvertently spread by humans. For example, commercial tree nurseries have been very important in aiding the spread of birch leafmining sawflies (Langor et al. 2000).

Knowledge of the current distribution of non-native species is not equivalent for all areas of the country, nor for all taxonomic groups. Hemiptera are best surveyed in ON and BC where most recent and current taxonomists working on this order were located. Historically, most coleopterists working in Canada were located in the eastern half of the country, and this area is likely best known, especially ON and QC. There are ongoing projects to inventory the beetles of the maritime provinces (Majka 2007) and NL (Biological Survey of Canada 2007b). The Symphyta are best known for ON, QC and the prairie provinces, as these are areas where taxonomists have been most recently active with collecting efforts. However, for the five species of exotic birch leafmining sawflies there has been a recent extensive survey of much of Canada, resulting in many new provincial records (Digweed and Langor, unpublished data), and this effort showed that there were large gaps in our knowledge about distribution even for species that we putatively know well. The macro-Lepidoptera has received much taxonomic and inventory focus throughout most of Canada, and this is one of the best known groups of insects in Canada. The distributions of non-native micro-moths are not nearly as well known. Similarly, there is a dearth of information about distribution of non-native Diptera and mites.

Host range

The high degree of taxonomic affinity (at the generic level) between European and North American woody plants (Huntley 1993) figures largely in the remarkably successful invasion of Canada by European phytophagous insects. In general, non-native insects and mites have colonized the same genera of woody plants in Canada that are hosts in their native range. However, in some cases, species have colonized host genera that have been extinct from Europe since the Pleistocene, e.g., *Taxodium*, *Thuja*, *Tsuga*, *Carya*, *Liriodendron*, *Magnolia*, *Robinia* and *Sassafrass* (Niemelä and Mattson 1996). Niemelä and Mattson (1996) suggest that some of the phytophagous insect fauna of tree genera that went extinct in Europe were able to adapt and persist on con-familial relatives. Some of these host-switching survivors may maintain the genetic capacity to recolonize their pre-Pleistocene relatives.

Woody plant genera with the widest distribution and highest local abundance within its range tend to have the greatest diversity of phytophages (Strong et al. 1984). While this has certainly been shown to be a common pattern for native phytophages, it also appears to hold up for non-native faunas. Among

gymnosperms, *Picea* and *Pinus* are the most widespread, diverse and locally abundant genera in Canada (Farrar 1995), and these also have the most diverse faunas of non-native phytophages. For angiosperms, *Malus*, *Prunus*, *Salix*, *Betula*, *Quercus* and *Populus* had the most diverse non-native fauna, and these are among the most widespread and abundant genera in Canada. It was notable that *Pyrus* also had a highly diverse fauna, even though this genus is large localized and abundant in only in a few fruit-growing regions of Canada. It seems that commercial fruit trees (*Pyrus*, *Malus* and *Prunus*) have been especially susceptible to invasive insects.

Many European woody plant species have been planted throughout Canada, especially in urban areas (Farrar 1995). The presence of their native hosts likely aids the establishment of some non-native phytophages. For example, the successful establishment of the pine shoot beetle, *Tomicus piniperda* (L.) in the Great Lakes region appears to have been aided by the presence of its native host, Scots pine, *Pinus sylvestris* L. (Niemelä and Mattson 1996).

Almost all native woody plant genera in Canada have been invaded by non-native phytophages. The only genera that appear to be spared thus far are *Cephalanthus*, *Gymnocladus*, *Hamamelus*, *Nyssa*, *Toxicodendron* and *Zanthoxylum*. In fact, it would not be surprising if these genera have also been attacked by non-native insects or mites but have thus far escaped attention. Angiosperms host 3.5 times more non-native phytophagous insects than gymnosperms. This is to be expected as angiosperms are much more diverse and have more diverse faunas in both Europe and North America (Strong et al. 1984). Phytophages on angiosperms also tend to be much more polyphagous than those on gymnosperms (Strong et al. 1984).

Temporal pattern of colonization

Estimation of the date of arrival of a non-native species is difficult even for species introduced relatively recently, let alone for those introduced centuries ago, even before the advent of modern taxonomy. Nonetheless, historical literature (e.g., diaries and almanacs) at times draws attention to pestiferous species on crops (Sailer 1983). The earliest record is the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), which was recorded from apple trees in Ontario in 1635.

As well, dating of insects found in old latrines can give insights into approximate arrival times of some species (Bain and LeSage 1998).

Examination of the dates of arrival in North America for the 419 non-native species on woody plants in Canada yielded a pattern virtually identical to that reported by Sailer (1983) for the almost 1,500 non-native species of insects then known from North America. Very few species were present before about 1840, and those were largely imported on crops, in ballast or on animal dung (Sailer 1983). After 1840, the rate of introduction of species into North America increased rapidly, largely through the accidental introduction of phytophagous insects and mites as the importation of foreign plants came into vogue in the mid-nineteenth century. The rate of introduction of non-native arthropods into the USA peaked between 1900 and 1919. The marked reduction in the rate of species introduction after 1920 likely reflects the deterrent effect of the Plant Quarantine Act which was enacted in 1912 (Sailer 1983). A similar temporal pattern of colonization is evident for Canada, although the period of rapid colonization did not commence until later (1860–1879) and reached a peak later (1940–1959) than for North America as a whole. Clearly the temporal pattern of colonization of Canada by non-native phytophages was influenced by the policies of the USA. Most of the earliest species introduced to Canada spread from the USA, and the enactment of the 1912 Plant Quarantine Act resulted in a decrease in species arriving in Canada via spread from the USA. However, the species introduced directly to Canada did not decline noticeably until the 1980s. In 1976 Canada enacted the Plant Quarantine Act, which more strictly regulated importation of exotic species. It may be that this legislation has been effective in reducing the rate of direct species introductions to Canada, and possibly the spread of exotic species from Canada to the USA.

The future

Canada and the USA will continue to receive new non-native species through direct accidental importation from other countries (Work et al. 2005; McCullough et al. 2006), albeit hopefully at an ever-decreasing rate. Legislation in the USA (1912 Plant Quarantine Act) and Canada (Plant Quarantine

Act of 1976) has apparently aided the fight against invasive species in North America, and it is clear that legislation and policies in each country will have implications for both countries. The North American Forestry Commission should continue to play a central role in fostering communication within North America concerning non-native species on trees. Furthermore, in Canada, federal regulatory controls have been adopted to prevent the introduction of new populations and spread of existing populations of non-native tree-feeding species such as the Asian longhorned beetle, the brown spruce longhorned beetle, the emerald ash borer, and the pine shoot beetle as well as inadvertent introduction of species associated with high-risk commodities, such as those requiring solid wood packaging (Canadian Food Inspection Agency 2007). The new international standards for treating wood packaging material (FAO 2002) should significantly reduce phytosanitary risks associated with such packaging materials, a known mode of entry for many non-native bark-and wood-boring insects in Canada (Humble and Allen 2001). However, as only a small proportion of shipping containers arriving from international destinations are ever inspected, and as containers can be moved practically anywhere in Canada before they are opened (Allen and Humble 2002), there are still many opportunities for non-native species to continue to invade Canada.

There is a large number of non-native species on woody plants in the northern USA that have not yet been collected in Canada. Undoubtedly, many or all of these will eventually spread northward. Some of the most important recent introductions into Canada have come via the USA, including the emerald ash borer and the pine shoot beetle. The most recent known introduced insect on trees, the banded elm bark beetle, *Scolytus schevyrewi* Semenov, was just detected in southern Alberta in 2006 and likely came across the border (possibly aided by humans) from the USA where it has been established for several years (Haack 2006). It may be that this species will vector Dutch Elm Disease and will be an important complicating factor in the fight against DED in Canada and the USA (Negrón et al. 2005).

An under-appreciated and underestimated threat associated with non-native phytophagous insects and mites is the potential danger posed by organisms vectored by these arthropods. For example, many introduced bark and wood-boring beetles have fungi associated with them (Hausner et al. 2005), and some of those fungi are potentially phytopathogenic. Some fungi introduced in association with non-native insects may also be transferred to native insect species that also serve as vectors (Jacobs et al. 2004). As well, aphids are well-known plant virus vectors (Chan et al. 1991). Humble and Allen (2006) argue persuasively that effective management of invasive insect species also requires a detailed understanding of their role as vectors of other organisms.

Detection and identification of non-native arthropod species (and associated species of fungi, viruses, etc.) is simply not possible without access to extensive taxonomic expertise (Huber and Langor 2004). Many introduced species, especially those from the Palearctic, have closely related species in Canada. Attempting to identify non-native species using existing keys to Nearctic species will often not allow non-specialists to realize that they have a non-native species in hand, and will lead to a misidentification and a failure to recognize a new introduction. For example, *Tetropium fuscum* was consistently misidentified as a native species for 10 years before it was recognized by an expert as a Palearctic species (Huber and Langor 2004). Continued investment in taxonomic research, regional and national faunistic inventories and maintenance of reference collections of native and non-native species is essential to maintaining domestic capacity to identify new biotic threats to Canada.

The sources of information about non-native species on woody plants in Canada are numerous. Specimens residing in Canadian collections provide information about presence (place and time) of non-native species, which is useful for assessing patterns and rates of spread. As well, specimen labels often contain host information. Since the early 1930s until the mid-1990s, the Canadian Forest Service (CFS)-Forest Insect and Disease Survey (FIDS) has routinely collected information about species affecting woody plants, and this information was published annually in regional and national reports. These reports contain a lot of information about notable invasive insects and fungi. In the near future the CFS will make those reports available in a searchable electronic format via the Internet. Many specimen and damage collections made by FIDS were accompanied by enclosure slips that contained an

abundance of ancillary information about damage symptoms, habitat and population levels. This information has been databased and is available for searches and analyses. A large number of web sites currently have information about non-native biota of North America, and most contain information relevant to species in Canada (Ricciardi et al. 2000; Crall et al. 2006). However, many of these are superficial and often do not do justice to the non-native biota of Canada, especially as regards distribution, phenology and hosts. Numerous journal papers and gray reports have been produced in Canada and the USA concerning non-native species, and many of those have extensive information about the biology, impacts, host, distribution and management of invasive species. As well, the taxonomic and faunistics literature contains a wealth of information about distribution, hosts and identity of non-native species. The Internet provides better access to published information than has ever previously been experienced, but still fails to capture (and certainly does not summarize or synthesize) much information concerning non-native species. A current initiative lead by the CFS aims at creating a one-stop-shop web site for information about invasive phytophagous arthropods and fungi on trees in Canada (Langor, unpublished). Clearly, the combined goals of protection of Canada against future invasions and minimization of the effects of current invasions, along with the development of science and policy to aid achievement of those goals, requires ready access to and synthesis of the most current information about non-native species. The catalogue of non-native insects and mites on woody plants will provide a key part of the foundation for development of this integrated information resource.

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