3 Exotic Bark and Ambrosia Beetles in the USA: Potential and Current Invaders

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3.1 Introduction

Bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are among the most important insects affecting trees and forests worldwide. There are approximately 6000 scolytine species worldwide, with species found on all continents except Antarctica (Table 3.1) (Wood and Bright, 1992; Bright and Skidmore, 1997, 2002; Wood, 2007). The majority of species are found in the tropics, but many also occur in boreal forests. Undoubtedly, there are hundreds of additional species that have not yet been described. Many authorities now consider the bark and ambrosia beetles a subfamily (Scolytinae) of the weevil family (Curculionidae) (Alonso-Zarazaga and Lyal, 2009), while others continue to treat them as a distinct family (Wood, 2007). In this chapter, we will use the subfamily ranking Scolytinae, but recognize that most plant protection agencies worldwide continue to use Scolytidae.

Although adults of all scolytine species bore into their host to lay eggs, they exhibit many different habits and utilize many different host tissues. True bark beetles bore through the outer bark to the phloem–cambial area where they construct characteristic galleries and lay eggs. Larval mines radiate out from the gallery as the larvae feed on the phloem (phloeophagous). Ambrosia beetle adults bore through the bark and into the xylem (wood) where they lay eggs. Ambrosia beetle adults and larvae cultivate and feed on symbiotic ambrosia fungi that grow in the galleries (xylomycetophagous). Most scolytine species in tropical regions exhibit the ambrosial habit, while most scolytines in temperate forests are true bark beetles. There are also a number of species that breed in seeds, cones, roots of woody plants, and stems and roots of non-woody plants (Wood, 1982; Sauvard, 2004).

Most species of bark and ambrosia beetles live in injured, weakened or dying woody plants, and are often among the first insects to colonize such host material (Haack and Slansky, 1987; Sauvard, 2004). A few species aggressively attack healthy trees, and during outbreaks cause extensive mortality of their host trees. Efficient host location is important, and is often mediated by olfactory responses to host odors, tree degradation products, or conspecific pheromones (Byers, 2004). Pheromones are used to attract potential mates, and in some scolytines are also used to mass attack host trees to overcome host resistance (Byers, 2004; Raffa *et al.*, 2008).

Mating systems and social organization vary among scolytines. Reproductive systems range from simple monogamy (one male with one female), to heterosanguineous polygyny (multiple members of one sex with one, unrelated member of the opposite sex), to consanguineous polygyny (multiple members of one sex with one,

Table 3.1. Approximate number of scolytine species worldwide and the number of those classified as ambrosia beetles by geographic area.

Continent or geographic area[a]	Approximate number of scolytine species[b]	
	Total	Ambrosia beetles[c]
Africa	1140	260
Asia	1920	500
Australia	130	50
Europe	230	25
North America	1700	400
South America	1250	450
Pacific Islands	220	100
Worldwide	6000	1800

[a]Geographic regions follow Wood and Bright (1992), Europe and Asia are divided by Ural Mountains, Asia includes Indonesia and Philippines, Africa includes Madagascar, North America includes Antilles Islands and Central America to Panama, New Zealand is included with Australia.
[b]Totals for each geographic area include all species in the region, not just the endemic species, therefore the sum of all world regions is greater than the worldwide totals.
[c]Ambrosia beetles are all genera in the tribes Corthylini, Hyorrhynchini, Premnobini, Scolytoplatypodini, Xyleborini, Xyloterini, and the genus *Camptocerus*.

related member of the opposite sex) (Wood, 1982; Kirkendall, 1983). Social organization ranges from parental care, to colonial breeding, and eusociality with division of labor and reproduction (Crespi, 1994; Kirkendall *et al*., 1997).

The cryptic nature of scolytines, along with their wide variety of mating systems, host finding behaviors, and abilities to utilize different host tissues, allow them to be very successful in their native habitats as well as efficient invaders of new habitats (Wood, 1977, 1982; Haack, 2001; Roques *et al*., 2009; Sauvard *et al*., 2010). Ecologically and economically, these beetles are a very important group. In North America, various members of *Dendroctonus* kill vast expanses of forests each year. The current outbreak of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, has killed c. 18 million acres (7.3 million ha) of pine (*Pinus*) forests across the western USA, and a similar acreage in western Canada (Raffa *et al*., 2008; USDA Forest Service, 2010). In Europe, the spruce bark beetle, *Ips typographus* (Linnaeus), historically has been the major pest of spruce (*Picea*), resulting in extensive areas of tree mortality (Wermelinger, 2004). Other species vector pathogenic fungi that cause tree diseases, for example the bark beetle *Scolytus multistriatus* (Marsham), which vectors the causal agents of Dutch elm disease (Evans and Finkral, 2010). Ambrosia beetles, and their associated fungi, often cause stain and degrade of valuable wood products, and in some cases, the fungal associates may be highly pathogenic to new hosts (Fraedrich *et al*., 2008). In this chapter, we will: (i) summarize recent US interceptions of scolytines with a focus on those that were intercepted in association with wood; (ii) discuss the 58 scolytine species that were known to be established in the continental USA as of 2010; (iii) briefly discuss the biology and impact of the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff; and (iv) discuss current international efforts aimed at reducing the international movement of exotic plant pests.

3.2 Scolytine Interceptions on Wood from 1984 to 2008

Since 1984, the United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) has maintained an electronic database for plant pests intercepted at US ports of entry (Haack, 2001, 2006; McCullough *et al*., 2006). At first, this database was known as the Port Information Network, or PIN, but is now called the Pest Interception Database, or PestID. The internal policies of every country influence how cargo is inspected and which interceptions are recorded. In the USA, not all interceptions are entered into PestID, but rather there is a bias towards pests of live plants that are considered of quarantine significance. This policy has affected the number and types of scolytine interceptions recorded over the years. For example, because true bark beetles more often infest live trees than do ambrosia beetles, it is more likely that interceptions of bark beetles will be entered into PestID than will interceptions of ambrosia beetles. In addition, given that Canada and the USA share many insect species, few interceptions from Canada are ever considered of quarantine importance and entered into PestID. For example, of the 195 scolytine species recorded in Canada, only five are unique to Canada, while 190 are also present in the USA (Wood and Bright, 1992; Bright and Skidmore, 1997, 2002). It is important to remember these policies when examining the interception data discussed below.

In our analysis, we used PestID interception records for scolytines associated with wood for the 25-year period from 1984 through 2008. The data set consisted of 8286 records. Note, that our data set did not include all scolytines, such as those found in food items like coffee and nuts (Haack, 2001), but rather focused on those associated with wood in the form of wood packaging material (e.g., crating, pallets and dunnage), lumber and logs. Of the 8286 interceptions, 3446 (42%) were identified to the species level; 2239 (27%) to only the genus level; and 2601 (31%) to only the family level (Table 3.2). In the discussion below, these 8286 interception records are presented as a means of suggesting which scolytines are most likely to invade the continental USA; however, it is important to realize that the pool of potential invaders will change in relation to changes in trading partners, types of imported products and the tree species utilized to manufacture wood packaging material.

3.3 Continent of Origin

Scolytines from eight continents or world regions were intercepted on wood in the USA from 1984 to 2008 (Table 3.2). For each interception record, we assigned the corresponding country of origin to a continent in a manner similar to that used in Haack (2001, 2006), which is slightly different to the world regions used in Table 3.1 in this chapter. For example, for the data that follow, we assigned all interceptions from Russia and Turkey to Asia, Mexico to Central America, and Australia and New Zealand to the Pacific region. Most of the 8286 interceptions originated in Europe (48%), Central America (32%) and Asia (15%) (Table 3.2). Overall, 46 genera and 107 species were identified among the intercepted scolytines (Table 3.2). The diversity of intercepted scolytines was greatest for Asia and Europe (Table 3.2); however, keep in mind that USDA APHIS historically identified more bark beetles than ambrosia beetles. The five scolytine genera that represented the most interceptions from each continent are given in Table 3.2.

Over the 25-year period from 1984 to 2008, the annual number of wood-associated scolytine interceptions was highest in 1985 (647 interceptions), then decreased during the 1990s (low of 161 in 1991), and increased again in the 2000s (high of 517 in 2002; Fig. 3.1). Note that the number of interceptions shown for 1984 is artificially low because the electronic PestID database actually began midway through 1984. The strong reduction in overall interceptions during the late 1980s and 1990s was related to a dramatic decline in interceptions from Europe (Fig. 3.1). By contrast, the increase in interceptions during the 2000s was primarily the result of more interceptions from Central America, especially Mexico (Fig. 3.1).

There are many factors that influence changes in interception rates (Haack, 2001). For example, exporters can change the type or quality of packaging materials they use, or they can treat the wood prior to export. Importing countries can also influence interception rates by changing their inspection policies, import regulations and major trading partners. For example, during the 1990s, the USA implemented two regulations on wood packaging material that likely affected interception rates. First, beginning in 1996, the USA required that all unmanufactured solid wood packaging be 'totally free from bark and apparently free from live plant pests' or else be certified as treated for wood pests by the exporting country (USDA APHIS, 1995). In addition, beginning in 1999, the USA imposed stricter regulations on wood articles exported from China to the USA (USDA APHIS, 1998). As for major changes in US trading partners, the most dramatic change has been with China, given that the value of imports from China to the United States increased from US$3.1 billion in 1984 when China was the 20th leading US trading partner, to US$338 billion in 2008 when China was the 2nd leading USA trading partner (US Census Bureau, 2011).

3.4 Country of Origin

Scolytines were intercepted on wood at US ports of entry from at least 85 distinct countries that exist today, plus two countries that no longer exist (USSR and Yugoslavia) and the US state of Hawai'i, for a total of 88 'countries'. Although Hawai'i is a US state, goods from Hawai'i are inspected when exported to the continental USA. Of the 85 countries that exist today, nine were in

Table 3.2. Summary data by continent of origin for 8286 scolytine interceptions made in association with wood products or wood packaging materials at USA ports of entry from 1984 to 2008.

Continent[a]	Number of interceptions	Number identified to only			Number of identified		Five most common genera in decreasing order
		Family level	Genus level	Species level	Genera	Species	
Africa	70	17	34	19	9	3	*Hypothenemus*, *Orthotomicus*, *Pityophthorus*, *Hylastes*, *Polygraphus*
Asia	1218	243	619	356	32	43	*Phloeosinus*, *Orthotomicus*, *Hypocryphalus*, *Hypothenemus*, *Pityogenes*
Central America	2690	1094	1113	483	24	28	*Pityophthorus*, *Ips*, *Gnathotrichus*, *Pseudopityophthorus*, *Dendroctonus*
Caribbean	9	0	8	1	7	1	*Hypothenemus*, *Pityophthorus*, *Xyleborus*, *Pseudothysanoes*, *Cryptocarenus*
Europe	3977	1155	324	2498	31	72	*Pityogenes*, *Ips*, *Orthotomicus*, *Hylurgops*, *Hylurgus*
North America	19	8	3	8	5	5	*Dendroctonus*, *Phloeosinus*, *Polygraphus*, *Scolytus*, *Dryocoetes*
Pacific	11	3	3	5	5	4	*Hylurgus*, *Hylurgops*, *Phloeosinus*, *Xyleborus*, *Crypturgus*
South America	209	54	117	38	22	11	*Hypothenemus*, *Xyleborus*, *Hylurgus*, *Coccotrypes*, *Pityophthorus*
Unknown[b]	83	27	18	38	18	16	*Pityogenes*, *Ips*, *Orthotomicus*, *Hylurgops*, *Scolytus*
Total	8286	2601	2239	3446	46	107	*Ips*, *Pityophthorus*, *Pityogenes*, *Orthotomicus*, *Hylurgops*

[a]See text for details on how countries were assigned to continents as well as Haack (2001).
[b]For some interceptions the country or likely country of origin was not listed. This can happen, for example, when a live insect is found walking freely inside a container and not associated closely with specific cargo. This is especially common when there is mixed cargo from multiple countries within a single container.

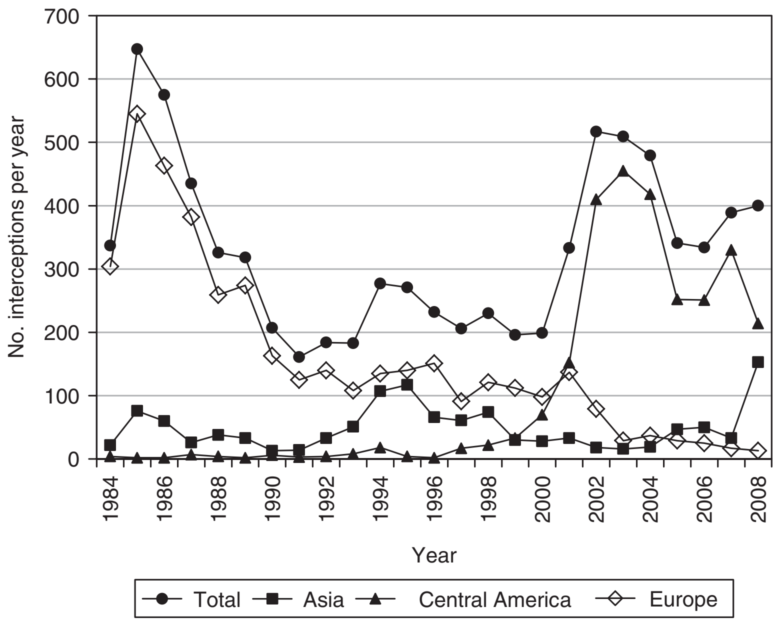

Fig. 3.1. Total number of annual wood-associated scolytine interception at US ports of entry and for selected continents of origin for the period 1984 through 2008.

Africa, 21 in Asia (which included Russia and Turkey), seven in Central America (including Mexico), four in the Caribbean, 29 in Europe, five in the Pacific region (including Australia, Hawai'i and New Zealand) and 11 in South America. There were 12 countries from which 100 or more interceptions were made from 1984 to 2008: Mexico (2581 interceptions), Italy (1322), Germany (715), Spain (533), China (428), Belgium (316), France (255), India (225), Turkey (180), Portugal (178), United Kingdom (137) and Russia (113). Additional details on scolytine interceptions by country can be viewed in Haack (2001) for the period 1985–2000.

3.5 Intercepted Scolytines by Receiving US State

Scolytines were intercepted on wood at ports of entry in 38 US states as well as in Puerto Rico and the US Virgin Islands. Puerto Rico and the US Virgin Islands serve as official US ports of entry for many foreign goods that are later shipped to the US mainland. Of the 8286 wood-associated scolytine interceptions, 5235 were made at maritime ports, 2572 at land borders with Canada and Mexico, 415 at airports, 55 at other US inspection stations, 6 at rail inspection centers, 2 at foreign sites (preclearance inspections) and 1 in Hawai'i during pre-departure inspection to the US mainland. Of the 2572 interceptions at land borders, only 19 (0.7%) were actually of Canadian origin, while 2534 (98.5%) were of Mexican origin, and the remainder (0.8%) were from other countries for products shipped to the USA through either Canada or Mexico.

There were 100 or more wood-associated scolytine interceptions made in 15 US states and Puerto Rico from 1984 to 2008, including Texas (3065 interceptions), Florida (890), Georgia (615), California (576), Louisiana (399), Ohio (340), South Carolina (339), Washington (272), New York (238), Kentucky (233), Maryland (208), North Carolina (191), Puerto Rico (160), New Jersey (131), Alabama (103) and Michigan (100). All of the states listed above have major maritime ports, international airports, or land border crossings with Canada or Mexico. Overall, most interceptions made along the US west coast were on goods shipped from Asia. By contrast, most interceptions made along the US east coast or at ports along the Great Lakes were of European origin, and most interceptions made along the US border with Mexico, including California, were of Central American origin, remembering that Mexico was classified as part of Central America in this analysis.

3.6 Genera of Intercepted Scolytines

Of the 8286 wood-associated scolytine interceptions, 5685 (69%) were identified to at least the genus level and represented 46 genera (Tables 3.2–3.3). Given that 31% of the interceptions were not identified beyond the family level it is likely that many more genera were intercepted. There were 14 genera with 100 or more interceptions from 1984 to 2008: *Ips* (917 interceptions), *Pityophthorus* (827), *Pityogenes* (618), *Orthotomicus* (591), *Hylurgops* (346), *Hylurgus* (291), *Gnathotrichus* (216), *Tomicus* (194), *Hypothenemus* (182), *Xyleborus* (181), *Dryocoetes* (166), *Phloeosinus* (160), *Hylastes* (135) and *Hypocryphalus* (115).

For each scolytine genus, the number of originating continents (world regions), countries and the top four originating countries are presented in Table 3.3. Individuals identified as *Xyleborus* were intercepted from seven continents, the most of any of the 46 identified genera, while two genera (*Phloeosinus* and *Pityophthorus*) were each intercepted from six continents. Eight genera were intercepted from 20 or more countries, including *Ips* (38 countries), *Pityogenes* (35), *Hypothenemus* (30), *Orthotomicus* (25), *Xyleborus* (25), *Hylurgops* (23), *Tomicus* (22) and *Dryocoetes* (21). A positive linear relationship was found between the number of interceptions for a given genus and the number of the originating countries ($F^{[1, 44]} = 57.7$, $P < 0.0001$, $R^2 = 0.57$).

The number of receiving US states and the number of years during the 25-year period from 1984 to 2008 that individuals of each scolytine genus were intercepted are provided in Table 3.3. *Ips* beetles were intercepted in the most US states (27) and specimens of five other genera were intercepted in 20 or more US states: *Orthotomicus* (25 US states), *Pityogenes* (25), *Dryocoetes* (22), *Hylurgops* (21) and *Hylurgus* (20) (Table 3.3). Five genera were intercepted during each year of the 25-year survey period (*Hylurgops*, *Hypothenemus*, *Ips*, *Pityogenes* and *Pityophthorus*), and individuals of three other genera were intercepted during 24 of the 25 years (*Hylurgus*, *Orthotomicus* and *Tomicus*) (Table 3.3).

3.7 Species of Intercepted Scolytines

Of the 8286 wood-associated scolytine interceptions, 3446 (42%) were identified to the species level and represented 107 species (Tables 3.2 and 3.4). As mentioned above for scolytine genera, many more species would likely have been identified as well, if more interceptions had been identified to the species level. Nevertheless, the species listed in Table 3.4 are probably representative of those commonly associated with wood packaging material used in international trade, but of course lack the scolytine species intercepted on US exports (Brockerhoff *et al*., 2006). The ten most commonly intercepted wood-associated scolytines were *Orthotomicus erosus* (Wollaston) (513 interceptions), *Pityogenes chalcographus* (Linnaeus) (512), *Ips typographus* (292), *Hylurgops palliatus* (Gyllenhal) (282), *Hylurgus ligniperda* (Fabricius) (239), *Ips sexdentatus* (Boerner) (189), *Tomicus piniperda* (Linnaeus) (159), *Ips integer* (Eichhoff) (82), *Hylastes ater* (Paykull) (67) and *Xyleborus eurygraphus* (Ratzeburg) (67) (Table 3.4). Of the 107 identified scolytine species, there were 15 species of *Ips*, 9 *Xyleborus*, 6 *Pityogenes*, 6 *Hylastes*, 5 *Scolytus*, and 4 each of *Crypturgus*, *Hylurgops*, *Orthotomicus* and *Polygraphus*. We recognize that several taxonomic changes have occurred in recent years for some of the species listed in Table 3.4; however, for the sake of consistency, we are presenting the species names as recorded by USDA APHIS.

As mentioned in Haack (2001), interception databases often include records that suggest range expansion of a species. The PestID database suggests several cases of range expansion if we consider the range data in Wood and Bright (1992) and Wood (2007) complete, and that there were no errors in identification or data entry. For example, there were interception records in the USA for several scolytine species originating from countries that were outside their published geographic ranges, including *Dendroctonus frontalis* Zimmermann from Turkey (1 interception), *Hylastes attenuatus* Erichson from South Africa (2), *Hylurgops palliatus* from Honduras (1) and Venezuela (1), *Hylurgus ligniperda* from Venezuela (1), *Phloeosinus rudis* Blandford from Belgium (1),

Table 3.3. Summary data by genus for the 8286 wood-associated interception records of scolytines intercepted at US ports of entry from 1984 to 2008.

Scolytine genus	Number of interceptions		Number of continents	Number of countries	Top four countries of origin in decreasing order[a]	Number of receiving US states	Number of years intercepted from 1984 to 2008
	Total	Identified to species level					
Araptus	2	0	1	2	BR, PE	2	2
Carphoborus	38	18	3	8	TR, ES, IT, BE	13	16
Chaetophloeus	3	3	1	1	MX	3	3
Cnemonyx	2	0	2	2	PE, TT	2	2
Coccotrypes	17	0	5	6	BR, IT, VE, CR	6	11
Cryphalus	57	7	4	13	CN, IT, IN, PH	11	16
Cryptocarenus	1	0	1	1	TT	1	1
Crypturgus	66	36	5	15	PT, ES, DE, IT	14	18
Cyrtogenius	20	10	1	6	CN, KR, SG, HK	9	11
Dendroctonus	54	32	3	3	MX, CA, TR	5	10
Dryocoetes	166	47	4	21	CN, IT, DE, BE	22	23
Euwallacea	6	6	1	2	CN, IN	3	5
Gnathotrichus	216	80	2	8	MX, IT, FR, HN	7	15
Hylastes	135	122	5	15	ES, IT, FR, DE	18	22
Hylesinus	16	11	3	6	UK, BE, UA, IT	7	13
Hylocurus	1	1	1	1	MX	1	1
Hylurgopinus	4	2	2	2	MX, IT	2	3
Hylurgops	346	301	5	23	DE, IT, BE, MX	21	25
Hylurgus	291	240	5	16	IT, PT, ES, CL	20	24
Hypocryphalus	115	4	4	10	IN, BR, TW, MY	16	18
Hypothenemus	182	2	5	30	IN, BR, VE, CN	13	25
Ips	917	808	5	38	MX, IT, DE, ES	27	25
Monarthrum	13	0	2	3	MX, PE, BR	2	4
Orthotomicus	591	552	3	25	IT, ES, CN, TR	25	24

Pagiocerus	2	0	2	2	BR, IN	2	2
Phloeosinus	160	16	6	9	CN, JP, MX, CA	17	20
Phloeotribus	4	2	2	3	JO, ES, IL	4	4
Pityogenes	618	591	4	35	DE, IT, ES, BE	25	25
Pityokteines	18	15	1	5	IT, FR, GR, DE	7	10
Pityophthorus	827	20	6	15	MX, BR, ZA, IT	19	25
Polygraphus	66	49	4	18	IT, DE, CN, RU	17	20
Pseudohylesinus	3	3	1	3	MX	1	2
Pseudopityophthorus	99	2	1	1	MX	1	10
Pseudothysanoes	1	0	1	1	DO	0	1
Pteleobius	1	1	1	1	IT	1	1
Scolytodes	2	0	2	2	DE, BR	2	2
Scolytogenes	1	0	1	1	ID	1	1
Scolytoplatypus	3	0	2	2	CN, PT	2	2
Scolytus	98	20	5	17	BE, CN, IT, FR	19	22
Taphrorychus	64	35	4	13	BE, DE, FR, TR	17	17
Tomicus	194	166	3	22	IT, FR, ES, UK	19	24
Trypodendron	38	29	2	12	IT, TR, DE, FR	10	17
Xyleborinus	17	11	2	8	CN, IT, KR, GR	7	8
Xyleborus	181	120	7	25	IT, CN, TR, MX	19	20
Xylechinus	12	2	2	2	IN, IT	6	6
Xylosandrus	17	17	4	8	CN, BE, IT, NG	10	10
Scolytidae[b]	2601	0	7	60	BE, CN, IT, FR	33	25
Total	8286	3446	8	87	MX, IT, DE, ES	38	25

[a]Country codes: AT Austria, AU Australia, AZ Azerbaijan, BE Belgium, BR Brazil, BZ Belize, CA Canada, CL Chile, CN China, CR Costa Rica, DE Germany, DO Dominican Republic, EC Ecuador, EE Estonia, ES Spain, FI Finland, FR France, GT Guatemala, GR Greece, GY Guyana, HK Hong Kong, HN Honduras, HR Croatia, ID Indonesia, IL Israel, IN India, IT Italy, JP Japan, JO Jordan, KR South Korea, LT Lithuania, LV Latvia, MX Mexico, MY Malaysia, NG Nigeria, NL Netherlands, PE Peru, PH Philippines, PL Poland, PT Portugal, RO Romania, RU Russia, SE Sweden, SG Singapore, SK Slovakia, TR Turkey, TT Trinidad and Tobago, TW Taiwan, UA Ukraine, UK United Kingdom, VE Venezuela, VN Vietnam, ZA South Africa.

[b]The interception records labeled Scolytidae were only identified to the family level.

Table 3.4. Summary data by species for the 3446 wood-associated interception records of scolytines that were intercepted at USA ports of entry from 1984 to 2008 and identified to the species level.

Species	No. interceptions	No. continents	No. countries	Top five originating countries in decreasing order[a]	No. receiving US states
Carphoborus bifurcus Eichhoff	1	1	1	MX	1
Carphoborus minimus (Fabricius)	11	2	4	ES, TR, IT, BE	8
Carphoborus pini Eichhoff	5	1	2	ES, IT	3
Carphoborus rossicus (Semenov)	1	1	1	DE	1
Chaetophloeus mexicanus Blackman	3	1	1	MX	3
Cryphalus abietis (Ratzeburg)	2	1	2	DE, IT	1
Cryphalus piceae (Ratzeburg)	5	1	2	IT, FR	4
Crypturgus cinereus (Herbst)	11	3	5	DE, ES, RU, BE, AU	6
Crypturgus mediterraneus Eichhoff	19	1	5	PT, ES, IT, FR, NL	8
Crypturgus numidicus Ferrari	4	1	2	ES, GR	4
Crypturgus pusillus (Gyllenhal)	2	2	2	CN, LV	2
Cyrtogenius luteus (Blandford)	10	1	4	CN, KR, SG, VN	6
Dendroctonus frontalis Zimm.	2	2	2	MX, TR	2
Dendroctonus mexicanus Hopkins	28	1	1	MX	3
Dendroctonus pseudotsugae Hopkins	2	1	1	CA	1
Dryocoetes autographus (Ratzeburg)	29	3	11	IT, BE, ES, BR, HR	14
Dryocoetes hectographus Reitter	1	1	1	IT	1
Dryocoetes villosus (Fabricius)	17	1	5	BE, DE, UK, FR, IT	9
Euwallacea andamanensis (Blandford)	1	1	1	IN	1
Euwallacea validus (Eichhoff)	5	1	1	CN	2
Gnathotrichus denticulatus Blackman	3	1	1	MX	1
Gnathotrichus materiarius (Fitch)	25	2	5	FR, IT, ES, DE, GT	6
Gnathotrichus sulcatus Leconte	52	1	1	MX	3

Continued

Table 3.4. Continued.

Species	No. interceptions	No. continents	No. countries	Top five originating countries in decreasing order[a]	No. receiving US states
Hylastes angustatus (Herbst)	4	1	2	BE, FR	3
Hylastes ater (Paykull)	67	2	10	ES, IT, FR, DE, UK	14
Hylastes attenuatus Erichson	23	2	7	ES, IT, PT, FR, ZA	8
Hylastes cunicularius Erichson	7	1	4	IT, DE, UK, BE	5
Hylastes linearis Erichson	10	1	3	ES, PT, IT	3
Hylastes opacus Erichson	1	1	1	PL	1
Hylesinus crenatus Fabricius	1	1	1	UK	1
Hylesinus varius (Fabricius)	10	1	3	UK, BE, IT	5
Hylurgopinus rufipes (Eichhoff)	2	2	2	MX, IT	2
Hylurgops glabratus (Zetterstedt)	3	2	2	IT, RU	2
Hylurgops incomptus (Blandford)	9	1	1	MX	1
Hylurgops palliatus (Gyllenhal)	282	5	21	DE, IT, BE, UK, ES	21
Hylurgops planirostris (Chapuis)	7	1	1	MX	1
Hylurgus ligniperda (Fabricius)	239	4	15	IT, PT, ES, FR, CL	16
Hylurgus micklitzi Wachtl	1	1	1	IT	1
Hypocryphalus mangiferae (Stebbing)	4	2	2	IN, BR	3
Hypothenemus birmanus (Eichhoff)	1	1	1	SG	1
Hypothenemus obscurus (Fabricius)	1	1	1	PT	1
Ips acuminatus (Gyllenhal)	40	2	9	TR, IT, ES, FR, CN	11
Ips amitinus (Eichhoff)	2	1	2	IT, FI	2
Ips apache Lanier	9	1	2	HN, MX	4
Ips bonanseai (Hopkins)	27	1	1	MX	3
Ips calligraphus (Germar)	13	1	3	MX, HN, GT	4
Ips cembrae (Heer)	9	2	4	IT, DE, TW, BE	5
Ips cribricollis (Eichhoff)	39	1	3	MX, HN, GT	4
Ips grandicollis (Eichhoff)	14	1	2	MX, GT	3
Ips integer (Eichhoff)	82	1	1	MX	3
Ips lecontei Swaine	43	1	2	MX, GT	4

Continued

Table 3.4. Continued.

Species	No. interceptions	No. continents	No. countries	Top five originating countries in decreasing order[a]	No. receiving US states
Ips mannsfeldi (Wachtl)	7	2	2	ES, TR	4
Ips mexicanus (Hopkins)	5	1	1	MX	1
Ips pini (Say)	37	1	1	MX	2
Ips sexdentatus (Boerner)	189	2	12	IT, ES, FR, TR, PT	19
Ips typographus (Linnaeus)	292	2	25	IT, DE, BE, RO, RU	22
Orthotomicus erosus Wollaston	513	3	20	IT, ES, TR, CN, PT	24
Orthotomicus laricis (Fabricius)	29	2	10	IT, FR, DE, ES, PL	12
Orthotomicus proximus (Eichhoff)	2	1	2	IT, FI	2
Orthotomicus suturalis (Gyllenhal)	8	1	3	UK, DE, EE	4
Phloeosinus canadensis Swaine	2	1	1	CA	2
Phloeosinus rudis Blandford	14	2	2	JP, BE	7
Phloeotribus scarabaeoides (Bernard)	2	2	2	ES, JO	2
Pityogenes bidentatus (Herbst)	23	2	7	ES, FR, DE, IT, SE	9
Pityogenes bistridentatus (Eichhoff)	42	2	7	ES, TR, IT, FR, UK	9
Pityogenes calcaratus (Eichhoff)	4	1	3	ES, FR, IT	4
Pityogenes chalcographus (Linnaeus)	512	3	31	DE, IT, BE, RU, ES	25
Pityogenes quadridens (Hartig)	9	2	5	FI, TR, ES, LT, PT	7
Pityogenes trepanatus (Nordlinger)	1	1	1	LT	1
Pityokteines curvidens (Germar)	3	1	3	FR, IT, GR	3
Pityokteines spinidens (Reitter)	12	1	4	IT, FR, AT, DE	5
Pityophthorus mexicanus Blackman	6	1	1	MX	1
Pityophthorus pityographus (Ratzeburg)	14	2	5	IT, DE, MX, NL, FR	8
Polygraphus poligraphus (Linnaeus)	44	2	10	IT, DE, CN, UK, BE	14
Polygraphus proximus Blanchard	1	1	1	IT	1
Polygraphus rufipennis (Kirby)	2	1	1	CA	2

Continued

Table 3.4. Continued.

Species	No. interceptions	No. continents	No. countries	Top five originating countries in decreasing order[a]	No. receiving US states
Polygraphus subopacus Thomson	2	2	2	IT, AZ	1
Pseudohylesinus variegatus (Blandford)	3	1	1	MX	1
Pseudopityophthorus pruinosus (Eichhoff)	1	1	1	MX	1
Pseudopityophthorus yavapaii Blackman	1	1	1	MX	1
Pteleobius vittatus Fabricius	1	1	1	IT	1
Scolytus intricatus (Ratzeburg)	12	1	4	BE, FR, IT, DE	8
Scolytus multistriatus (Marsham)	2	2	2	IT, CA	2
Scolytus ratzeburgi Janson	1	1	1	FI	1
Scolytus schevyrewi Semenov	4	2	2	CN, CA	4
Scolytus scolytus (Fabricius)	1	1	1	UK	1
Taphrorychus bicolor (Herbst)	21	1	5	BE, DE, FR, FI, NL	10
Taphrorychus villifrons (Dufour)	14	2	5	BE, DE, FR, LV, TR	9
Tomicus minor (Hartig)	7	2	3	TR, BR, IT	3
Tomicus piniperda (Linnaeus)	159	2	21	IT, FR, ES, UK, DE	19
Trypodendron domesticum (Linnaeus)	10	2	4	IT, TR, BE, FR	4
Trypodendron lineatum (Olivier)	12	2	7	IT, TR, CH, SK, IL	4
Trypodendron signatum (Fabricius)	7	1	4	DE, FR, PO, BE	4
Xyleborinus saxesenii (Ratzeburg)	11	2	7	IT, CN, GR, TR, KR	6
Xyleborus affinis Eichhoff	22	6	5	GY, MX, ID, HN, BR	8
Xyleborus apicalis Blandford	1	1	1	MY	1
Xyleborus dispar (Fabricius)	2	1	1	IT	1
Xyleborus eurygraphus (Ratzeburg)	67	2	4	IT, TR, ES, GR	9
Xyleborus ferrugineus (Fabricius)	2	2	2	BR, BZ	2
Xyleborus glabratus Eichhoff	1	1	1	CN	1
Xyleborus intrusus Blandford	9	1	3	HN, NI, MX	3

Continued

Table 3.4. Continued.

Species	No. interceptions	No. continents	No. countries	Top five originating countries in decreasing order[a]	No. receiving US states
Xyleborus similis Ferrari	1	1	1	VN	1
Xyleborus volvulus (Fabricius)	15	4	11	PE, GY, HN, VE, EC	7
Xylechinus pilosus (Ratzeburg)	2	1	1	IT	1
Xylosandrus crassiusculus (Motschulsky)	10	3	4	CN, IT, NG, ID	8
Xylosandrus germanus (Blandford)	6	3	5	JP, PE, DE, BE, IT	5
Xylosandrus morigerus (Blandford)	1	1	1	BE	1

[a]Country codes for Tables: AT Austria, AU Australia, AZ Azerbaijan, BE Belgium, BR Brazil, BZ Belize, CA Canada, CL Chile, CN China, CR Costa Rica, DE Germany, DO Dominican Republic, EC Ecuador, EE Estonia, ES Spain, FI Finland, FR France, GT Guatemala, GR Greece, GY Guyana, HK Hong Kong, HN Honduras, HR Croatia, ID Indonesia, IL Israel, IN India, IT Italy, JP Japan, JO Jordan, KR South Korea, LT Lithuania, LV Latvia, MX Mexico, MY Malaysia, NG Nigeria, NL Netherlands, PE Peru, PH Philippines, PL Poland, PT Portugal, RO Romania, RU Russia, SE Sweden, SG Singapore, SK Slovakia, TR Turkey, TT Trinidad and Tobago, TW Taiwan, UA Ukraine, UK United Kingdom, VE Venezuela, VN Vietnam, ZA South Africa.

Pityogenes chalcographus from Brazil (1) and *Tomicus minor* (Hartig) from Brazil (1). Although the above interceptions should not be considered authoritative records that these species are established in these countries, it is of interest to note that Kirkendall and Faccoli (2010) recently reported that *Phloeosinus rudis* is established in France and The Netherlands.

The number of originating continents and countries for each of the 107 identified scolytine species intercepted in the USA, as well as the top five originating countries, are presented in Table 3.4. There were six countries from which 20 or more wood-associated scolytine species were intercepted and identified: Italy (50 species), France (29), Germany (28), Spain (28), Belgium (24) and Mexico (24).

The number of US states in which each of the 107 identified scolytines were intercepted is presented in Table 3.4. Overall, there was a significant and positive linear relationship between the number of interceptions for a given scolytine species and the number of the originating countries ($F^{[1,105]}$ = 300.7, $P < 0.0001$, $R^2 = 0.74$), and similarly between the number of interceptions and the number of receiving US states ($F^{[1,105]}$ = 212.5, $P < 0.0001$, $R^2 = 0.67$) (Table 3.5). There were seven US states where 25 or more species were identified among the intercepted scolytines: Texas (67 species), Florida (55), California (40), Louisiana (33), Georgia (30), South Carolina (30) and New York (25).

3.8 Currently Established Exotic Scolytines

As of 2010, we are aware of 58 scolytine species in 27 genera that are established in the continental USA (Table 3.5). Many of the species listed in Table 3.5, especially in the Xyleborini, had been transferred to new genera since publication of the world catalog by Wood and Bright (1992), including *Ambrosiophilus atratus* (Eichhoff), *Anisandrus dispar* (Fabricius), *A. maiche* Stark, *Cnestus mutilatus* (Blandford), *Cyclorhipidion californicus* (Wood), *C. pelliculosum* (Eichhoff), *Dryoxylon onoharaensum* (Murayama), *Wallacellus similis* (Ferrari), *Xyleborinus octiesdentatus* (Murayama) and *Xylosandrus amputatus* (Blandford). In Wood and Bright (1992), all of the above species were formerly members of the genus *Xyleborus* except *Cnestus mutilatus* (formerly in *Xylosandrus*), and *X. amputatus* (formerly in *Amasa*). The pine shoot beetle, *Tomicus piniperda*, is the only scolytine of

Table 3.5. Summary data for the 58 exotic scolytines recognized as being established in the continental United States as of 2010.

Tribe	Species	Feeding guild[a]	Record or report of first collection: Year	Record or report of first collection: State[b]	Native range	No. US states where found as of 2010[c]	Reference of first USA collection record[d]
Hylastini							
	Hylastes opacus Erichson	BB	1987	NY	Eurasia	17	37
	Hylurgops palliatus (Gyllenhal)[e]	BB	2001	PA	Eurasia	3	14
Hylesinini							
	Hylastinus obscurus (Marsham)	R	1878	NY	Europe	20	29
Tomicini							
	Hylurgus ligniperda (Fabricius)	BB	1994	NY	Eurasia	2	13
	Tomicus piniperda (Linnaeus)	BB	1991	MI	Eurasia	18	10
Phloeosinini							
	Phloeosinus armatus Reitter	BB	1992	CA	Asia	1	37
Scolytini							
	Scolytus mali (Bechstein)	BB	1868	NY	Europe	10	18
	Scolytus multistriatus (Marsham)	BB	1909	MA	Europe	48	6
	Scolytus rugulosus (Muller)	BB	1877	NY	Europe	48	7
	Scolytus schevyrewi Semenov[e]	BB	1994	CO	Asia	29	23
Ipini							
	Orthotomicus erosus (Wollaston)	BB	2004	CA	Eurasia	1	20
	Pityogenes bidentatus (Herbst)	BB	1988	NY	Europe	2	11
Dryocoetini							
	Coccotrypes advena Blandford	ST	1956	FL	Asia	1	36
	Coccotrypes carpophagus (Hornung)	ST	1926	FL	Africa	2	36
	Coccotrypes cyperi (Beeson)	ST	1934	LA	Asia	2	36
	Coccotrypes dactyliperda (Fabricius)	ST	1915	AZ, FL	Africa	4	16
	Coccotrypes distinctus (Motschulsky)	ST	1939	FL	Asia	2	36
	Coccotrypes rhizophorae (Hopkins)	ST	1910	FL	Asia	1	16
	Coccotrypes rutschuruensis Eggers	ST	1992	CA	Africa	1	38
	Coccotrypes vulgaris (Eggers)	ST	1985	FL	Asia	1	3
	Dactylotrypes longicollis (Wollaston)	ST	2009	CA	Europe	1	17
	Dryoxylon onoharaensum (Murayama)[fg]	AB	1982	LA	Asia	18	5

Continued

Table 3.5. Continued.

Tribe	Species	Feeding guild[a]	Record or report of first collection		Native range	No. US states where found as of 2010[c]	Reference of first USA collection record[d]
			Year	State[b]			
Crypturgini							
	Crypturgus pusillus (Gyllenhal)	BB	1868	NY	Eurasia	9	18
Xyloterini							
	Trypodendron domesticum (Linnaeus)	AB	2008	WA	Europe	1	22
Premnobini							
	Premnobius cavipennis Eichhoff	AB	1939	FL	Africa	1	4
Xyleborini							
	Ambrosiodmus lewisi (Blandford)	AB	1990	PA	Asia	1	12
	Ambrosiodmus rubricollis (Eichhoff)	AB	1942	MD	Asia	21	4
	Ambrosiophilus atratus (Eichhoff)	AB	1988	TN	Asia	27	2
	Anisandrus dispar (Fabricius)	AB	1817	MA	Europe	24	25
	Anisandrus maiche Stark	AB	2005	PA	Asia	3	27
	Cnestus mutilatus (Blandford)[h]	AB	1999	MS	Asia	8	30
	Cyclorhipidion californicus (Wood)[h]	AB	1944	CA	Asia	28	34
	Cyclorhipidion pelliculosum (Eichhoff)[h]	AB	1987	PA	Asia	18	2
	Euwallacea fornicatus (Eichhoff)	AB	2002	FL	Asia	2	31
	Euwallacea validus (Eichhoff)	AB	1976	NY	Asia	23	36
	Wallacellus similis (Ferrari)[eh]	AB	2002	TX	Asia	2	26
	Xyleborinus alni (Niisima)	AB	1996	WA	Eurasia	13	21
	Xyleborinus andrewesi (Blandford)	AB	2009	FL	Asia	1	25
	Xyleborinus octiesdentatus (Murayama)[e]	AB	2008	LA	Asia	2	28
	Xyleborinus saxesenii (Ratzeburg)	AB	1911	CA	Eurasia	43	16
	Xyleborus glabratus Eichhoff[e]	AB	2002	GA	Asia	4	26
	Xyleborus pfeilii (Ratzeburg)	AB	1992	MD	Eurasia	6	32
	Xyleborus seriatus Blandford[e]	AB	2005	MA	Asia	3	15
	Xylosandrus amputatus (Blandford)[e]	AB	2010	FL	Asia	1	8
	Xylosandrus compactus (Eichhoff)	AB	1941	FL	Asia	10	36
	Xylosandrus crassiusculus (Motschulsky)	AB	1974	SC	Asia	29	1
	Xylosandrus germanus (Blandford)	AB	1931	NY	Asia	32	9

Cryphalini							
	Hypocryphalus mangiferae (Stebbing)	BB	1949	FL	Asia	1	33
	Hypothenemus areccae (Hornung)	ST	1960	FL	Asia	1	36
	Hypothenemus birmanus (Eichhoff)	ST	1951	FL	Asia	1	33
	Hypothenemus brunneus (Hopkins)	ST	1904	TX	Africa	3	16
	Hypothenemus californicus Hopkins	ST	1895	CA	Africa	14	16
	Hypothenemus columbi Hopkins	ST	1881	SC	Africa	6	16
	Hypothenemus crudiae (Panzer)	ST	1868	GA, LA	Asia	20	18
	Hypothenemus erectus LeConte	ST	1876	TX	Africa	1	19
	Hypothenemus javanus (Eggers)	ST	1977	FL	Africa	1	35
	Hypothenemus obscurus (Fabricius)	ST	1977	FL	S America	1	35
	Hypothenemus setosus (Eichhoff)	ST	1982	FL	Africa	1	36

[a]Feeding guilds: AB = ambrosia beetles, feed primarily on fungus (xylomycetophagous), BB = bark beetles, feed primarily on inner bark or phloem (phloeophagous), R = roots of herbaceous plants, e.g. Trifolium, (herbiphagous), ST = most are seed and twig beetles, feeding in seeds (spermophagous), or the pith (myelophagous) or phloem of twigs.

[b]US state abbreviations: AZ = Arizona, CA = California, CO = Colorado, FL = Florida, GA = Georgia, LA = Louisiana, MA = Massachusetts, MD = Maryland, MI = Michigan, MS = Mississippi, NY = New York, PA = Pennsylvania, SC = South Carolina, TN = Tennessee, TX = Texas, and WA = Washington.

[c]Number of US states where reported in literature or found in the USDA Forest Service Early Detection & Rapid Response surveys as of 2010, exclusive of Hawai'i.

[d]References: 1= Anderson (1974), 2= Atkinson *et al*. (1990), 3 = Atkinson *et al*. (1991), 4 = Bright (1968), 5 = Bright and Rabaglia (1999), 6 = Chapman (1910), 7 = Chittenden (1898), 8 = Cognato *et al*. (2011), 9 = Felt (1932), 10 = Haack and Poland (2001), 11 = Hoebeke (1989), 12 = Hoebeke (1991), 13 = Hoebeke (2001), 14 = Hoebeke and Acciavatti (2006), 15 = Hoebeke and Rabaglia (2008), 16 = Hopkins (1915), 17 = LaBonte (unpublished data), 18 = LeConte (1868), 19 = LeConte (1876), 20 = Lee *et al*. (2005), 21 = Mudge *et al*. (2001), 22 = NAPIS (2008), 23 = Negrón *et al*. (2005), 24 = Okins and Thomas (2010), 25 = Peck (1817), 26 = Rabaglia *et al*. (2006), 27 = Rabaglia *et al*. (2009), 28 = Rabaglia *et al*. (2010), 29 = Riley (1879), 30 = Schiefer and Bright (2004), 31 = Thomas (2004), 32 = Vandenberg *et al*. (2000), 33 = Wood (1954), 34 = Wood (1975), 35 = Wood (1977), 36 = Wood (1982), 37 = Wood (1992), 38 = Wood and Bright (1992).

[e]These species were first detected in the USA by the USDA Forest Service Early Detection & Rapid Response project.

[f]Bright and Rabaglia (1999) recorded this species from Delaware in 1977; the correct Delaware record is from 1997.

[g]These three species names have commonly been misspelled in the scientific literature. The current correct spellings are: *D. onoharaensum* not *D. onoharaensis*; *X. saxesenii* not *X. saxeseni*; and *Xyleborus pfeilii* not *Xyleborus pfeili*.

[h]Recent taxonomic changes have affected the nomenclature of these species as follows: *Xylosandrus mutilatus* to *Cnestus mutilatus* (Dole and Cognato, 2010); X*yleborus californicus* and *X. pelliculosus* to *Cyclorhipidion*; *Xyleborus similis* to *Wallacellus similis* (Hulcr and Cognato, 2010).

the 58 exotics for which there is a USDA federal quarantine that regulates movement of pine host material to areas outside the known current US range of this bark beetle (Haack and Poland, 2001). This US federal quarantine was enacted soon after discovery of *T. piniperda* in 1992 and it is still in effect as of 2010, even though this bark beetle has caused minimal damage in the currently infested portions of the eastern USA.

Overall, 19 of the 107 intercepted scolytines listed in Table 3.4, and an additional two intercepted species listed in Haack (2001), which included US interceptions for scolytines on all products, are among the 58 exotic scolytines now established in the continental USA (Table 3.5). The 21 species, listed in the order they appear in Table 3.5, include: *Hylastes opacus* Erichson, *Hylurgops palliatus*, *Hylurgus ligniperda*, *Tomicus piniperda*, *Scolytus multistriatus*, *S. schevyrewi* Semenov, *Orthotomicus erosus*, *Pityogenes bidentatus* (Herbst), *Coccotrypes carpophagus* (Hornung) (in Haack, 2001), *Dactylotrypes longicollis* (Wollaston) (in Haack, 2001), *Crypturgus pusillus* (Gyllenhal), *Trypodendron domesticum* (Linnaeus), *Euwallacea validus* (Eichhoff), *Xyleborinus saxesenii* (Ratzeburg), *Xyleborus glabratus*, *Wallacellus similis* (Ferrari), *Xylosandrus crassiusculus* (Motschulsky), *X. germanus* (Blandford), *Hypocryphalus mangiferae* (Stebbing), *Hypothenemus birmanus* (Eichhoff) and *H. obscurus* (Fabricius). Undoubtedly, if more of the intercepted scolytines had been identified to the species level (Tables 3.2, 3.4), then more of the scolytine species listed as established in the USA (Table 3.5) would have been found among the intercepted scolytines. This is especially true for species of *Coccotrypes* and *Hypothenemus*, which were seldom identified beyond genus in the PestID database. For example, only 3 of 502 *Coccotrypes* interceptions and 63 of 821 *Hypothenemus* interceptions were identified to species during 1985–2000 (Haack, 2001). For those scolytines considered true bark beetles, a significant positive relationship was found between interception frequency and likelihood of establishment (Brockerhoff *et al*., 2006; Haack, 2006).

The species *Hypothenemus africanus* (Hopkins) was included by Haack (2001) in an earlier list of exotic scolytines that were considered to be established in the continental USA. However, even though the type specimen of *H. africanus* was first described from South Africa (Hopkins, 1915), it is now considered more likely that this species is native to the Americas given its current worldwide geographic distribution (Wood and Bright, 1992).

Kirkendall and Faccoli (2010) recently reported that there are 18 species of exotic scolytines established in Europe, of which seven are also established in the USA: *Ambrosiodmus rubricollis* (Eichhoff), *Ambrosiophilus atratus*, *Coccotrypes dactyliperda* (Fabricius), *Dactylotrypes longicollis*, *Xyleborus pfeilii* (Ratzeburg), *Xylosandrus crassiusculus* and *X. germanus*. In addition, Kirkendall and Faccoli (2010) list *Cyclorhipidion bodoanum* (Reitter) as established in Europe, and state that this species will be synonymized with *C. californicus*, which is established in the USA (Table 3.5). Once this occurs there will be eight exotic scolytines in common between Europe and the USA. Note that we listed Europe as the native range of *D. longicollis* in Table 3.5 given that this species is native to the Canary Islands, which are an autonomous territory of Spain. However, Kirkendall and Faccoli (2010) treat this species as an exotic to continental Europe.

Of the 58 exotic scolytines in the USA, one – *Hylastinus obscurus* (Marsham) – breeds in roots of herbaceous legumes, while the others breed primarily in woody plants and palms. We categorized 25 of the 58 scolytines as ambrosia beetles (43%), 13 as bark beetles (22%), 19 as seed and twig feeders (33%) and one as a root feeder of herbaceous plants (2%; Table 3.5). In general, considering the 58 species listed in Table 3.5, the ambrosia beetles in the tribes Premnobini and Xyleborini are polyphagous, inbreeding species and breed primarily in broadleaf woody plants; bark beetles are outbreeding with the species of Hylastini, Ipini, Phloeosinini, and Tomicini breeding in conifers while the Scolytini breed in broadleaf woody plants; *Coccotrypes* species are inbreeders and reproduce mostly in the seeds of palms and broadleaf woody plants; and *Hypothenemus* species are inbreeders, generally polyphagous, and reproduce in seeds and twigs of broadleaf woody plants (Wood, 1982; Wood and Bright, 1992; Jordal *et al*., 2002). Considering the feeding guilds of the 58 exotic scolytines and their interception histories (Haack, 2001), it is likely that some of the ambrosia beetles and most seed and twig feeders arrived in association with seeds, fruit, cuttings and live plants, whereas the remaining ambrosia beetles and nearly all bark beetles arrived in association with wood packaging material, logs, lumber and perhaps fuel wood. In the case of fuel wood, for example, from

1996 to 2009 the USA imported fuel wood from 34 countries in Africa, Asia, the Caribbean, Central America, Europe, North America (Canada) and South America, with a total declared value on arrival of >US$98 million for the 14-year period (Haack *et al*., 2010b). Overall, the majority of exotic scolytines in both the USA and Europe are inbreeding, polyphagous species, which are traits that favor invasiveness (Kirkendall and Faccoli, 2010).

We attempted to locate in the scientific literature the earliest year of collection or the first year of reporting for each of the 58 exotic scolytines. In addition, we tried to identify the US state in which the first collection of each species was made. We recognize that nearly all exotic insects are present for many years before they are first collected, and similarly that the founding population of each exotic may enter the USA at a location that is very distant from where it is later first collected. For two species, *Coccotrypes dactyliperda* and *Hypothenemus crudiae* (Panzer), we were not able to determine the US state in which the first collections were made. In both cases, the first reports listed two US states in which each was collected but did not provide any dates of collection (LeConte, 1868; Hopkins, 1915). Nevertheless, we feel that such data can be used to approximate the historical arrival rate and the areas of the country where the founding population first became established.

Seven of the exotic scolytines first reported since 2000 were discovered as part of the United States Department of Agriculture, Forest Service 'Early Detection and Rapid Response' (EDRR) project (Table 3.5; Rabaglia *et al*., 2008). The EDRR project was initiated as a pilot project in 2001 and in 2007 the program was expanded to full implementation. Approximately 15 different US states now participate in the survey each year, which utilizes pheromone- and karimone-baited traps at 12 sites per state (Rabaglia *et al*., 2008). The relatively steep rate of new scolytine detections since 2000 is in part a reflection of the increased survey efforts such as EDRR. Given the success of the EDRR project in locating previously unknown exotic scolytines, as well as increasing public awareness and surveys by other groups, it is likely that more exotics will be found in the years ahead.

Anisandrus dispar, formerly in the genus *Xyleborus*, was the earliest recorded exotic scolytine in the continental USA (Peck, 1817; Table 3.5). Overall, about 16% (n = 9) of the 58 exotic scolytines were first collected or reported during the 1800s, 24% (14) during 1900–1949, 40% (23) during 1950–1999 and 21% (12) during 2000–2010. Taken as a whole, the species accumulation curve for exotic scolytines in the USA has shown accelerated growth over the past two centuries (Fig. 3.2), reflecting a similar steep increase in US imports (Haack, 2001; US Census

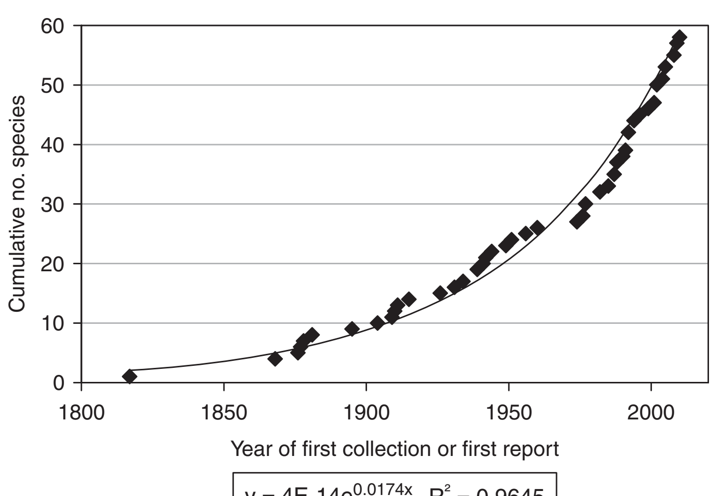

Fig. 3.2. Cumulative number of detections of new exotic scolytines in the continental USA by year of first collection or first published report. Data are from Table 3.5. Exponential equation fitted to the data.

Bureau, 2011). Similarly, accelerating species accumulation curves have been documented for exotic phloem and wood borers in the USA (Aukema *et al*., 2010) as well as for exotic scolytines in Europe (Kirkendall and Faccoli, 2010). If we consider the 57 exotic scolytines on palms and woody plants, and the three major feeding guilds they represent, a pattern emerged where most early invaders were seed and twig feeders while most recent invaders were ambrosia beetles (Table 3.5).

The 58 exotic scolytines were first reported from 16 US states (Fig. 3.3; Table 3.5). As expected, 14 of these 16 states have major maritime or land-based ports of entry given that they border oceans, the Great Lakes or neighboring countries. The five states where the most exotic scolytines were first found were Florida (17 species), New York (8), California (7), Louisiana (4) and Pennsylvania (4). There were only two interior US states where new exotics were first reported: *Ambrosiophilus atratus* in Tennessee and *Scolytus schevyrewi* in Colorado (Table 3.5); however, it is likely that Colorado and Tennessee were not the initial states where these two species first became established, given that each scolytine was found in several states when first reported (Atkinson *et al*., 1990; Negrón *et al*., 2005). When considering the US states in which the 58 exotic scolytines were first reported, along with their assigned feeding guild, there was a tendency for ambrosia beetles to establish in the south-eastern USA, bark beetles in the north-east, and seed and twig beetles along the southern tier of states from California to Florida (Fig. 3.3). Overall, Florida was the state in which most exotic ambrosia beetles (5 of 25), as well as seed and twig beetles (11 of 19) were first found,

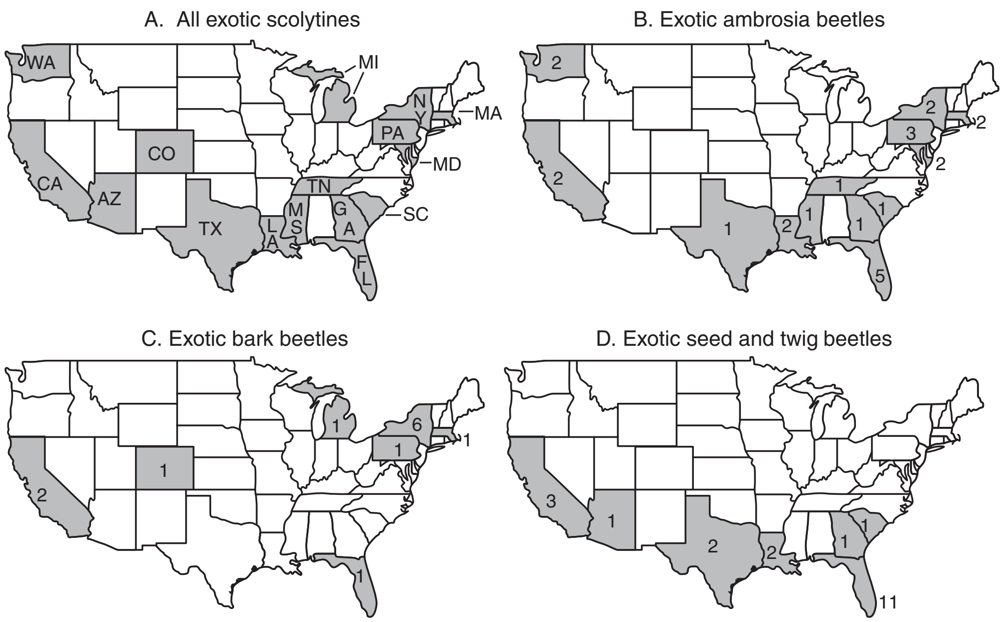

Fig. 3.3. Maps of the contiguous 48 US states indicating the states (shaded) where the established exotic scolytines were first reported in the continental USA by feeding guild. Map A indicates the 16 US states where one or more of the 58 exotic scolytines now established in the USA were first reported, and also provides the state abbreviations as given in Table 3.5. Similarly, maps are presented for the first US state of detection for the 25 exotic scolytines classified as ambrosia beetles (Map B), the 13 species of exotic bark beetles (Map C), and the 19 seed and twig feeders (Map D). Data are from Table 3.5. Numbers within each US state (Maps B–D) indicate the number of exotic scolytines that were first found in each state by feeding guild. For the two exotic seed and twig feeders (*Coccotrypes dactyliperda* and *Hypothenemus crudiae*) that were each initially reported from two US states (Table 3.5), we credited each state for each scolytine. No map is shown for *Hylastinus obscurus*, which is a root feeder of herbaceous legumes that was first found in New York.

whereas 6 of the 13 exotic bark beetles were first found in New York (Fig. 3.3). These geographic patterns may reflect historical trade routes for specific imports and their typical scolytine associates, or they may indicate strict biological (hosts) and environmental (temperature and humidity) conditions that some scolytines require for successful establishment. For example, it is logical that many of the exotic *Coccotrypes* species would be restricted to the relatively warm southern tier of states, given that they breed in seeds of palm trees.

Spread is the third step in the invasion process after arrival and establishment (Liebhold and Tobin, 2008). Using the scientific literature and trapping data from the US Forest Service EDRR project (Rabaglia *et al*., 2008), we calculated the number of states in the continental USA in which each of the current 58 exotic scolytines was reported as of 2010 (Table 3.5). We recognize that these numbers underestimate the true range of these exotics, given that extensive sampling has not occurred in all US states. Moreover, because no exotic scolytines have been reported from Alaska as of 2010, the values given in Table 3.5 refer to only the 48 contiguous US states. Of the 58 exotic scolytines listed in Table 3.5, 19 species were still only reported from a single state, whereas 39 were reported from two or more states each (Table 3.5). *Scolytus multistriatus* and *S. rugulosus* (Muller) were the only two exotics found in all 48 contiguous US states as of 2010. As expected, there was a weak but significant positive linear relation between the number of years since initial discovery in the USA and the number of states currently occupied by the exotic scolytines as of 2010 ($F^{[1, 56]} = 8.3$, $P < 0.0055$, $R^2 = 0.13$).

The native range of the 58 exotic scolytines currently established in the USA include the continents of Africa (10 species), Asia (30), Europe (8), Eurasia (9) and South America (1) (Table 3.5). Note that we considered Eurasia separately from Europe and Asia for those species whose native range extends widely over both continents. Most species of ambrosia beetles were of Asian origin (76%), most bark beetles were native to Eurasia (46%), and most seed and twig feeders were of African origin (47%; Table 3.5). It is possible that some exotic scolytines now established in the USA arrived from locations outside their native ranges, given that several of the 58 species listed in Table 3.5 were established elsewhere in the world prior to their initial detection in the USA (Wood and Bright, 1992; Haack, 2001, Brockerhoff *et al*., 2006; Kirkendall and Faccoli, 2010).

3.8.1 Redbay ambrosia beetle, *Xyleborus glabratus*

Very few of the 58 exotic scolytines currently established in the continental USA have been reported to cause widespread ecological and economic damage in recent decades. Three notable exceptions include one bark beetle (*Scolytus multistriatus*) and two ambrosia beetles (*Xylosandrus crassiusculus* and *Xyleborus glabratus*). *S. multistriatus* is associated with widespread mortality of elm (*Ulmus*) in North America, primarily as a result of vectoring fungi that are the causal agents of Dutch elm disease (Evans and Finkral, 2010). *X. crassiusculus* has caused extensive mortality of broadleaf trees, especially small-diameter trees, both in the USA and in other countries where it has been introduced (Kirkendall and Ødegaard, 2007). Details on the discovery, biology and impact of *X. glabratus* are presented below.

The redbay ambrosia beetle, *X. glabratus*, was first reported in the USA in 2002. The initial collection consisted of three adult specimens captured in traps near Port Wentworth, Georgia, that were deployed as part of the USDA Forest Service EDRR project (Rabaglia *et al*., 2006, 2008). Additional delimiting trapping in 2002 and 2003 around Port Wentworth and Savannah, Georgia, found no additional beetles and therefore it was thought that *X. glabratus* was not actually established. In 2003 significant redbay (*Persea borbonia*) mortality was reported on Hilton Head Island, South Carolina. Although this mortality was first thought to be the result of drought or fluctuations in the local water table, *X. glabratus* and an unidentified fungus were recognized as the cause of the redbay mortality by 2004. Since 2004, *X. glabratus* was reported in Florida in 2005, Mississippi in 2009 and Alabama in 2010. Although natural spread has occurred through adult flight, human-assisted movement of infested host material is suspected in cases of long-distance spread. There is no USDA federal quarantine that regulates movement of potential host material of *X. glabratus* as of 2010.

It was soon realized that the symbiotic fungal associate of *X. glabratus* was extremely pathogenic to redbay (Fraedrich *et al*., 2008). Harrington *et al*. (2008) described the fungus as a new species (*Raffaelea lauricola*) and also identified it as the causal agent of the disease now known as laurel wilt.

X. glabratus is native to Bangladesh, India, Japan, Myanmar and Taiwan, and in Asia it is reported to infest *Leucaena glauca*, *Lindera latifolia*, *Lithocarpus edulis*, *Litsea elongata*, *Phoebe lanceolata* and *Shorea robusta* (Rabaglia *et al*., 2006). *X. glabratus* carries spores of *R. lauricola* in its mandibular mycangia and inoculates a tree as it bores through the bark and enters the xylem. The fungus causes disruption of water flow in the xylem, which results in vascular wilt and a characteristic discolouration or 'streaking' of the outer sapwood. In Asia, neither *R. lauricola* nor *X. glabratus* has been reported to cause laurel wilt. In North America, *R. lauricola* has been isolated only from members of the family Lauraceae, i.e., redbay, avocado (*Persea americana*), swampbay (*P. palustris*), camphor tree (*Cinnamomum camphora*), pondberry (*Lindera melissifolia*), pondspice (*Litsea aestivalis*) and sassafras (*Sassafras albidum*).

Of the 22 exotic Xyleborini established in the USA (Table 3.5), most species, with the exception of some *Xylosandrus* species, attack injured, weakened or dying trees. *Xyleborus glabratus* appears to be similar to these non-aggressive species with the exception of its highly pathogenic, symbiotic fungus. Dispersing *X. glabratus* adult females appear to be attracted to host odors, and after landing they initiate tunneling on the main trunk and branches. If the tree is healthy, colonization may be unsuccessful, but in the process of tunneling the beetle can inoculate the tree with the fungus. The fungus grows quickly in the sapwood, restricting water flow that leads to wilting foliage. In redbay, which seems to be the most susceptible North American host, the entire crown will wilt over a period of a few weeks to a few months, resulting in eventual tree death (Fraedrich *et al*., 2008). As a tree declines, *X. glabratus* adults are attracted to the tree and soon colonize and produce brood in the sapwood. Adult females bore into the xylem where they lay eggs and cultivate the symbiotic fungus on which the larvae feed. As is typical for xyleborine ambrosia beetles, female progeny greatly outnumber the flightless males, and mate with their siblings in the parental gallery. In the south-eastern USA there are overlapping generations throughout the year with one generation requiring about 60 days (Hanula *et al*., 2008). As the female brood adults feed in the gallery and become reproductively mature, *R. lauricola* fungal spores become packed in the mycangia near their mandibles. After mating, the female brood adults emerge from the dead or dying host trees and either reinfest the same tree if there is suitable wood moisture, or fly off to infest new host trees.

For many native and exotic xyleborine ambrosia beetles, ethanol is an effective attractant. The first specimens of *X. glabratus* in North America were collected in ethanol-baited funnel traps (Rabaglia *et al*., 2006). However, additional trapping using ethanol showed that it was only weakly attractive to *X. glabratus*, whereas manuka oil and phoebe oil were shown to be highly attractive (Hanula and Sullivan, 2008). Hanula *et al*. (2008) also showed that *X. glabratus* was attracted to cut redbay bolts or injured redbay trees. Current survey efforts for laurel wilt and *X. glabratus* focus on visual detection of wilted host trees or traps baited with manuka oil.

Although *X. glabratus* has been found infesting sassafras, Hanula *et al*. (2008) noted that *X. glabratus* was not attracted to cut bolts of sassafras. Even though this may slow the spread of the disease in sassafras, observations in Georgia indicate that laurel wilt is able to persist in counties where sassafras is common but redbay is rare (Mayfield *et al*., 2009).

Laurel wilt is well established from coastal South Carolina to Florida, as well as along the Gulf coast of Mississippi, and eradication is no longer feasible. Due to the extreme virulence of *R. lauricola*, the ability of *X. glabratus* to initiate populations from single unmated females and its efficiency in vectoring the fungus, continued high levels of redbay mortality are expected. Management of laurel wilt in forested areas where redbay is common will be difficult. Limiting long-distance, human-assisted spread of the beetle could delay the impacts of the disease in currently unaffected areas. Efforts such as germplasm conservation or screening for tree resistance may be the best long-term hope for redbay and other affected species. For high-value landscape trees, chemical treatments may be an option. Mayfield *et al*. (2008a) demonstrated the ability of macro-infusion of the fungicide propiconazole to protect redbay trees from laurel wilt. The movement of *X. glabratus* and laurel wilt into the commercial avocado-growing region of southern Florida threatens the avocado industry, as well as in other US states, Mexico and elsewhere in the Americas (Mayfield *et al.*, 2008b). Members of the Lauraceae are primarily woody plants and number about 3000 species worldwide, reaching their greatest diversity in the tropical and subtropical latitudes of Asia and the Americas (Chanderbali *et al.*, 2001), and therefore there are hundreds of plant species that are potentially at risk from this insect–fungus disease complex.

3.9 Future Prospects

The world community has taken positive steps to reduce the risk of pests being moved inadvertently in international trade. For example, in 2002, signatories to the International Plant Protection Convention (IPPC) adopted International Standards for Phytosanitary Measures No. 15 (ISPM No. 15), which was entitled 'Guidelines for Regulating Wood Packaging Material in International Trade' (IPPC, 2002). ISPM No. 15 was first revised in 2006 and most recently in 2009 (IPPC, 2009). The goal of ISPM No. 15 is to 'reduce significantly the risk of introduction and spread of most quarantine pests' (IPPC, 2009). The two currently approved phytosanitary treatments for wood packaging material include heat treatment to a minimum temperature of 56°C for 30 min throughout the profile of the wood and including the core, and fumigation with methyl bromide following prescribed schedules (IPPC, 2009). New methods are under development and when approved they will be added to ISPM No. 15.

After approval of ISPM No. 15 in 2002, individual countries or groups of countries began to require their trading partners to follow ISPM No. 15 protocols over the succeeding years. For example, Canada, Mexico and the USA began full implementation of ISPM No. 15 in 2006.

Very few surveys were ever conducted for insects of quarantine significance on wood packaging material prior to initiation of ISPM No. 15. In the paper by Bulman (1992), based on a random survey for pests in wood packaging material during 1989–1991 in New Zealand, 2.7% of the consignments with wood were infested with insects. By contrast, in three surveys conducted after implementation of ISPM No. 15, insect infestation rates of imported wood packaging material were reported as 0.1% in the USA (Haack and Petrice, 2009), 0.3% in the EU (IFQRG, 2006; Haack and Brockerhoff, 2011) and 0.5% in Australia (Zahid *et al.*, 2008). If these values are representative of actual pre- and post-ISPM No. 15 infestation rates, they suggest that implementation of ISPM No. 15 has lowered the occurrence of live wood-infesting insects moving in wood packaging material. Nevertheless, it is important to note that in all three surveys, live bark- and wood-infesting insects were still present in some wood packaging items that had been stamped with the ISPM No. 15 logo. The presence of live insects on wood marked with the ISPM No. 15 logo could indicate improper treatment, pest tolerance to the treatment, infestation after treatment or fraud. To reduce the possibilities that bark-infesting insects could survive or infest after treatment (Evans, 2007; Haack and Petrice, 2009), ISPM No. 15 was revised in 2009 to set maximum size limits for individual pieces of residual bark on wood packaging material (IPPC, 2009). The approved tolerance limits for residual bark allow for bark pieces of any length if they are less than 3 cm in width (as may occur along the edge of a board) or if a bark piece is wider than 3 cm, the total surface area must be less than 50 cm^2 (slightly larger than a typical credit card) (IPPC, 2009). Worldwide implementation of the recent revisions in ISPM No. 15 (IPPC, 2009) should further reduce the phytosanitary risk of wood packaging material.

It should be noted that most, if not all, of the exotic scolytines (Table 3.5) and other wood-infesting insects (Haack, 2006; Haack *et al.*, 2009, 2010a) discovered in the USA since approval of ISPM No. 15 in 2002 very likely became established prior to 2002. Therefore, future discoveries of exotic bark- and wood-infesting insects should not be considered as evidence that ISPM No. 15 has failed, unless the pest population can be dated accurately and linked to wood packaging material. Here again, it should be noted that the stated goal of ISPM No. 15 is not zero risk but rather to significantly reduce risk (IPPC, 2009).

Scolytines can move internationally in many other products besides wood. Many scolytines are intercepted in food items such as fruits and nuts, cut plants, nursery stock (plants for planting) and wooden handicrafts (Haack, 2001, 2006; Kirkendall and Faccoli, 2010; USDA APHIS, 2010). In recognition of the phytosanitary risk of international trade of live plants, a draft ISPM was released in 2010 for country consultation entitled 'Integrated Measures Approach for Plants for Planting in International Trade' (IPPC, 2010). This draft ISPM does not provide specific treatments, as does ISPM No. 15 for wood packaging material, but rather provides guidelines for exporting countries to follow in the areas of production practices, such as use of pest-free mother stock, isolation of introduced plant material, best management practices and treatments, and quality control (standard operating procedures, record keeping, training, internal audits and traceability). If approved and implemented, an ISPM that deals with plants for planting would certainly help reduce the phytosanitary risk now associated with international trade in live plants.

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