Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide[1]

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Abstract: Scolytinae species are among the most damaging forest pests, and many of them are invasive. Over 1500 Scolytinae interceptions were recorded at New Zealand's borders between 1950 and 2000. Among the 103 species were *Dendroctonus ponderosae*, *Ips typographus*, and other high-risk species, but actual arrivals probably included many more species. Interceptions were primarily associated with dunnage, casewood (crating), and sawn timber, and originated from 59 countries, mainly from Europe, Australasia, northern Asia, and North America. New Zealand and United States interception data were highly correlated, and 7 of the 10 most intercepted species were shared. Interception frequency and establishment in New Zealand were not clearly related. By combining New Zealand and United States interceptions of true bark beetles we obtained data on species found in shipments from around the world. Logistic regression analysis showed that frequently intercepted species were about four times as likely as rarely intercepted species to be established somewhere. Interception records of wood and bark borers are valuable for the prediction of invaders and for our general understanding of invasions. The use of alternatives to solid wood packaging, such as processed wood, should be encouraged to reduce the spread of invasive wood and bark borers.

Résumé : Les scolytinés sont parmi les ravageurs forestiers les plus dommageables et ils comptent plusieurs espèces envahissantes. Plus de 1500 interceptions de scolytinés ont été enregistrées aux frontières de la Nouvelle-Zélande entre 1950 et 2000. Parmi les 103 espèces, on trouvait *Dendroctonus ponderosae*, *Ips typographus* et d'autres espèces à haut risque mais les arrivées incluaient en réalité probablement beaucoup plus d'espèces. Les interceptions étaient principalement associées au bois d'arrimage, au bois de caisserie (emballages à claire-voie) et au bois scié et provenaient de 59 pays, surtout de l'Europe, de l'Australasie, du nord de l'Asie et de l'Amérique du Nord. Les données d'interception de la Nouvelle-Zélande et des États-Unis étaient étroitement corrélées et sept des dix espèces les plus souvent interceptées étaient communes. En Nouvelle-Zélande, la fréquence d'interception et l'établissement n'étaient pas clairement reliés. En combinant les interceptions des scolytes de l'écorce faites en Nouvelle-Zélande et aux États-Unis, les auteurs ont obtenu des données sur les espèces retrouvées dans les expéditions partout dans le monde. L'analyse de régression logistique a démontré que les espèces fréquemment interceptées avaient environ quatre fois plus de chances d'être établies quelque part que les espèces rarement interceptées. Les données d'interception des xylophages et des insectes qui s'attaquent à l'écorce sont précieuses pour faire des prédictions au sujet des envahisseurs et pour notre compréhension générale des envahissements. L'utilisation de solutions de rechange à l'empaquetage avec du bois solide, telles que le bois transformé, devrait être encouragée pour réduire la dispersion des xylophages et des insectes envahissants qui s'attaquent à l'écorce.

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Introduction

Biotic invasions are a major threat to indigenous biodiversity and economic activities. The effects of intentionally or accidentally introduced, nonindigenous invasive species are diverse and can include (*i*) changes in the composition of biological communities, (*ii*) extinction of native species, and (*iii*) impacts on ecosystem functioning such as nutrient cycling or productivity (Atkinson and Cameron 1993; Vitousek et al. 1997; Mack et al. 2000). Forest insect pests and diseases constitute

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some of the most dramatic examples of invasions. Well-known cases are gypsy moth (*Lymantria dispar* L.), chestnut blight (caused by *Cryphonectria parasitica* (Murrill) Barr), and white pine blister rust (caused by *Cronartium ribicola* (J.C. Fischer ex Rabenh.)) in North America (Liebhold et al. 1995), Dutch elm disease (caused by *Ophiostoma ulmi* (Buisman) Nannf. and *Ophiostoma novo-ulmi* Brasier) in Europe and North America (Brasier 1991), and pine wilt disease (caused by *Bursaphelenchus xylophilus* (Steiner et Bührer)) in Japan (Mamiya 1988).

Forest insect pests continue to be spread to new territories at unprecedented rates, assisted by global trade (Liebhold et al. 1995; Haack 2001). Wood borers and bark beetles feature prominently among invasive species because they are easily transported inside wooden products and wood packaging materials in which they are concealed and protected. Furthermore, such insects represent some of the worst forest pests, including the bark beetles (Scolytinae) *Scolytus multistriatus*, a vector of the fungal pathogen causing Dutch elm disease (Webber 2000), and *Dendroctonus valens*, an invasive bark beetle that kills pines in China (Gao et al. 2005); the longhorn beetles (Cerambycidae) *Monochamus* spp., vectors of the nematode that causes pine wilt disease (Mamiya 1988); *Anoplophora glabripennis*, a major pest of broadleaved trees in its native and introduced ranges (Nowak et al. 2001); and the jewel beetle (Buprestidae) *Agrilus planipennis*, a recent introduction to parts of North America where it kills ash trees (Haack et al. 2002).

Biotic invasions are caused by the transport of species to areas beyond their indigenous geographic range followed by their successful establishment and spread. Numerous factors impact on each of these stages, and collectively they influence which species eventually become established and which of these become invasive (Mack et al. 2000). Species associated directly or indirectly with traded products are more likely to be dispersed to new territories. Some species, such as wood borers and bark beetles, are in a better position to survive travel to a distant location than others that do not possess amenable life stages and would perish en route. When nonindigenous species arrive at a location, their survival and establishment depend, among other things, on the suitability of the local climate and, in the case of phytophagous insects, the availability of host plants. Other characteristics of the receiving environment are also important; for example, islands and species-poor communities are thought to be particularly susceptible to invasion (Elton 1958).

The number of individuals that arrive at a location is another factor that is intuitively important in determining a species' probability of becoming established at a new location. In fact, it has been shown for birds and plants that species that have been released in greater numbers or more frequently became established at a greater rate (Kolar and Lodge 2001; Duncan et al. 2003). For other taxa there is limited information on the relationship between "propagule pressure" and successful establishment (Kolar and Lodge 2001), although there is good information on marine species transported in the ballast water of ships and by similar means (Leung et al. 2004). For insects, few analyses exist (e.g., Berggren 2001) except for studies on the success rates of biological control introductions (Hopper and Roush 1993). However, data on of exotic insects in incoming cargo are available from border inspections in several countries. A large data set (Port Information Network (PIN)) of nearly 600 000 insect interceptions in the United States (US) has been examined for Scolytinae (Haack 2001) but no mathematical analysis was made to relate interception rates and establishments of species. These data may not always be appropriate for calculating propagule pressure because of certain biases in the inspections of different goods and in the way interceptions were recorded (Work et al. 2005). Another US interception data set (Agricultural Quarantine Inspection Monitoring (AQIM)) with fewer such biases was used by Work et al. (2005) to calculate propagule pressure; however, that data set is much smaller and it covers only a relatively short period of about 5 years. Possibly one of the best data sets on interceptions of wood- and bark-boring insects is New Zealand's Wood- and Bark-Borer Interception Database (Bulman 1990). The New Zealand data set has fewer biases than PIN, covers a much longer period (1950–2000) than either PIN or AQIM, and thus gives a good representation of the wood- and bark-boring insects that arrived in New Zealand.

The objectives of this paper were to document the interceptions of introduced Scolytinae at New Zealand's borders, to compare interception rates with those in other countries, and to determine whether interception rates are related to establishments in New Zealand and other parts of the world. Two earlier reviews of interceptions of Scolytinae at New Zealand ports were published by Milligan (1970) and Bain (1977).

Material and methods

Interceptions of exotic bark and ambrosia beetles in New Zealand

Data on intercepted specimens were obtained from the Wood- and Bark-Borer Interception Database (also known as BUGS) maintained by Forest Research (Bulman 1990). This database holds information on insect specimens that were found between 1950 and 2000 by quarantine officers working for the Forest Service, and subsequently for the Ministry of Forestry and the Ministry of Agriculture and Forestry, during inspections of imports of timber and wooden materials to New Zealand (Bulman 1990). The original database contained a total of 9620 entries of interceptions, of which 1468 entries were Scolytinae. A preliminary review of the Scolytinae was given by Brockerhoff et al. (2003). During the review of the database and collection that was carried out for the present paper, several corrections were made, and 37 new records were added based on collection specimens and information on specimen labels. Thus the new total of records of interceptions of Scolytinae is 1505.

The records held originate from inspections of dunnage (wood used to brace and support cargo), casewood (crating), pallets, sawn timber, logs, and other wooden imports. Usually about 10% of consignments were examined by quarantine officers. Although inspections were not applied at random but with some preference for inspection of shipments from countries that were known to be more frequently infested (Bulman 1992), many shipments from "lower risk" countries

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were also inspected. Thus, we believe there was no serious bias in the way shipments were inspected. When insects were found, a form was completed recording information on the type of cargo and wooden material associated with the interception, the origin of the shipment, the type of insect or symptom, and the location where it was found (e.g., city and port or airport) (Bulman 1990). The completed form and sample specimens were sent to Forest Research for identification and entry of records into the database. In addition to the information provided with the sample, the database contains information on insect order, family (Scolytinae are actually listed under the old classification as a family), genus, and species.

Of the 1505 Scolytinae records 71.5% (1076 records) were identified to species level, an additional 17.9% were identified only to genus level (or tentatively to species), and 1.8% were tentatively identified to genus. Only 8.8% (133 specimens) were identified just to tribe or subfamily level. Previously we reported a slightly lower percentage of records that were identified to species (Brockerhoff et al. 2003); this difference is due to improved identifications. Poor condition of specimens and samples containing only larvae were the main reasons why generic- or specific-level identifications were not possible. The database also contains information on the life stage of intercepted specimens (e.g., larva, pupa, adult), the location in the wooden material (e.g., under bark, in the wood, on the surface), and whether it was alive or dead.

The number of specimens entered into the database varied over time but overall the number of records per year was relatively even. However, during the period from 1950 to 1958, when the inspection of imports had just begun, few specimens were received. The database also contains few records from 1966 to 1971 because rules for examination of quarantine specimens had temporarily changed. In 1999 and 2000 the number of specimens sent declined sharply, as the Ministry decided to fumigate all imports that were infested by insects, without determining their identity.

Taxonomy and distribution of species

We refer to the bark and ambrosia beetles as “Scolytinae”, a subfamily of the Curculionidae according to Lawrence and Newton (1995) and Marvaldi et al. (2002). However, the group used to be, and is still sometimes, considered a family, “Scolytidae”. The taxonomy of species follows the catalogue of Wood and Bright (1992) and its supplements (Bright and Skidmore 1997, 2002).

Information on the establishment of species outside their native range is according to Haack (2001), which is based mainly on the catalogue of Wood and Bright (1992). Additional establishments and corrections are given in the results.

Definition of biogeographic regions

Where data for individual countries were grouped by geographical regions, we largely followed the zoogeographic realms or regions of Wallace (1876, in Price 1997). However, for simplicity we usually refer to continents rather than to the actual zoogeographic regions as follows: “Africa” is basically equivalent to the Ethiopian region (because there were no interceptions from North Africa in the New Zealand database). Asia is either referred to as “Asia” as a whole or as “northern Asia” and “southern Asia”, which are equivalent to the Palaearctic and Oriental regions, respectively. “Australasia” consists of Australia, New Zealand, New Guinea, and the South Pacific Islands. “Europe” is either listed separately or as part of the Palaearctic region, which also includes North Africa and northern Asia. “North America” is equivalent to the Nearctic region. “South and Central America” (all countries south of Mexico and Florida) is equivalent to the Neotropical region. Species from the Neotropical, Ethiopian, and Oriental regions are also referred to as “subtropical and tropical”. Names of countries that changed over the time period covered by the data were combined to one country name. For example, most interceptions in imports from the former USSR are thought to have originated from Russia, and thus, they were all treated as “Russia”.

Data analysis

To compare interception data from New Zealand with those from another country we used data from the Port Information Network (PIN) database of the US Department of Agriculture, Animal and Plant Health Inspection Service (Haack 2001). The Pearson’s correlation coefficient between interception counts of each species in New Zealand and the US was calculated. This analysis included only true bark beetle species because US PIN data are not reliable for interceptions of ambrosia beetles and other Scolytinae that were considered of lower risk and were often not recorded (Haack 2001). The US data included several species that are native to the US, and these were also excluded. There were no New Zealand natives in the New Zealand or US data. Because the distributions of interceptions were highly skewed for both countries, they were transformed (using $\ln(N + 1)$) for the correlation analysis.

To assess whether there is a relationship between interception frequency and establishment, we calculated for each species its percentage of the total number of interceptions. For New Zealand data, this was attempted for all Scolytinae species either included in the New Zealand database or established in New Zealand, but the small number of established species was not sufficient to assess this. A separate analysis using the combined New Zealand and US interception data was performed. This was done on a subset of the data that included only true bark beetle species, using the mean percentage of each such species in the New Zealand and US data. These combined data included interceptions of bark beetles in a wide range of imports from all continents and most countries over a substantial period of time and were thus assumed to give an approximation of the worldwide relative arrival rate. Species were classified into four interception classes: low, <0.5%; medium–low, 0.5%–1%; medium–high, 1%–3%; high, >3%. Species that were native to the US were classified on the basis of the New Zealand interception percentages only, and all other species were classified on the basis of the average of the New Zealand and US interception percentages. Species were then classified as having successfully established (where the species was recorded as having established in any country) or not. A logistic regression analysis was performed to determine whether the probability of a species establishing differed significantly between interception classes by fitting the latter as a class

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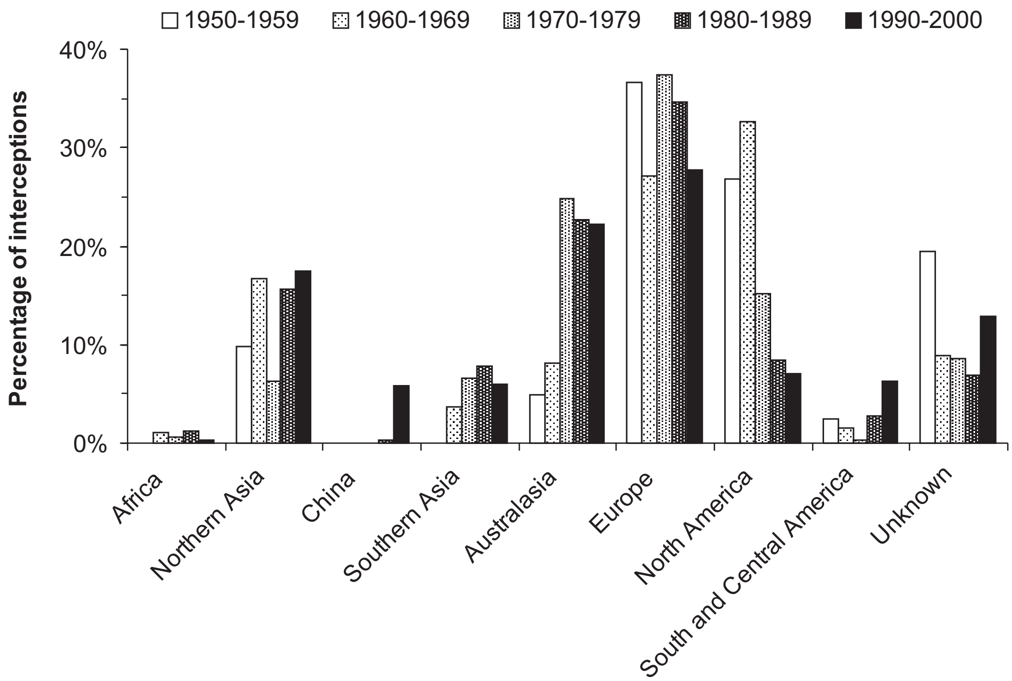
Fig. 1. Origin of intercepted Scolytinae by continent or region for each decade from 1950 to 2000. Note: Northern Asia consists of the Palaearctic part of Asia excluding the Asian part of Russia and the former USSR and Northern India; China is included with Northern Asia but also shown separately; data for Russia and the former USSR were added to Europe.



factor using the SAS procedure GENMOD (SAS Institute Inc. 2000).

Results

The 1505 records of Scolytinae interceptions at New Zealand's borders provide a comprehensive overview of the species that arrived between 1950 and 2000. Fifty-nine countries from all continents (except Antarctica) were represented among the origins of infested shipments, and Europe was the biggest source continent, as it accounted for 31.3% of total interceptions (Fig. 1). Other major sources were Australasia (19.8%), northern Asia (ca. 14.5%), and North America (ca. 14.2%) (Fig. 1). Interceptions from Europe remained at a broadly similar level over the period from 1950 to 2000, while the percentage of interceptions from North America decreased over time (Fig. 1). The percentage of records from Australasia increased early on but remained stable over the last three decades, and recent increases were noted for China as an individual country (Fig. 1). Among individual countries Japan ranked top with 139 interceptions followed by the United States (129 interceptions), Fiji (104), Australia (86), United Kingdom (76), Germany (75), China (including Hong Kong) (52), Papua New Guinea (45), Sweden (43), Italy and Netherlands (each 38), and Canada and Russia (including all other countries of the former USSR) (32 each). Because 13.6% of interceptions could not be traced to an individual country, the actual numbers would have been slightly higher. For example, 41 interceptions from North America are probably predominantly from the US, with some from Canada.

A total of 38 Scolytinae genera were recorded; the 10 most frequently intercepted genera were *Xyleborus* (351 interceptions), *Ips* (173), *Hylurgops* (110), *Pityogenes* (87), *Dryocoetes* (62), *Scolytus* (61), *Orthotomicus* (56), *Hylastes* (49), *Polygraphus* (49), and *Phloeosinus* (48). There were 103 species of Scolytinae. The most commonly intercepted true bark beetles are listed in Table 1 and other Scolytinae are listed in Table 2. These included many significant forest pests such as *Dendroctonus ponderosae*, *Ips sexdentatus*, *Ips typographus*, *Scolytus scolytus*, *Tomicus piniperda*, *Xyleborus ferrugineus*, *Xyleborus perforans*, and *Xylosandrus germanus*. The origins of interceptions mirrored the native range of species. For instance, *Hylurgops palliatus* and *Pityogenes chalcographus*, two of the most frequent interceptions, were exclusively intercepted in shipments from their native ranges in Europe and Asia. But interceptions from the introduced range of species were also common. For example, of the 49 interceptions of *Ips grandicollis*, 20 were from Australia, where this North American species is introduced. Likewise, of the 30 interceptions of *Hylurgus ligniperda*, 19 were from Australia and three from Chile, where the species is introduced, and the remainder were from its native Eurasia. There were few interceptions where the origin of shipments did not match the known distribution of species. An example was one interception of *Scolytus scolytus* from India, where it is not thought to occur.

Materials most commonly associated with interceptions were dunnage, casewood (crating), and sawn timber, whereas logs accounted for few records (Table 3). Most of the frequently intercepted species followed this pattern and were primarily found in dunnage and casewood. However, 76% of the interceptions of *Xyleborus perforans*, the most frequently intercepted species overall, were found in sawn timber of numerous tree species from Fiji, Papua New Guinea, Solomon Islands, Indonesia, and other countries.

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Table 1. The 35 true bark beetle species most frequently intercepted in New Zealand (N.Z.) plus less frequently intercepted species that are known to be established anywhere outside their native range, their origin and introduced range, and comparison with United States (US) interception data (N = 722 interceptions for New Zealand and 2626 interceptions for the US).

	Interceptions (%)				
Species	N.Z.	US*	Origin†	Countries where the species has become established‡	Most common hosts
Hylurgops palliatus (Gyllenhal)	13.4	11.2	AS, EUR, NAF	US	*Pinus, Picea*
Pityogenes chalcographus (L.)	9.1	21.5	AS, EUR	Jamaica§	Conifers
Ips grandicollis (Eichhoff)	6.8	0.0‖	CAR, NAM	Australia	*Pinus*
Dryocoetes autographus (Ratzebg.)	6.2	0.8‖	AS, EUR, NAM, NAF	Brazil§	*Picea, Pinus*
Ips typographus (L.)	6.0	10.9	AS, EUR		*Picea*
Hylastes ater (Paykull)	5.1	2.9	AS, EUR, NAF	N.Z., Australia, Chile	*Pinus*
Hylurgus ligniperda (Fabricius)	4.2	8.3	AS, EUR, NAF	N.Z., Australia, Japan, Chile, US, Brazil§, Uruguay§, South Africa	*Pinus*
Scolytus scolytus (Fabricius)	4.2	0.0	AS, EUR		*Ulmus*
Tomicus piniperda (L.)	3.6	5.9	AS, EUR, NAF	Canada, US	*Pinus*
Polygraphus rufipennis Kirby	3.0	0.0‖	NAM	South Africa§	*Picea*
Polygraphus poligraphus (L.)	2.5	1.8	AS, EUR	South Africa§	*Picea*
Orthotomicus angulatus (Eichhoff)	2.1	0.0	AS	Fiji	*Pinus, Tsuga*
Hylesinus varius (Fabricius)	1.9	0.3	AS, EUR, NAF		*Fraxinus*
Phloeosinus perlatus Chapuis	1.8	0.0	AS		Conifers
Ips calligraphus (Germar)	1.5	0.0‖	CAR, NAM	Phillipines	*Pinus*
Ips cembrae (Heer)	1.5	0.4	AS, EUR		*Larix*
Pityogenes bidentatus (Herbst)	1.5	1.0	AS, EUR	Madagascar, US	*Pinus*
Scolytus multistriatus (Marsham)	1.5	0.0	AS, EUR, NAF	N.Z., Canada, US	*Ulmus*
Taphrorychus villifrons (Dufour)	1.5	0.6	AS, EUR, NAF		*Quercus, Fagus, Castanea*
Orthotomicus erosus (Wollaston)	1.4	14.7	AS, EUR, NAF	Chile, South Africa	*Pinus*
Phloeosinus rudis Blandford	1.2	0.8	AS	France, Netherlands	Conifers
Scolytus intricatus (Ratzeburg)	1.2	0.4	AS, EUR, NAF		*Quercus*
Orthotomicus caelatus (Eichhoff)	1.1	0.0‖	NAM	South Africa§	*Pinus*
Orthotomicus laricis (Fabricius)	1.1	1.1	AS, EUR, NAF	Chile§	*Picea, Pinus*
Dryocoetes villosus (Fabricius)	1.0	0.8	EUR, NAF		*Quercus*
Ips amitinus (Eichhoff)	1.0	0.1	AS, EUR		*Picea*
Ips acuminatus (Gyllenhal)	0.8	1.0	AS, EUR		*Pinus*
Ips pini (Say)	0.8	0.0‖	CA, NAM		*Pinus*
Ips sexdentatus (Boerner)	0.8	6.0	AS, EUR		*Pinus*
Cyrtogenius fijianus (Schedl)	0.7	0.0	AUS (Fiji)		*Agathis*
Hylesinus crenatus (Fabricius)	0.7	0.0	AS, EUR, NAF		*Fraxinus*
Pityogenes quadridens (Hartig)	0.7	0.3	EUR		*Pinus*
Carphoborus ponderosae Swaine	0.4	0.0‖	NAM		*Pinus*
Dendroctonus ponderosae Hopkins	0.4	0.0‖	NAM		*Pinus*
Taphrorychus bicolor (Herbst)	0.4	0.9	AS, EUR		*Fagus*
Orthotomicus proximus (Eichhoff)	0.3	0.1	AS, EUR	Madagascar§	*Pinus*
Pityokteines curvidens (Germar)	0.3	0.1	AS, EUR	Argentina, South Africa§	*Abies*
Scolytus mali (Bechstein)	0.3	0.0	AS, EUR, NAF	Canada, US	*Rosaceae*
Crypturgus pusillus (Gyllenhal)	0.1	0.0	AS, EUR, NAF	Canada, US	Conifers
Dendroctonus micans (Kugelann)	0.1	0.0	AS, EUR	UK	*Picea*
Hylastes angustatus (Herbst)	0.1	0.2	AS, EUR	Swaziland, South Africa	*Pinus, Picea*
Hylesinus toranio (Danthione)	0.1	0.0	AS, EUR, NAF	Argentina	*Fraxinus*
Phloeosinus armatus Reitter	0.1	0.0	AS	US	Conifers
Scolytus schevyrewi Semenov	0.1	0.0	AS	US	*Ulmus*
Cryphalus wapleri Eichhoff	0.0	0.0	AUS (Australia)	N.Z.	*Ficus*
Dendroctonus valens LeConte	0.0	0.0‖	NAM	China	*Pinus*
Hylastes lineariz Erichson	0.0	0.3	AS, EUR, NAF	South Africa	*Pinus*
Hylastes opacus Erichson	0.0	0.1	AS, EUR	US	*Pinus, Picea*
Phloeosinus cupressi Hopkins	0.0	0.0‖	NAM	N.Z., Australia, Panama	*Cupressus*
Scolytus rugulosus (Müller)	0.0	0.0	AS, EUR, NAF	Argentina, Canada, Mexico, Peru, US, Uruguay	Broad-leaved trees

*US interceptions data according to Haack (2001).
†Native range: AF, Africa; AS, Asia; AUS, Australasia (i.e., Australia, New Zealand, New Guinea, and the South Pacific Islands); CAR, Caribbean; EUR, Europe; NAF, North Africa; NAM, North America.
‡Mainly according to Wood and Bright (1992), Haack (2001), see text for others.
§The status of the species marked has not been verified by the authors.
‖Species native to North America.

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Table 2. Ambrosia beetles and seed-feeding Scolytinae that were intercepted in New Zealand (N.Z.) and species that were not intercepted but have become established in New Zealand, their origin, and comparison with United States (US) interception data (*N* = 356 interceptions for New Zealand and 114 interceptions for the US).

	Interceptions (%)				
Species	N.Z.	US*	Origin†	Established in New Zealand?	Most common hosts
Xyleborus perforans (Wollaston)	59.3	0.0	Tropics		Polyphagous
Trypodendron lineatum (Olivier)	7.6	0.0§	AS, EUR, NAF, NAM		Conifers
Euwallacea valida (Eichhoff)	4.8	6.1§	AS		Polyphagous
Xyleborus affinis Eichhoff	4.8	0.0	Tropics		Polyphagous
Xylosandrus germanus (Blanford)	3.7	0.0	AS		Polyphagous
Xyleborus ferrugineus (Fabricius)	3.4	0.0	Tropics		Polyphagous
Gnathotrichus sulcatus (LeConte)	2.8	0.0§	NA		Conifers
Xyleborinus saxesenii (Ratzeburg)	2.8	0.0§	EUR (?)	Yes	Polyphagous
Xyleborus similis Ferrari	1.7	0.0	Tropics		Polyphagous
Arixyleborus rugosipes Hopkins	1.4	0.0	AS (Philippines)		Polyphagous
Gnathotrichus materiarius (Fitch)	1.4	0.0§	CAR, NAM		Conifers
Gnathotrichus retusus (LeConte)	1.4	0.0§	NAM		Conifers
Xyloterinus politus (Say)	0.8	0.0§	NAM		Polyphagous
Coccotrypes dactyliperda (Fabricius)	0.6‡	0.0	Subtropics and tropics	Yes	Polyphagous seed borer
Trypodendron domesticum (L.)	0.6	6.1	AS, EUR		Broad-leaved trees
Xyleborus eurygraphus (Ratzeburg)	0.6	18.4	AS, EUR, NAF		*Pinus*
Xylosandrus crassiusculus (Motschulsky)	0.6	0.0	Subtropics and tropics		Polyphagous
Xylosandrus solidus (Eichhoff)	0.6	0.0	AUS (Australia)		*Diploglottis*, *Eucalyptus*
Cyclorhipidion sexspinatum (Schedl)	0.3	0.0	AS		Broad-leaved trees
Euwallacea andamensis (Blanford)	0.3	0.0	AS, AUS (New Guinea)		Polyphagous
Leptoxyleborus sordicauda (Motschulsky)	0.3	0.0	AS, AUS (New Guinea)		Broad-leaved trees
Trypodendron rufitarsis (Kirby)	0.3	0.0§	NAM		*Pinus*
Xyleborus intrusus Blandford	0.3	0.0§	CAR, NAM		*Pinus*, *Pseudotsuga*
Amasa truncata (Erichson)	0.0	0.0	AUS (Australia)	Yes	Polyphagous
Ambrosiodmus apicalis (Blandford)	0.0	0.9	AS		Polyphagous
Ambrosiodmus compressus (Lea)	0.0	0.9	AUS (Australia)	Yes	Polyphagous
Coccotrypes carpophagus (Hornung)	0.3‡	2.6	Subtropics and tropics		Polyphagous seed borer
Coptodryas eucalyptica (Schedl)	0.0	0.0	AUS (Australia)	Yes	Polyphagous
Dactylotrypes longicollis (Wollaston)	0.0	0.9	AF		Polyphagous seed borer
Hypothenemus birmanus (Eichhoff)	0.0	0.9	Subtropics and tropics		Polyphagous
Hypothenemus hampei (Ferrari)	0.3‡	54.4	Subtropics and tropics		*Coffea*
Trypodendron signatum (Fabricius)	0.0	4.4	AS, EUR		Broad-leaved trees
Xylosandrus morigerus (Blandford)	0.0	4.4	Subtropics and tropics		Polyphagous
Xylosandrus pseudosolidus (Schedl)	0.0	0.0	AUS (Australia)	Yes	Polyphagous

*US interceptions data according to Haack (2001).
†Native range — see Table 1.
‡These three species are recent additions to the data set.
§Species native to North America.

Table 3. Representation of various wooden goods and packaging materials in which Scolytinae were intercepted in New Zealand.

Material	No. (%) of interceptions
Dunnage	522 (34.7)
Casewood (crating)	427 (28.4)
Sawn timber	266 (17.7)
Pallets	156 (10.4)
Logs	48 (3.2)
Other materials or not recorded	86 (5.7)

Of the 11 Scolytinae species that have become established in New Zealand, five are true bark beetles (Table 1), five are ambrosia beetles, and one is a seed feeder (Table 2). More detailed information on the Scolytinae established in New Zealand is given by Brockerhoff et al. (2003). Three of the five true bark beetles that have become established in New Zealand were intercepted more or less frequently (Table 1) but *Cryphalus wapleri* and *Phloeosinus cupressi* were not intercepted once. Among the six other Scolytinae that have become established in New Zealand, two (*Xyleborinus saxesenii* and *Coccotrypes dactyliperda*) were intercepted, whereas the four others (*Amasa truncata*, *Ambrosiodmus compressus*, *Coptodryas eucalyptica*, and *Xylosandrus pseudosolidus*) were not. Almost half of the established species are of

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Table 4. Origin of Scolytinae that were intercepted in New Zealand and of those that have become established in New Zealand.

Bioregion	No. (%) of interceptions	No. (%) of establishments
Palaearctic	681 (51.0)	4 (36.4)
Australasia	295 (22.1)	5 (45.5)
Nearctic	211 (15.8)	1 (9.1)
Subtropical and tropical	149 (11.2)	1 (9.1)

Note: The percentages of interceptions were based on a corrected total that excludes 10.2% of interceptions of unknown origin.

Australasian origin, although only about a fifth of interceptions were from there (Table 4). Palaearctic species, probably from Europe, represent about a third of establishments but they account for half of the interceptions. A Nearctic (North American) species and one from subtropical and tropical regions made up the remainder, and percentages of interceptions from these regions were about similar (Table 4).

The fact that not all established species had been intercepted is an indication that many more species must have arrived at New Zealand's borders without being detected in incoming cargo. The actual number of species that arrived can be expected to be much higher than the 103 species that were intercepted.

Our examination suggests that there is no clear relationship between the number of interceptions of a species and its probability of becoming established in New Zealand. However, the small number of established species and the stochastic nature of establishments limit the ability to detect a response in a data set from a single country. Therefore, we explored the use of a larger interception data set, together with worldwide information on known establishments. To obtain interception data that are representative of a wider cross-section of originating countries we combined the New Zealand interception records with those from the US, as published by Haack (2001). This was limited to true bark beetle species because the US data are not thought to be reliable for other Scolytinae (see Material and methods). A comparison of these two data sets showed a remarkable similarity in relative interception frequency of true bark beetles. For example, the bark beetle that was most commonly intercepted in New Zealand (*Hylurgops palliatus*) was ranked third in the US, and the second species in New Zealand (*Pityogenes chalcographus*) was ranked first in the US. In fact, among the top 10 interceptions of true bark beetles (excluding US natives) seven species were shared. The two data sets were strongly correlated (r = 0.75 without transformation; r = 0.55 with log(N + 1) transformation; P < 0.0001 in both cases), indicating considerable similarities between interceptions in the two countries (Fig. 2).

The combined interception data of true bark beetles contained 80 species from the New Zealand data set and 56 species from the US data set. Of these, 35 were shared, giving a combined number of 101 species. In addition to the information provided by Wood and Bright (1992) and Haack (2001) on species recorded as established outside their native range, we added two species, *Cryphalus wapleri* and *Scolytus multistriatus*, as established in New Zealand. Furthermore, we changed the establishment record of *Orthotomicus erosus* in Fiji to *Orthotomicus angulatus* (R. Beaver, personal communication, 2004; unpublished identification of specimens by M. Knizek), we changed the introduced range of *Orthotomicus caelatus* from Australia to South Africa (Wood and Bright 1992) and that of *Ips calligraphus* from Australia to the Philippines (Lapis 1985), we expanded the range of *Phloeosinus rudis* to the Netherlands (L.G. Moraal, personal communication, 2004), and we added *Scolytus schevyrewi* (Liu and Haack 2003) and *Orthotomicus erosus* (Haack 2004) as established in the US. Thus we determined a total of 32 true bark beetles that are thought to have become established outside their native range (Table 1). Four of these did not appear in the combined New Zealand and US interception data set.

When the combined data set of true bark beetles was used, the logistic regression analysis of the relationship between the frequency of interceptions of a species and establishment outside its native range was highly significant ($\chi^2_{[3]}$ = 29.2, P < 0.0001). Among those species that were intercepted, 82% of the most frequently intercepted species have become established compared with only 10%–14% of the more rarely intercepted species (Table 5). When species that had become established but had not been intercepted in either New Zealand or the US were included in this analysis (in the <0.5% class), the proportion of establishments for this class increased from 0.16 to 0.20. Statistically, this does not alter the conclusion that there is a highly significant association between interception and establishment ($\chi^2_{[3]}$ = 25.4, P < 0.0001).

Discussion

The total of 103 Scolytinae species that were intercepted in New Zealand is considerable but the actual number of species that arrived in traded wooden goods is likely much higher given that only a small proportion (about 10%) of shipments were examined. Furthermore, the period under investigation covered only a third of the time since the European colonization of New Zealand began over 150 years ago. Compared with the worldwide total of about 6000 Scolytinae (Bright and Skidmore 2002; Knížek and Beaver 2004), which are predominantly xylomycetophagous and phloeophagous species and hence associated with wood and bark, only a small fraction of the species were intercepted. However, many Scolytinae that are globally recognised as significant forest pests were represented among the interceptions. For over 80% of species, interceptions included live specimens (Brockerhoff et al. 2003). These observations illustrate the risks associated with trade in wooden goods and solid wood packing materials and confirm that this is justifiably considered to be a major pathway for the introduction of wood- and bark-boring species into new territories (e.g., USDA APHIS 2000). Thus, it is no surprise that so many of these species have indeed become established outside their native range.

Information on the establishment of nonindigenous Scolytinae in New Zealand is reliable, as efforts to detect such species in the field are substantial, albeit somewhat biased towards conifers in plantation forests and other economically important trees (Brockerhoff et al. 2003). New Zealand data on interception rates and establishments of Scolytinae do not

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Fig. 2. Relationship between interception counts of true bark beetle species in New Zealand and the United States using log-transformed data.

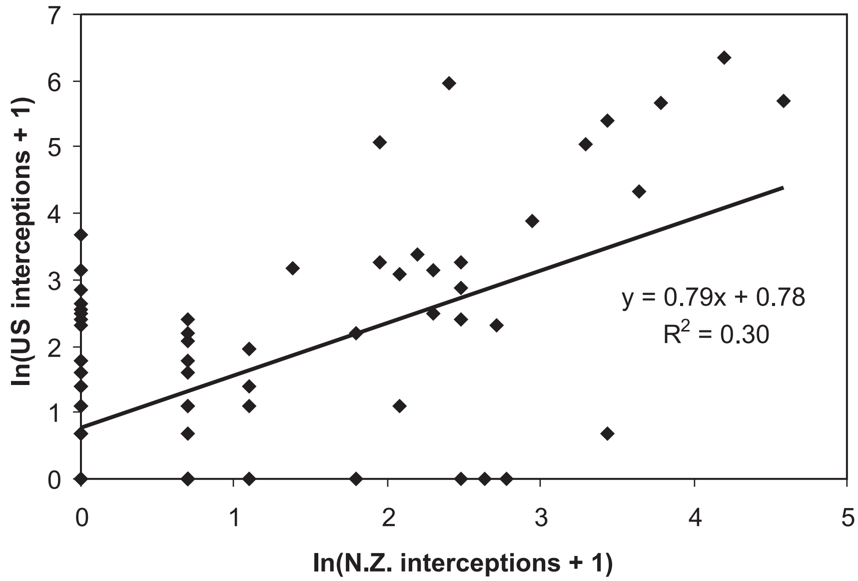

Table 5. Proportions of true bark beetle species that have become established worldwide in relation to their interception frequency in New Zealand and the United States (see methods for calculation).

Interception class*	$n^{\dagger}$	Proportion of species that have become established‡
High (>3%)	11	0.82a
Medium–high (1%–3%)	10	0.70a
Medium–low (0.5%–1%)	10	0.10b
Low (<0.5%)	70, 74§	0.16b, 0.20b§

*The interception classes are defined by percentages of interceptions.
†Sample size is the number of species.
‡Values followed by the same letter do not differ significantly (least significant difference test; α = 0.05).
§Proportions and sample sizes are excluding and including established species that were not intercepted, respectively.

show that frequently intercepted species are necessarily more likely to become established than those that are rarely encountered. Also, the majority of species that were often intercepted have not (yet) become established. This illustrates that establishment is a rare chance event despite favourable conditions (e.g., Niemelä and Mattson 1996) due to the presence of numerous exotic (host) tree species (Weston 1957), a temperate to subtropical climate, and a relative shortage of natural enemies that would be expected in an invaded area. One of the reasons why there are in fact not more species that have become permanently established can probably be found in the Allee effect (after Allee et al. 1949), which explains that small founder populations have a high chance of extinction for several reasons, including difficulty of finding mates and inbreeding depression (Stephens et al. 1999; Liebhold and Bascompte 2003). Hence establishments of Scolytinae are probably more common than our data suggest but many settlements are not permanent and become extinct before populations have built up to self-sustaining levels.

The similarity between the New Zealand and US interceptions independent data sets corroborates their accuracy and suggests that it is valid to combine the data to provide a larger data set that better describes which species are commonly shipped around the world in wooden goods and packaging materials. The combined data set covers a greater species pool and is likely to be more representative of the spread of Scolytinae through global trade. To begin with, the US data do not provide useful insights into the species that originate from the US, whereas the New Zealand data do, and vice versa. Unfortunately, neither New Zealand nor US inspections were applied at random, and there was a certain preference for inspection of shipments from countries that were known to be more frequently infested. Nevertheless, these data sets can still be expected to reflect the relative arrival frequency of such species. Another US interception data set (AQIM) with random sampling and fewer biases exists (Work et al. 2005), but it could not realistically have been used to relate propagule pressure and establishment because the AQIM data set is much smaller, covers only a relatively short period of about 5 years, and includes data on only 559 insect interceptions, across all taxa, of which just 69 were identified to species.

Our examination of the relationship between the combined New Zealand and US interception rates and the worldwide establishment of true bark beetles showed a clear pattern of preferential establishment of frequently intercepted species. This is a rare example where a link between propagule pressure and establishment has been shown for a taxon other than birds (Kolar and Lodge 2001; Duncan et al. 2003). Unfortunately, compilations of established insect species are innately imperfect, and this is probably also true for Scolytinae, despite the interest in this particular group. Establishments of birds are likely to be noticed more easily because of their larger body size and the attention they receive. Scolytinae are relatively small and cryptic, many are associated with plants that are not commercially important, and their identification is difficult. Also, some established species do not become invasive and remain at low population levels and with limited distribution (Mack et al. 2000), mak-

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ing their detection difficult. On the other hand, over-reporting has occurred when quarantine interceptions that were lodged with museums have been mistaken as establishments. This was noticed in several cases of establishments reported for New Zealand (Brockerhoff et al. 2003). Thus we attempted to verify the worldwide establishments reported here but uncertainties remain about some records. However, it is encouraging that even when all unverified establishments are excluded from the analysis, "high-interception" species (Table 5) still have a much greater share of establishments (63%) than less frequently intercepted species. Despite some shortcomings in the worldwide establishment data, the interception and establishment data set we used is likely to be among the best available for insects.

The strength of the correlation between New Zealand and US interception data is notable and perhaps an indication of the degree of globalization in trade patterns. Similarities in both interceptions and establishments have been noted for other wood-borer taxa. Over the last decade, the so-called Asian longhorned beetle (*Anoplophora glabripennis*) appeared in the US, Austria, France, Germany, and Canada, and it was also intercepted in New Zealand. This is probably related to the increase in trade with China and Korea. Once a species has become established in a new territory, its likelihood of further spread is increased. For example, more *Hylurgus ligniperda* were intercepted in New Zealand in shipments from its exotic range in Australia and Chile than from its native Eurasia. *Hylurgus ligniperda* is now established in countries on all continents and likely to become a cosmopolitan species.

Niemelä and Mattson (1996) suggest that the predominance of species established in the US that originated from Europe is related to a combination of abundant arrivals, the availability of host plants, and their apparent superiority as invaders over the native US species. It is noteworthy that European, or Palaearctic, Scolytinae also dominated the interceptions in both the US (Haack 2001) and New Zealand. However, contrary to their predominance in interceptions, European Scolytinae were less successful as invaders in New Zealand, in absolute numbers and even less so relative to their share of interceptions compared with Australasian (Australian) species. Although this observation is based on a small number of established species, it suggests that European species are perhaps not universally superior as invaders. Interestingly, among the approximately 50 Scolytinae established in the US, not one is from Australia, and this appears to correlate with the small number of Australian species intercepted in the US (Haack 2001). The high representation of Australian species among establishments in New Zealand is probably related to the proximity of the two countries, which are separated by only about 2000 km of ocean.

Another factor that needs to be considered when relationships between interceptions and establishments are examined is the possibility that temporal changes in trade and propagule pressure of species may affect the result. For example, over the last decade there has apparently been an increase in interceptions and incursions of the Asian longhorned beetle, probably as a result of outbreaks in its native China and increased trade with that region. Such temporal changes may explain why there are six established Scolytinae in New Zealand that were not represented in the interception data. At least three of these were already present before 1950 when interception records began (Brockerhoff et al. 2003), and their arrival rate may have been higher in the more distant past. The other three species were detected between 1972 and 1978 but they may also have been present before 1950 because the potentially long lag period at the beginning of an invasion (e.g., Mack et al. 2000) can cause long delays before a species is detected.

More research into historical interceptions and establishments combined with ongoing monitoring of interceptions should improve our ability to predict which species are probable invaders. Also, we need to learn more about the biological characteristics that determine why some species are more likely than others to become established when they are transported with wooden goods and packaging materials in relatively small numbers. For example, small founder populations of Scolytinae that infest dead or dying trees can successfully colonize host material, whereas "primary" species, such as *Dendroctonus ponderosae*, which tend to mass attack live trees, may not succeed unless they are abundant (Haack 2001). This may reflect differences between inbreeding and outbreeding species (Haack 2001). So far, few primary species appear to have become established outside their native range, and it would be encouraging if such species are in fact less invasive. However, contrary to expectation, even species that preferably attack dead or dying trees in their native range can become aggressive invasive species and cause much tree mortality, as shown with *Dendroctonus valens* in China (Gao et al. 2005).

Our study of interceptions and establishments of Scolytinae contributes to the knowledge of the arrival and establishment stages of invasion processes of this group of significant forest pests. We can expect that there will be more invasions of Scolytinae despite the increase in quarantine efforts resulting from our growing awareness about the impacts of invasive species. However, given the potential economic and ecological implications of the spread of wood and bark borers trough global trade, particularly in solid wood packaging, the use of alternative materials such as processed wood should urgently be considered to reduce the risks associated with this pathway.

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