A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe

Alain Roques, Marie-Anne Auger-Rozenberg, Solen Boivin

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Abstract: We compared the recruitment of phytophagous arthropod pests onto exotic conifers introduced in Europe without any congeners with that of exotic conifers that have native congeners. In 130 years of extensive plantation forestry in Europe, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) recruited only 87 arthropod species, i.e., only 33.9% of the number of associated arthropod species in its native range (257 spp.). Exotic species of Cupressaceae without indigenous congeners also recruited only a portion (3.4% to 57.9%) of the arthropod fauna observed in their native range. In both cases, the majority of the recruited species were polyphagous, i.e., that they can feed on plants of different families of conifers and (or) angiosperms. In contrast, exotic conifers with native congeners recruited most of the insects colonizing the native congeneric conifers. Differences in arthropod recruitment were observed according to both guild and feeding habit, with the externally feeding herbivores being dominant. Typically, the damage caused by native insects that had been recruited by exotic conifers without congeners was limited, whereas the damage caused by native insects that had been recruited by exotic conifers with congeners often led to severe outbreaks at the time the shift between hosts occurred. However, when a highly specialized exotic insect was introduced along with the host, the invasive insect tended to occupy the entire niche, causing more damage than in the original range, in the absence of natural enemies and indigenous competitors.

Résumé : Le recrutement d'arthropodes phytophages par des conifers exotiques introduits en Europe sans congénères autochtones a été comparé à celui de conifères exotiques présentant des congénères natifs. En 130 ans de plantations importantes en Europe, le sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) n'a recruté que 87 espèces d'arthropodes, soit seulement 33,9 % du total des 257 espèces qui y sont associées dans la zone d'origine. Les espèces exotiques de Cupressacées sans congénères natifs n'ont recruté que de 3,4 à 57,9 % autant d'espèces que dans leur zone native. Dans tous ces cas, la plupart des insectes sont polyphages et capables de se nourrir sur différentes familles de conifères et (ou) d'angiospermes. A l'opposé, la plupart des insectes colonisant les conifères présentant des congénères proviennent de ces congénères. On a aussi observé des différences de recrutement selon la guilde et les types alimentaires, avec une dominance des herbivores se nourrissant de manière externe sur le feuillage. Les insectes recrutés ne produisent que rarement des dégâts, voire des pullulations, sur les conifères sans congénères natifs. En revanche, l'introduction d'insectes exotiques hautement spécialisés (comme le chalcidien des graines de Douglas) se traduit par une occupation maximale de la niche considérée, en l'absence d'ennemis naturels comme de compétiteurs indigènes.

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Introduction

During the 20th century, exotic conifers have increasingly been planted all over the world to meet the demand for wood products as well as for ornamental purposes (Zobel et al. 1987). In Western and Northern Europe, several exotic species of Pinaceae, namely Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Doug. ex. Loud. var. *latifolia* Engelm.), Monterey pine (*Pinus radiata*

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D. Don.), and Sitka spruce (*Picea sitchensis* (Bong.) Carrière), presently constitute important portions of the forested ecosystems. For instance, Douglas-fir was first introduced from western North America to Europe in 1827 and has been extensively planted since the 1860s–1870s, with a noticeable acceleration following World War II (De Champs 1997). Today, there are about 650 000 ha of Douglas-fir planted in Europe; 357 000 ha are located in France, where the species represents 7.1% of the total area covered by conifers (AFOCEL 2004). Similarly, most European hedgerows are increasingly dominated by exotic conifers of the family Cupressaceae such as *Chamaecyparis lawsoniana* (A. Murray) Parl., *Cryptomeria japonica* (L. f.) D. Don, *Thuja plicata* Donn ex D. Don, and *Cupressus sempervirens* L. The latter species, also known as the evergreen cypress, was introduced two millenniums ago by the Ancient Greeks and the Romans (Baumann 1982).

The increase in the surface planted with exotic conifers has resulted in native insects being more regularly exposed to such species. From a scientific perspective, tree introduc-

tions can be viewed as large-scale manipulative experiments that test the response of insects to novel hosts. In such experiments, controls are represented either by the tree's herbivore assemblage from its native range (Strong et al. 1977) or by the assemblages on native plants coexisting with the exotic tree in the area of introduction (Strong 1974a; Leather 1986). Such experiments also provide a rare opportunity to study phytophagous communities as they are being assembled from the local pool of insect species with no history of contact with their new hosts, and to determine the relative importance of ecological and evolutionary processes in shaping herbivorous assemblages (Novotny et al. 2003).

The literature contains contradictory results on the relative susceptibility of exotic and native tree species to phytophagous insects (DeGomez and Wagner 2001). Based on the observation of a few outbreaks (e.g., Drooz and Bustillo 1972), the rate of insect recruitment by exotic trees has probably been overemphasized because of experiences with cosmopolitan cultivated crops such as cocoa, tea, coffee, rice, sugarcane, maize, and soya bean (Tahvanainen and Niemelä 1987). These plants show low chemical defences following their cultivation as monoculture crops under high fertilization regimes, and they rapidly accumulated herbivores from the native faunas, mostly polyphagous externally feeding insects, without a need of evolutionary adaptation (Strong et al. 1984; Janzen 1986). According to Strong et al. (1984), such colonization is typically asymptotic, and recruitment of insect populations stabilizes within ca. 300 years of the introduction of the host. Similarly, Evans (1987) found that Sitka spruce introduced in Great Britain has recruited more species of acquired phytophagous insects than in its native North American range. Conversely, very slow insect recruitment has been observed for some tree species transferred from one continent to another, such as oaks from Europe to South Africa (Moran and Southwood 1982) and *Eucalyptus* spp. from Australia to Africa and America (Strong et al. 1984). Tahvanainen and Niemelä (1987) pointed out that strongly defended or chemically isolated newly introduced plants probably require special adaptations before local insects are able to utilize them, and therefore they can be colonized only through evolutionary processes, leading to a very slow recruitment. In such cases, the equilibrium could be achieved only over a geological time scale (Southwood 1960). However, both processes — rapid initial colonization, which is mainly governed by ecological factors, and slow evolutionary recruitment — could be superimposed based on the level of the plant's resistance and the colonization ability of the local insect species (Tahvanainen and Niemelä 1987).

The taxonomic isolation or relatedness of the introduced trees from the local flora has been suspected to explain, at least partly, the variation in the rate of insect recruitment among tree species (Lawton and Schröder 1977; Connor et al. 1980; Neuvonen and Niemelä 1981). Few insects specialize on just a single plant species, and even the more specialized monophagous feeders tend to be able to feed on congeneric species (Niemelä and Mattson 1996). The degree of taxonomic isolation of the exotic species is, however, difficult to determine. Among the various approaches detailed by Kennedy and Southwood (1984), the most convenient one seemed to consist of ranking tree species as subgeneric, congeneric, confamilial, or only non-confamilial, in the area of introduc-

tion (Connor et al. 1980). After the Quaternary glacial periods Europe was left with a limited number of conifer species and genera. Genera such as *Chamaecyparis*, *Thuja*, and *Pseudotsuga*, which were formerly present in Europe, went extinct during late Tertiary period and Pleistocene (Sauer 1988; Czaja 2000). As a result, many monophagous and oligophagous European insect species undoubtedly went extinct along with these host plants (Niemelä and Mattson 1996). This context provides an opportunity to assess the importance of taxonomic isolation on recruitment rate by comparing phytophage colonization among introduced conifers with and without native congeneric taxa, and comparing conifer families. However, only a few synthetic studies are available, essentially dealing with species having native congeners in Europe in the genera *Pinus* (*Pinus contorta*, Lindelöw and Björkman 2001) and *Picea* (*Picea sitchensis*, Evans 1987). In spite of its use in large plantations, Douglas-fir has been little studied for its entomofauna, and most of the available information is scattered in "grey" literature. The situation is no better for the other conifer species without native European congeners (*Chamaecyparis*, *Cryptomeria*, and *Thuja* in the family Cupressaceae; *Cedrus* and *Tsuga* in the family Pinaceae).

In this paper, current knowledge on the arthropod species associated with Douglas-fir and several Cupressaceae introduced into Europe is summarized and used to compare the community structure in Europe with that in the native range of each tree species. Also, this information was used to compare the colonization processes of exotic conifer species without congeneric species in the area of introduction (i.e., Douglas-fir, *Chamaecyparis lawsoniana*, *Cryptomeria japonica*, and *Thuja plicata*) with that observed on an exotic conifer species with native congeners in the area of introduction, lodgepole pine.

Material and methods

Data on the arthropod fauna of Douglas-fir in Europe were extracted from published reports (e.g., France: Legrand 1990, 1997, 2004; Italy: Roversi et al. 1993; Poland: Dominik 1972, 1979; Borowski 1997), from records dealing with specific guilds (foliage: Hatcher and Winter 1990; cones and seeds: Roques 1981, 1983; Křístek et al. 1992; Skrzypczyńska 1996), from observations in arboreta (Čzermák 1952; Hrubík 1973), and from various unpublished reports by foresters, especially those following the 1999 windstorm that hit forests of Western Europe. A colonized host is defined by Fraser and Lawton (1994) as one with two or more records of an arthropod species that is normally associated with other plants and is found feeding (as an adult) and (or) completing larval development under field conditions. The entomofauna of Douglas-fir in North America was compiled from Furniss and Carolin (1992) and Wood et al. (2003) for the western United States, from Holsten et al. (1985) for Alaska, and from the list of conifer defoliating insects of British Columbia (http://www.pfc.forestry.ca/entomology/defoliators/). We also examined more specific publications for cone and seed insects (Keen 1958; Hedlin 1974; Hedlin et al. 1980; Yates 1986) and bark beetles (Bright 1976). We finally developed a bibliographical analysis for both geographic areas using CAB abstracts 1972–2004 as a primary source to find addi-

Fig. 1. Comparison of the percentage of species in the arthropod orders that have colonized Douglas-fir in Europe and in its natural North American range.
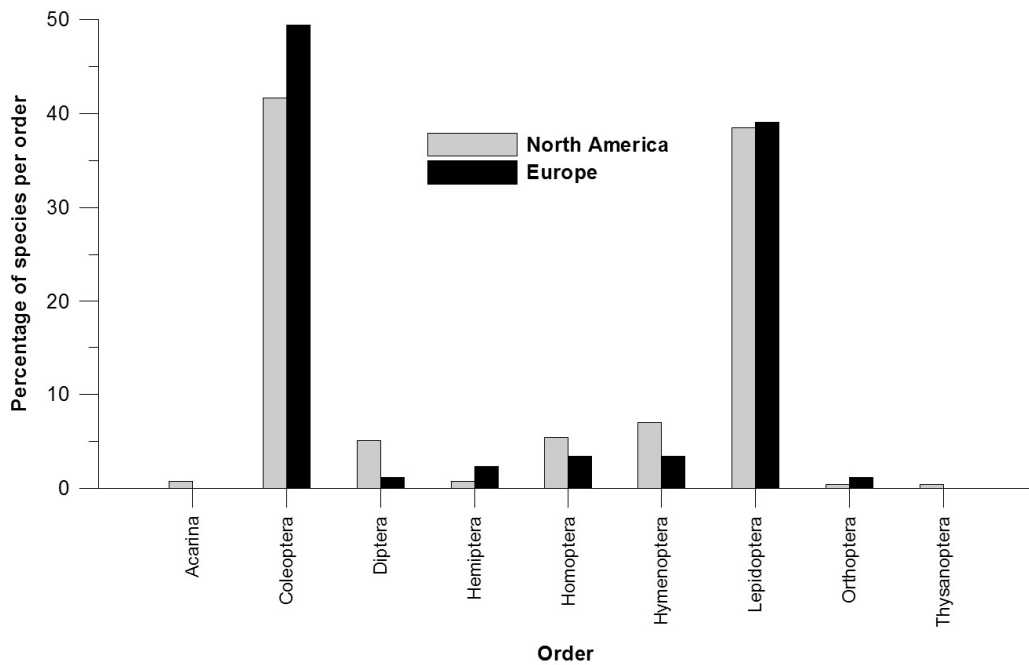
tional species records that were not mentioned in the studies cited above or discovered after their publication.

To compare the degree of host specialisation for the insects colonizing Douglas-fir in its native range with that of the insects recruited in the area of introduction, several parameters were established. Each insect species was assigned to one of the following categories (Lindelöw and Björkman 2001): (*i*) monophagous (i.e., feeding apparently restricted to plants from a single genus); (*ii*) oligophagous (i.e., feeding on plants from several genera of the same family); and (*iii*) polyphagous (i.e., feeding on plants from more than one family). Furthermore, species feeding only on conifers were distinguished from those feeding on both conifers and angiosperms. Whenever possible, we tried to identify the original host tree species from which an insect species shifted to the exotic tree, but in most cases literature data only allowed us to determine the main host (i.e., the host onto which insect records are the more frequent). The type of tree tissue fed upon by immature stages was also used to further define the level of host specialization. Insects were first assigned to one of the following two categories: (*i*) herbivores, which feed on foliage and reproductive structures, and xylophages, which feed in phloem and xylem of living, dying, or dead trees, and include root feeders; and (*ii*) external chewers, sap feeders, leaf miners, gall formers, bud and shoot borers, or pollen and seed-cone feeders.

The list of insects recruited by *Cryptomeria japonica*, the North American species of *Chamaecyparis*, and *Thuja plicata* (= *Thuja orientalis* L.) introduced in Europe was established from Hrubik (1973), Schwenke (1982), Roques (1983), Hatcher and Winter (1990), and various other sources (e.g., Golan 2003; Golan and Jaskiewicz 2002; Gomboc 2003; Rouault 2002). The entomofauna present in the native areas of these tree species could be ascertained for only three guilds (external chewers, cone and seed insects, and xylo-

phages). They were extracted from Kobayashi (1976, 1981), Li and Li (1997), and Liu (1987) for *Cryptomeria japonica* in eastern Asia, while the data for *Chamaecyparis lawsoniana*, *Chamaecyparis nootkatensis* (D. Don) Spach, and *Thuja plicata* in North America were compiled from Keen (1958), Hedlin et al. (1980), Holsten et al. (1985), Yates (1986), Furniss and Carolin (1992), Duncan (1996), and the list of conifer defoliating insects of British Columbia (cf. above).

Faunal records were compared between native and introduced ranges of the tree species using contingency tables and log likelihood ratio G test (Sokal and Rohlf 1995).

Results

Patterns of colonization of Douglas-fir in Europe

A total of 87 indigenous species have been recruited by Douglas-fir in Europe (Appendix A, Table A1). This value represents only 33.9% of the overall species richness observed in the native North American range of Douglas-fir, where a total of 257 arthropod species (255 insects and two mites) belonging to nine orders and 45 families have been recorded. In addition, we observed six species that were introduced from North America together with the host tree and one species of Asian origin (*Xylosandrus germanus* (Blandford)). The species recruited in Europe belonged to seven orders (Fig. 1) and 24 families of insects (Fig. 2). Coleoptera predominated (43 species, i.e., 49.4%) with Lepidoptera second (34 species, i.e., 39.1%), followed by, in decreasing importance, a few Hymenoptera, Homoptera, Hemiptera, Diptera, and Orthoptera. Native European mites as well as thrips (Thysanoptera) have not yet colonized Douglas-fir, but the relative proportion of species in each insect order did not differ significantly between North America and Europe (Fig. 1; $G = 8.22$, df = 7, $P = 0.223$). Similarly, the relative proportion of insect species in each family did not differ globally

Fig. 2. Comparison of the number of species per arthropod family that have colonized Douglas-fir in Europe and in its natural North American range.
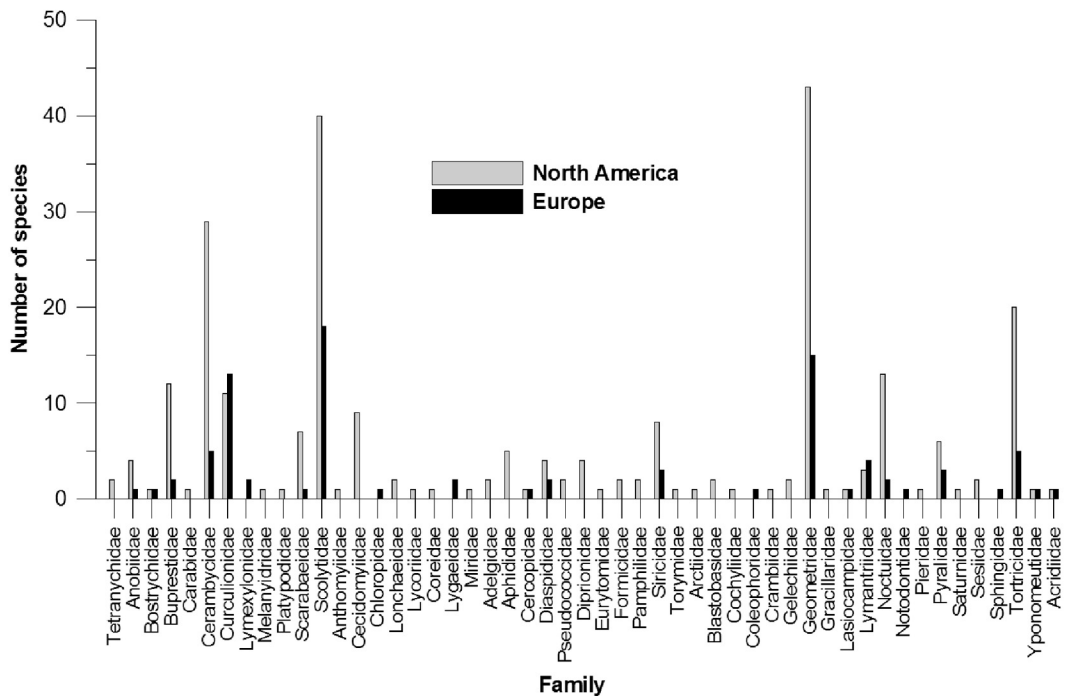
between the native and introduced ranges of Douglas-fir (Fig. 2; G = 112.65, df = 51, P = 0.083). However, recruitment has not yet occurred in Europe in some families that are well represented in the native range, e.g., Diprionidae (Hymenoptera) and Aphididae (Homoptera), whereas recruitments were observed in six insect families not recorded in the native range (Notodontidae, Coleophoridae, Sphingidae, Lymexylonidae, Chloropidae, Lygaeidae). The proportion of Lepidopteran species was quite similar between Europe and North America (39.1% vs. 38.5%) but there was a proportionally larger recruitment of Coleoptera in Europe (49.4% vs. 41.6%). This difference was mainly due to a higher number of phyllophagous weevils in Europe than in the native range (13 species, 14.9% of the total richness vs. 11 species, 4.3% of the total richness).

The degree of host specialization among the recruited insects is shown in Fig. 3. Polyphagous species (originally feeding on different conifer families and (or) on angiosperms) were dominant, representing 42.5% of the total species recruited. Oligophagous species (feeding on different genera of Pinaceae) and monophagous species accounted for 27.6% and 29.9% of the shifts, respectively (Fig. 3a). Most of the monophagous insects colonising Douglas-fir in Europe came from *Abies alba* Mill. and *Pinus* spp. rather than from *Picea abies* (L.) Karst. and *Larix decidua* Mill. A few species were recruited from junipers. However, when only the main host of the recruited insects was considered, most recruited species came from *Picea* rather than from the other genera of Pinaceae (Fig. 3b).
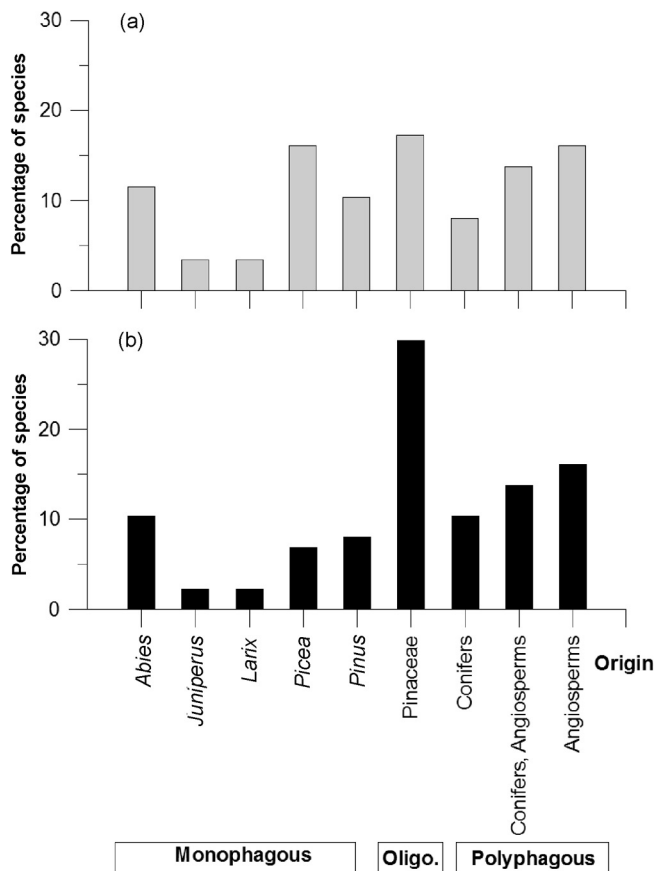
Despite the absence of native gall maker in Europe, the guild structure of Douglas-fir did not differ significantly between the original and introduced ranges (Fig. 4; G = 5.003, df = 6, P = 0.416). It consisted predominantly of xylophages and external chewers in both areas. Another striking pattern was that the colonizing external chewers were predominantly

generalists, whereas the xylophagous colonizers mostly consisted of monophagous species, essentially originating from *Abies alba*, and oligophagous species related to Pinaceae (Table 1). Cones and buds have not been colonized by specialists. Most of the phyllophagous weevils cited above as contributing to a higher proportion of Coleoptera on Douglas-fir in Europe were highly polyphagous species. When the feeding habits of the recruited insects were examined, one could see a preponderance of externally feeding herbivores (i.e., feeding on the exterior of plants), such as chewers and sap feeders, over endophagous herbivores (i.e., feeding within plant tissues), such as bud and cone feeders and gall makers. Thus, the externally feeding herbivores were 5.9 times as numerous as the endophages in Europe (41:7; Fig. 4), whereas they were only 2.5 times as numerous in North America (i.e., 107:42).

The recruited insects feeding behaviour on the exotic hosts was usually the same as that on the original host (Appendix A, Table A1). A noticeable exception was a pine cone pyralid, *Dioryctria simplicella* Hein. (= *Dioryctria mutatella* Fuchs), whose larvae originally feed on cones and shoots of Scots pine (*Pinus sylvestris* L.) On Douglas-fir, however, *D. simplicella* larvae girdled branches and trunks and fed on seed cones (Vouland et al. 1990; Roques 1983).

Native species shifting onto Douglas-fir rarely caused outbreaks. A few records concerned polyphagous Lepidopteran defoliators. A lymantrid, *Orgyia antiqua* L., caused large defoliation in Poland (Burzyński 1978). Elswhere than in Europe, Kay (1983) also recorded several outbreaks of a geometrid native to New Zealand, *Pseudocoremia suavis* Butler. Damage by a notodontid pine specialist, the winter pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiff.), also increased in southern Europe, as the moth has become more frequently encountered in Douglas-fir stands along its latitudinal and altitudinal range extension with global
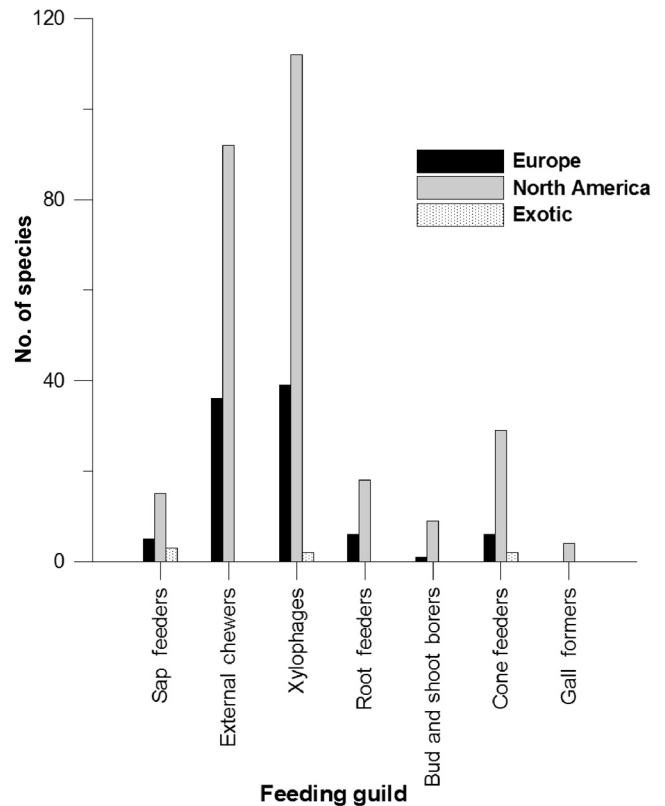
Fig. 3. Degree of host specialization of the arthropod species that have colonized Douglas-fir in Europe. (*a*) Percentage of species calculated with regard to the main host of the arthropod (see text). (*b*) Percentage of species calculated with regard to the host range exhibited by the arthropod.

Fig. 4. Comparison of the guild structure of the entomofauna exploiting Douglas-fir in the natural range (North America) and in the introduced range (Europe) (a species may belong to several feeding guilds). Exotic insect species introduced to Europe are also shown.

warming (Battisti et al. 2005). None of the 18 native scolytids developing in trunks and logs of Douglas-fir (Fig. 2) have caused severe damage yet. Even following the 1999 wind-storm, which felled large areas planted with Douglas-fir in Western Europe, the percentage of trees attacked by bark beetles remained significantly lower in Douglas-fir than in native Pinaceae species. A survey conducted during 2000–2001 in France revealed that only 2.6% of the Douglas-fir trees surveyed had been attacked by autumn 2000 and only 6% had been attacked by autumn 2001, while the attack rate reached 36% and 72% for *Picea abies* (Nageleisen 2002).

In contrast, an invasive chalcid specialist of Douglas-fir seeds, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), destroyed most (up to 100%) of the annual seed crop in the majority of European plantations, especially in the seed orchards (Roques 1981; Rappaport and Roques 1991; Jarry et al. 1997), whereas less than 20% of the seeds were generally infested in the native American range (Rappaport and Volney 1989; Schowalter and Haverty 1989). *Megastigmus spermotrophus* was probably introduced during the last part of the 19th century, along with its host, to Europe and New Zealand (Roques and Skrzypczyńska 2003). In the newly colonized areas, only a few insects shifted to cones, mostly polyphagous and oligophagous species that caused very limited damage to cones and seeds (Roques 1983). In the near

absence of competitors and natural enemies, the invasive chalcid tended to occupy the entire seed niche. The same process was observed in New Zealand (Bain 1977). In contrast, the presence of a large number of competing cone insects in the native range probably explains the limited seed infestation by *M. spermotrophus* because the chalcid is the last species to oviposit into cones (Fig. 5; Roques et al. 2003). However, the recent introduction in Italy and Slovenia of another exotic cone feeder, the western conifer-seed bug, *Leptoglossus occidentalis* Heid. (Hemiptera: Coreidae), may further limit the preeminence of *M. spermotrophus* in Europe (Bernardinelli and Zandigiacomo 2002; Gogala 2003).

A similar situation was observed for the Cooley spruce gall aphid, *Gilletteella cooleyi* (Gill.), which induced severe defoliation on Douglas-fir in several European countries after having been introduced from North America in the early 1900s (Goix 1982; Parry and Spires 1982; Stephan 1987; Legrand 1990; Roversi and Nocentini 1996). The presence of a larger number of competing native defoliators and the need for a primary host to complete its cycle, namely a spruce species, may, however, have prevented the aphid's damage from reaching levels similar to those observed with the seed chalcid.

Patterns of colonization of exotic Cupressaceae in Europe

Insect recruitment largely differed among exotic species of Cupressaceae introduced into Europe (Table 2; Appendix A,

Table 1. Number of arthropod species per feeding guild that have colonized Douglas-fir in Europe according to original host (a species may belong to several feeding guilds, e.g., external chewer as adult and root feeder as larva for several weevils).

Origin	Sap feeders	External chewers	Xylophages	Root feeders	Bud and shoot borers	Cone and seed feeders
Abies	0	1	7	0	1	0
Juniperus	0	1	1	0	0	0
Larix	0	2	0	0	0	0
Picea	0	2	3	0	0	1
Pinus	1	2	4	0	0	1
Pinaceae	2	7	15	1	0	3
Conifers	1	6	2	0	0	0
Conifers and angiosperms	0	7	5	3	0	0
Angiosperms	1	8	2	2	0	1
Exotic species	3	0	2	0	0	2

Fig. 5. Comparison of the entomofauna exploiting cones and seeds in the introduced range (Europe) with that observed in the natural range (North America) of Douglas-fir. Each arrow indicates the approximate period of oviposition or predation (seed bug) of the corresponding species with regard to the phenology of cone development. The histograms figure the relative impact on seeds of *Megastigmus* seed chalcids compared with that of the other insects in both areas.
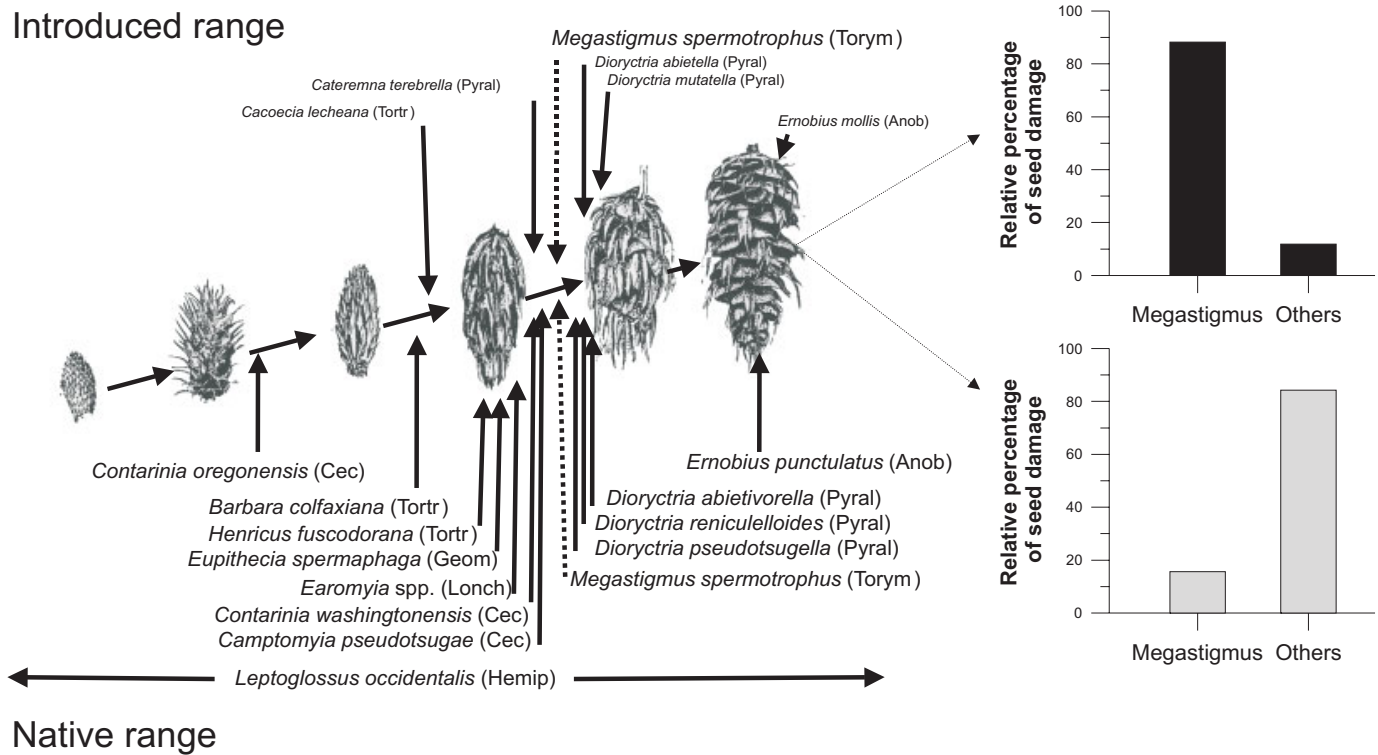

Table A2). Recruitment by *Cryptomeria japonica* was extremely limited, whereas that on *Thuja* spp. and *Chamaecyparis* spp. reached 28 and 16 indigenous insects, respectively. Given that reliable data about the native range's entomofauna existed for only a subset of the three guilds (i.e., external chewers, cone and seed feeders, and xylophages), the overall species richness for these three guilds in the area of introduction amounted only to 3.4%, 25.4%, and 57.9% of that observed in the native range of the three Cupressaceas genera, respectively ($G = 11.694$, df = 2, $P = 0.003$; Table 2).

Recruitment also differed significantly among the feeding guilds for *Thuja* spp. ($G = 13.131$, df = 2, $P = 0.001$; Table 2) because of a very limited recruitment of external chewers (four species) compared with the richness of the native range (46 species), but there was no such difference for *Chamaecyparis* spp. ($G = 0.303$, df = 2, $P = 0.860$). The number of xylophagous species recruited by the *Thuja* spp. and *Chamaecyparis* spp. introduced into Europe was less than half of that in their native range. Cones and seeds were almost unexploited by insects except in *Chamaecyparis*. Not

Table 2. Colonization by insects of exotic Cupressaceae introduced in Europe compared with the entomofauna observed in the original range of the tree species (North America for *Chamaecyparis* spp. and *Thuja* spp., eastern Asia for *Cryptomeria japonica*), and degree of host specialization of the arthropod species.

Species	Range	Total insect species	External chewers	Xylophages	Cone and seed feeders	Exotic species	Monophages (%)	Oligophages (%)	Polyphages (%)
Chamaecyparis spp.	Europe	16	2	6	3	2	0.0	60.0	40.0
	Native	22*	5	10	4	0	36.4	50.0	13.6
Cryptomeria japonica	Europe	2	1	0	0	0	0.0	0.0	100.0
	Native	30*	7	6	16	0	53.3	23.3	23.3
Thuja spp.	Europe	28	4	14	0	1	0.0	50.0	50.0
	Native	81*	46	20	5	0	8.6	37.1	54.3

*Data only partial.

one monophagous species was recruited, whatever the guild and the tree species (Table 2). The colonizing insect assemblage consisted equally of oligophagous species, capable of attacking several native Cupressaceae, and polyphagous species, developing on a large set of conifer species and even angiosperms (Appendix A, Table A2). The entomofauna observed in the native range of *Cryptomeria* and, to a lesser degree, *Chamaecyparis* spp. was more specialized. However, polyphagous species were dominant in the native range of *Thuja* spp.

An outbreak of indigenous insects has not yet been recorded in the introduced range of the three exotic Cupressaceae; however, a juniper flat-headed borer, *Lampra festiva* L., is causing increased damage on *Thuja* spp. in France, probably because of the drought conditions currently being observed (Chauvel 1997; A. Roques, unpublished results). Only two invasive species were observed. The midge, *Janetiella siskiyou* Felt, which exploits *Chamaecyparis* spp. seed cones, was recorded for the first time in 1931 in the Netherlands (De Meijère 1935). Being the sole occupant of the cone niche in Europe, it is now found all over Europe where *Chamaecyparis* plantations exist (Coutin 1976; Roques 1983). A similar process probably occurred with an arborvitae leafminer, *Argyresthia thuiella* (Packard), which was introduced from Canada during the 1970s (van Frankenhuizen 1974; Csóka 2001).

Discussion

In all of the cases we examined, an exotic conifer species introduced into Europe without any native congeners had fewer insects associated with it than in its native range. However, large differences existed among species, with *Cryptomeria* having recruited only 3.4% of the number of associated species in its native Asian range, whereas this proportion reached 25.3% in *Thuja*, 33.9% in *Pseudotsuga menziesii*, and 57.9% in *Chamaecyparis*. Obviously, a bias was likely to exist because of differences in sampling efforts according to the economic value of the tree species, especially for *Cryptomeria*, but the data concerning the three last species generally supported the predictions of Strong (1974a, 1974b) regarding the asymptotic accumulation of species richness on new host trees. Strong's model predicted that more than 60% of the original value of the species richness is reached over an ecological time period, i.e., within ca. 300 years following introduction. Douglas-fir, which has been present in

Europe as large plantations for ca. 130 years, has accumulated ca. 60% of the original value.

It has also been speculated that the number of newly recruited species depends on the size of the plantations (Strong 1974c). This might explain the differences in recruitment observed in the exotic Cupressaceae. Although we cannot obtain precise data about the respective areas of plantations in Europe because they consist mostly of hedgerows, the comparatively lower number of species observed on *Cryptomeria* might be attributable to the smaller plantings of this tree species. On the other hand, a survey carried out in New Zealand revealed that introduced Douglas-fir accumulated 77 insect species there (Zondag 1982; USDA 1992), i.e., 88.5% of the number of species recruited in Europe, although the plantation area is about six times as small (109 000 vs. 650 000 ha). In addition, the total arthropod recruitment on Douglas-fir in Europe was not so different from that observed for an exotic conifer with native congeners, lodgepole pine. Lindelöw and Björkman (2001) counted a total of 81 species of indigenous insect species that shifted to this exotic species in 600 000 ha of plantations in Sweden. This corresponded roughly to 20% of the species richness in the native American range, which we estimated (ca. 400 species) using data from Furniss and Carolin (1992). By contrast, Evans (1987) found that Sitka spruce had more species of acquired phytophages in Great Britain than in its native North America (90 vs. 59). However, the plantation area reached ca. 700 000 ha in Great Britain in 1995 (from National Forest inventories of England, Wales, and Scotland; Forestry Commission 2001a, 2001b, 2002), which corresponds to about two times that of its natural area in the native range (calculated from map supplied in Burns and Honkala 1990).

Although the total number of recruited species was rather similar, a comparison of the number of European species respectively observed per insect order on Douglas-fir and lodgepole pine (using data from Lindelöw and Björkman 2001) revealed significant differences in the faunal patterns ($G = 10.304$, df = 5, $P = 0.0356$; analysis with Hemiptera and Homoptera grouped together). This was due to a proportionally more important recruitment of Lepidoptera in Douglas-fir (39.1% vs. 23.5% in lodgepole pine) and of Hymenoptera in lodgepole pine (14.8% vs. 3.4% in Douglas-fir).

Not surprisingly, polyphagous species tended to be better colonizers of alien plants than specialists (Strong et al. 1984; Zwölfer 1988; Fraser and Lawton 1994). Novotny et al. (2003)

showed that the probability that a caterpillar species colonizes alien *Piper* spp. in Papua New Guinea increases with the host range from 3% for the species feeding on a single plant family to 92% for the species with a host range greater than 10 families. This pattern was clearly observed for Douglas-fir as well as for the three species of exotic Cupressaceae, where generalists feeding on several plant families, often including angiosperms, represented 42.5% (Douglas-fir) to 100% (*Cryptomeria*) of the colonizing insects. The opposite pattern was observed for the recruitment of insect species by lodgepole pine, where monophagous and oligophagous species showed greater colonization compared with species with broader host-plant ranges (58.0% and 30.9% vs. 11.1%; Lindelöw and Björkman 2001). Moreover, in that case, specialist lepidopteran species originating from congeneric native Scots pine were significantly more likely to be recruited than were insects originating from other hosts. Lindelöw and Björkman (2001) suggested that dominance of specialists among the species that shifted to the exotic tree is related to the similarity in chemistry and morphology between the two *Pinus* species. Similar trends were difficult to observe in conifers without native congeners, Douglas-fir as well as exotic Cupressaceae. According to recent phylogenetic analyses, the closest relative of Douglas-fir (*Pseudotsuga*) appears to be the genus *Larix*, and the sister group of *Pseudotsuga–Larix* is considered to be *Pinus–Picea* (Wang et al. 2000). Actually, *Larix* contributed very little to the recruitment, whereas most of the monophagous colonizers came from *Abies alba* and *Pinus* spp., and *Picea* when the primary host was considered for the species capable of shifting on several Pinaceae. In exotic Cupressaceae, where no specialist has yet been recorded, the relative importance of oligophagous insects related to the family Cupressaceae in the recruitment on *Thuja* (50%) and, even more, *Chamaecyparis* (60%) suggested closer relationships among tree species of this family than in Pinaceae. On the contrary, the case of *Cryptomeria* showed that this mechanism was not efficient for all species, and that other barriers probably existed. As pointed out by Hatcher (1994), it was not the taxonomic relationship per se that seemed to be important, but the associated similarities in host plants, especially in the secondary chemicals.

Differences in phytophage recruitment by exotic introduced plants were also observed according to guilds and insect feeding habits (Cornell and Khan 1989; Fraser and Lawton 1994; DeGomez and Wagner 2001). The time available for colonization appeared to be important. Strong et al. (1984) suggested that the externally feeding herbivores are more likely to rapidly colonize alien hosts than are insects feeding within plant tissue (endophagous), and certain specialized guilds, such as those exploiting flowers and seeds, may even be totally absent in recently colonized areas (Zwölfer 1988). This pattern was clearly observed for cone and seed insects of both Douglas-fir and exotic Cupressaceae, which were hardly or not at all colonized. By contrast, the pine cone weevil, *Pissodes validorostris* Gyll., shifted from Scots pine to lodgepole pine all over Europe, to the point where the latter species tended to become its preferred host (Annila 1975; Roques 1983; Delplanque et al. 1988). The other kinds of endophagous insects (e.g., bud and shoot borers) were still absent on Douglas-fir and exotic Cupressaceae in Europe,

whereas ectophagous species such as external chewers and sap suckers dominated together with xylophages. Although the overall composition of the feeding guilds recruited by Douglas-fir in Europe and lodgepole pine in northern Europe did not differ significantly by the number of species ($G = 9.717$, df = 6, $P = 0.083$), the proportion of bud- and shoot-boring insects (9.3% vs. 1.1%) and that of foliage-feeding sawflies (12.0% vs. 0%) were noticeably more important in lodgepole pine. Moreover, when Lindelöw and Björkman (2001) calculated the proportion of lepidopteran species recruited by lodgepole pine with regard to the pool present in Sweden, the proportion was highest for shoot- and bud-boring insects and lowest for externally feeding species. These authors suggested that the differences in guild pattern may be due to the specific chemical and morphological properties of the different types of plant tissues. Such a calculation was difficult to accomplish in our case because all forest insects would have to be considered. Fraser and Lawton (1994) also identified a suite of features in British moths that could be associated with the propensity to undergo host range expansion onto introduced conifers, and they suggested that ecological opportunity is an important factor in host range expansion. Such features included feeding on a wide range of woody trees and shrubs, overwintering as ova, and eclosing from the egg in early spring or summer. In addition, the occurrence of grassland, heath, and upland habitats and feeding on certain plant families that are ecologically associated with conifer afforestation (Ericaceae, Salicaeae) increased the likelihood of host shifting. It would be interesting to test the pertinence of these criterion for the insects that have colonized Douglas-fir in Europe.

In contrast to the limited number of outbreaks as yet observed on exotic conifers without native congeners in Europe, many native herbivorous insects were observed to develop outbreaks on lodgepole pine. Lindelöw and Björkman (2001) noticed four species of lepidopteran defoliators (*Dendrolimus pini*, *Lymantria monacha*, *Bupalus piniara*, *Panolis flammea*). Most of these species have also colonized Douglas-fir (see Appendix A, Table A1) but have not develop into outbreaks on this tree species. In addition, larch budmoth, *Zeiraphera diniana* Guénée (Baltensweiler et al. 1977), sawflies (*Neodiprion sertifer*), shoot borers (*Rhyacionia buoliana*), and cone feeders (*Pissodes validirostris*) were capable of outbreaks on lodgepole pine (Delplanque et al. 1988). In the latter case, the difficulty for native parasitoids in locating the weevil larvae developing in an exotic introduced host was assumed to be the major factor allowing such damage on cones of lodgepole pine compared with Scots pine (Annila 1975; Delplanque et al. 1988). Similarly, there were several examples of outbreaks on Sitka spruce of insects coming from congeneric Norway spruce (*Picea abies*), such as European spruce sawfly, *Gilpinia hercyniae* (Hartig) (Williams et al. 2003), green spruce aphid, *Elatobium abietinum* (Walker) (Hendry et al. 2001; Halldorsson et al. 2003), and galling adelgids (Jaskiewicz et al. 2002). A polyphagous defoliator, winter moth, *Operophtera brumata* L., which is primarily associated with deciduous trees, also expanded its range to outbreak on Sitka spruce (Vanbergen et al. 2003).

The enemy-free-space hypothesis, such as formulated by Lawton and McNeill (1979) and Price et al. (1980), may also elucidate relative success of exotic introduced insects in

colonizing trees without congeners. In the near absence of natural enemies and indigenous competitors, exotic introduced insects such as the Douglas- fir seed chalcid, *M. spermotrophus*, and the yellow-cedar seed midge, *Janetiella siskyiou*, tended to occupy the whole seed-cone niche and caused more damage than in their native ranges (Coutin 1976; Rappaport and Roques 1991; Roques et al. 2003). Besides cone and seed insects, Fabre (1994) and Fabre et al. (1999) observed a similar situation for true cedar (*Cedrus atlantica* (Endl.) Manetti) planted in southern Europe without native congeners, which was severely damaged by exotic aphids (*Cedrobium laportei* Remaud. and *Cinara cedri* Mimeur) and torticids (*Epinotia cedricida* Diak.) introduced along with the tree species. However, exotic introduced insects may also outbreak on exotic trees with congeners, although these insects have to cope with a number of competitors. For example, such outbreaks were observed in fir woolly adelgid, *Dreyfusia nordmaniannae* (Eckstein) on *Abies nordmanianna* (Stev.) Spach. (Bejer 1981), and in a North American fir seed chalcid, *Megastigmus rafni*, on *Abies* spp. (Fabre et al. 2004).

Conclusions

Douglas-fir and the exotic Cupressaceae that were introduced into Europe without indigenous congeners tended to recruit native arthropods in a different way than did lodgepole pine, a species with native congeners. Recruitment of the former species, which is rather high considering the limited duration of exposure to native insects, mainly originated from polyphagous species that were not yet capable of saturating the new niches, whereas the recruitment mostly proceeded from monophagous and oligophagous species coming from congeneric tree species in the latter case. However, before drawing any definite conclusions, it would be necessary to examine a larger set of data including several species of exotic conifers with indigenous congeners such as Sitka spruce, Japanese larch (*Larix leptolepis*, (Siebold & Zucc.) Gord.), and Monterey pine, which have been densely planted in some parts of Europe.

An increase in arthropod species diversity on exotics over time is to be expected, especially if the range size increases. However, the introduction in Europe of exotic insect species highly adapted to the exotic host tree might create much more problems when conifers have no indigenous congeners because guilds are yet unsaturated, and the introduction of related exotic species, such as a Douglas-fir bark beetle, *Dendroctonus pseudotsugae*, is likely to result in a full occupancy of the niche. In this respect, quarantine procedures probably need to be reinforced for conifers without any congeners.

Acknowledgements

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Appendix A

Appendix appears on the following page.

Table A1. List of the arthropod species having colonized Douglas-fir in Europe, with their primary host plant (main host genus) and global host range.

Arthropod species and order	Family	Guild	Primary host*	Host range*	Reference
Coleoptera					
Ernobius mollis L.	Anobiidae	Cone feeder, xylophagous	Pinaceae	Pinaceae	Roques 1983
Stephanopachys substriatus Paykull	Bostrychidae	Xylophagous	Pinaceae	Pinaceae	Schwenke 1982
Antaxia helvetica Stierlin	Buprestidae	Xylophagous	*Juniperus*	*Juniperus*	Roversi et al. 1993
Chrysobothris solieri Laporte & Gory	Buprestidae	Xylophagous	*Pinus*	*Pinus*	Roversi et al. 1993
Corymbia rubra L.	Cerambycidae	Xylophagous	Pinaceae	Pinaceae	Dominik 1972
Morimus asper (Sulzer)	Cerambycidae	Xylophagous	Polyphagous (c, a)	Polyphagous (c, a)	Roversi et al. 1993
Prionus coriarus (L.)	Cerambycidae	Xylophagous	Polyphagous (c, a)	Polyphagous (c, a)	Dominik 1972
Tetropium castaneum (L.)	Cerambycidae	Xylophagous	*Picea*	Pinaceae	Dominik 1972
Tetropium fuscum (F.)	Cerambycidae	Xylophagous	*Picea*	Pinaceae	Dominik 1972
Hylastes sp.	Curculionidae	Xylophagous	*Picea*	Pinaceae	Legrand 1997
Hylobius abietis (L.)	Curculionidae	Xylophagous	*Pinus*	Pinaceae	Dominik 1972
Hylobius piceus (De Geer)	Curculionidae	Xylophagous	Conifers	Conifers	Dominik 1972
Hylobius pinastri (Gyll.)	Curculionidae	Xylophagous	*Picea*	Pinaceae	Dominik 1972
Metacinops calabrus Stierlin	Curculionidae	External chewer	Polyphagous (a)	Polyphagous (a)	Roversi et al. 1993
Otiorhynchus armadillo Rossi	Curculionidae	External chewer	Polyphagous (a)	Polyphagous (a)	Roversi et al. 1993
Otiorhynchus multipunctatus (F.)	Curculionidae	External chewer, root feeder	Polyphagous (c, a)	Polyphagous (c, a)	Borowski 1997
Otiorhynchus niger (F.)	Curculionidae	Root feeder	*Abies*	*Abies*	Legrand 1997
Otiorhynchus singularis (L.)	Curculionidae	External chewer, root feeder	Polyphagous (c, a)	Polyphagous (c, a)	Borowski 1997
Pissodes piceae Illiger	Curculionidae	Xylophagous	*Abies*	*Abies*	Legrand 1990
Polydrusus marginatus Stephens	Curculionidae	External chewer	Polyphagous (c, a)	Polyphagous (c, a)	Legrand 1997
Strophosoma capitatum De Geer	Curculionidae	External chewer, root feeder	Pinaceae	Pinaceae	Schwenke 1982
Strophosoma melanogrammus (Förster)	Curculionidae	External chewer, root feeder	Polyphagous (c, a)	Polyphagous (c, a)	Legrand 1990
Lymexylon navale (L.)	Lymexylonidae	Xylophagous	Polyphagous (a)	Polyphagous (a)	A. Roques, unpubl.
Hylecoetus dermestoides (L.)	Lymexylonidae	Xylophagous	Polyphagous (a)	Polyphagous (a)	Dominik 1972
Melolontha melolontha L.	Scarabaeidae	Root feeder	Polyphagous (a)	Polyphagous (a)	Abgrall 1991
Cryphalus abietis (Ratzeburg)	Scolytidae	Xylophagous	Pinaceae	Pinaceae	Roversi et al. 1993
Cryphalus piceae (Ratzeburg)	Scolytidae	Xylophagous	*Abies*	*Abies*	Legrand 1997
Dryocoetes autographus (Ratzeburg)	Scolytidae	Xylophagous	Pinaceae	Pinaceae	Dominik 1972
Gnathotrichus materiarius (Fitch)	Scolytidae	Xylophagous	Pinaceae	Pinaceae	Schwenke 1982
Ips acuminatus Gyllenhall	Scolytidae	Xylophagous	*Pinus*	*Pinus*	Legrand 1997
Ips cembrae Heer	Scolytidae	Xylophagous	*Larix*	Pinaceae	Stoakley 1975
Ips typographus L.	Scolytidae	Xylophagous	*Picea*	*Picea*	Grüne 1979
Pityogenes bidentatus (Herbst)	Scolytidae	Xylophagous	*Pinus*	Pinaceae	Schwenke 1982
Pityogenes chalcographus L.	Scolytidae	Xylophagous	*Picea*	Picea	Schwenke 1982
Pityogenes quadridens Hartig	Scolytidae	Xylophagous	*Abies*	*Abies*	Schwenke 1982
Pityokteines curvidens Germar	Scolytidae	Xylophagous	*Abies*	*Abies*	Legrand 1997
Pityokteines spinidens Reitter	Scolytidae	Xylophagous	*Abies*	*Abies*	Legrand 1997
Pityokteines vorontsovi Jakobson	Scolytidae	Xylophagous	*Abies*	*Abies*	Grüne 1979
Pityophthorus carniolicus Wichmann	Scolytidae	Xylophagous	*Pinus*	*Pinus*	A. Roques, unpubl.
Pityophthorus pityographus Ratzeburg	Scolytidae	Xylophagous	*Picea*	*Picea*	Dominik 1972
Trypodendron lineatus Olivier	Scolytidae	Xylophagous	Pinaceae	Pinaceae	Dominik 1972
Xyleborus dispar F.	Scolytidae	Xylophagous	Polyphagous (c, a)	Polyphagous (c, a)	Dominik 1972
Xyleborus saxeseni Ratzeburg	Scolytidae	Xylophagous	Polyphagous (c, a)	Polyphagous (c, a)	Legrand 1997
Diptera					
Hapleginella laevifrons (Loew)	Chloropidae	Cone feeder	Pinaceae	Pinaceae	Roques 1983
Hemiptera					
Gastrodes abietum Bergroth	Lygaeidae	Sap sucker, cone feeder	Pinaceae	Pinaceae	Roques 1983
Kleidocerys resedae (Panzer)	Lygaeidae	Sap sucker	Polyphagous (a)	Polyphagous (a)	Borowski 1997
Homoptera					
Haematoloma dorsatum (Ahrens)	Cercopidae	Sap sucker	Conifers	Conifers	Roversi et al. 1993
Lepidosaphes newsteadi (Sulc)	Diaspididae	Sap sucker	*Pinus*	*Pinus*	Roversi et al. 1993
Nuculaspis abietis (Schrank)	Diaspididae	Sap sucker	Pinaceae	Pinaceae	Roversi et al. 1993
Hymenoptera					
Urocerus augur (Klug)	Siricidae	Xylophagous	Conifers	Conifers	
Urocerus gigas (L.)	Siricidae	Xylophagous	Polyphagous (c, a)	Polyphagous (c, a)	Dominik 1972
Xeris spectrum (L.)	Siricidae	Xylophagous	Pinaceae	Pinaceae	Roversi et al. 1993

Table A1 (*concluded*).

Arthropod species and order	Family	Guild	Primary host*	Host range*	Reference
Lepidoptera					
Coleophora laricella (Hübner)	Coleophoridae	External chewer	*Larix*	*Larix*	Borowski 1997
Alcis repandata (L.)	Geometridae	External chewer	Polyphagous (c, a)	Polyphagous (c, a)	Hatcher and Winter 1990
Biston betularia (L.)	Geometridae	External chewer	Polyphagous (a)	Polyphagous (a)	Borowski 1997
Bupalus piniaria (L.)	Geometridae	External chewer	*Pinus*	Pinaceae	Bevan and Brown 1978
Deileptenia ribeata (Clerck)	Geometridae	External chewer	Conifers	Conifers	Hatcher and Winter 1990
Eupithecia intricata arceuthata (Frey.)	Geometridae	External chewer	*Juniperus*	Conifers	Hatcher and Winter 1990
Eupithecia lariciata (Freyer)	Geometridae	External chewer	*Larix*	*Larix*	Borowski 1997
Eupithecia pusillata (Den. & Schiff.)	Geometridae	External chewer	*Juniperus*	*Juniperus*	Borowski 1997
Eupithecia tantillaria Boisduval	Geometridae	External chewer	*Picea*	Pinaceae	Hatcher and Winter 1990
Hylaea fasciaria (L.)	Geometridae	External chewer	Pinaceae	Pinaceae	Hatcher and Winter 1990
Macaria liturata (Clerck)	Geometridae	External chewer	Conifers	Conifers	Hatcher and Winter 1990
Macaria signaria (Hübner)	Geometridae	External chewer	*Picea*	Pinaceae	Borowski 1997
Operophtera brumata (L.)	Geometridae	External chewer	Polyphagous (a)	Polyphagous (a)	Hatcher and Winter 1990
Thera britannica Turner	Geometridae	External chewer	*Picea*	Conifers	Hatcher and Winter 1990
Thera obeliscata (Hübner)	Geometridae	External chewer	Conifers	Conifers	Hatcher and Winter 1990
Thera variata (Den. & Schiff.)	Geometridae	External chewer	*Picea*	Pinaceae	Roversi et al. 1993
Dendrolimus pini (L.)	Lasiocampidae	External chewer	Conifers	Conifers	Borowski 1997
Calliteara pudibunda (L.)	Lymantriidae	External chewer	Polyphagous (a)	Polyphagous (a)	Borowski 1997
Lymantria dispar (L.)	Lymantriidae	External chewer	Polyphagous (a)	Polyphagous (a)	Legrand 1997
Lymantria monacha (L.)	Lymantriidae	External chewer	Polyphagous (c, a)	Polyphagous (c, a)	Legrand 1990
Orgyia antiqua (L.)	Lymantriidae	External chewer	Polyphagous (a)	Polyphagous (a)	Burzynski 1978
Agrotis segetum (Den. & Schiff.)	Noctuidae	Root feeder	Polyphagous (a)	Polyphagous (a)	Borowski 1997
Panolis flammea (Den. & Schiff.)	Noctuidae	External chewer	*Pinus*	*Pinus*	Borowski 1997
Thaumetopoea pityocampa (Den. & Schiff.)	Notodontidae	External chewer	*Pinus*	*Pinus*	Roversi et al. 1993
Cateremna terebrella (Zinck)	Pyralidae	Cone feeder	*Picea*	*Picea*	Roques 1983
Dioryctria abietella (Den. & Schiff.)	Pyralidae	Cone feeder	Pinaceae	Pinaceae	Roques 1983
Dioryctria simplicella Heinemann	Pyralidae	Cone feeder, bud borer, xylophagous	*Pinus*	*Pinus*	Roques 1983
Hyloicus pinastri (L.)	Sphingidae	External chewer	Pinaceae	Pinaceae	Roversi et al. 1993
Choristoneura murinana (Hübner)	Tortricidae	External chewer	*Abies*	*Abies*	Du Merle et al. 1992
Ditula angustiorana (Haworth)	Tortricidae	External chewer	Polyphagous (c, a)	Polyphagous (c, a)	Roversi et al. 1993
Epinotia fraternata (Haworth)	Tortricidae	Buds borers	*Abies*	*Abies*	Roversi et al. 1993
Epinotia tedella (Clerck)	Tortricidae	External chewer	*Picea*	*Picea*	Borowski 1997
Ptycholoma lecheana (L.)	Tortricidae	Cone feeder	Polyphagous (a)	Polyphagous (a)	A. Roques, unpubl.
Arghyrestia glabratella (Zeller)	Yponomeutidae	External chewer	*Picea*	*Picea*	Borowski 1997
Orthoptera					
Tetrix bipunctata (L.)	Tetrigidae	External chewer	Polyphagous (a)	Polyphagous (a)	Borowski 1997
Exotic species introduced in Europe					
Oligonychus ununguis (Jacobi)	Tetranychidae	Sap sucker			Borowski 1997
Gilletteella cooleyi (Gilette)	Adelgidae	Sap sucker			Dominik 1972
Elatobium abietinum (Walker)	Aphididae	Sap sucker			Szelegiewicz 1975
Buprestis aurulenta L.	Buprestidae	Xylophagous			Dominik 1980
Leptoglossus occidentalis Heidemann	Coreidae	Cone feeder			Bernardinelli and Zandigiacomo 2001
Xylosandrus germanus Blandford	Scolytidae	Xylophagous			Legrand 1997
Megastigmus spermotrophus Wachtl	Torymidae	Cone feeder			Roques 1983

*a, angiosperms; c, conifers.

Table A2. List of the arthropod species having colonized exotic Cupressaceae introduced in Europe, with their host range.

Arthropod species	Family	Guild	Host range	Reference
***Chamaecyparis* spp.**				
Cinara cupressi (Buckton)	Aphididae	Sap sucker	Cupressaceae	Winter 1989
Palmar festiva (L.)	Buprestidae	Xylophagous	*Juniperus*	Hellrig 1978
Hylotrupes bajulus (L.)	Cerambycidae	Xylophagous	Conifers	Dominik 1972
Planococcus vovae (Nassonov)	Coccidae	Sap sucker	*Juniperus*	Golan and Jaskiewicz 2002
Hylobius abietis L.	Curculionidae	Root feeder	Conifers	Dominik 1972
Carulaspis minima Targioni	Diaspididae	Sap sucker	Cupressaceae	Ülgentürk et al. 2004
Diaspis visci (Schrank)	Diaspididae	Sap sucker	Conifers	Hrubik 1973
Orsillus depressus Muls & Rey	Lygaeidae	Cone feeder	Cupressaceae	Rouault 2002
Orsillus maculatus Fieber	Lygaeidae	Cone feeder	Cupressaceae	Rouault 2002
Cryphalus abietis Ratzeburg	Scolytidae	Xylophagous	*Picea*	Schwenke 1982
Phloeosinus thujae (Perris)	Scolytidae	Xylophagous, shoot borer	Cupressaceae	Hrubik 1973
Urocerus gigas gigas (L.)	Siricidae	Xylophagous	Conifers	Viitasaari 1984
Xeris spectrum spectrum (L.)	Siricidae	Xylophagous	Conifers	Viitasaari 1984
Pseudococcyx tessulatana (Stgr.)	Tortricidae	Cone feeder	Cupressaceae	Hrubik 1973
Argyresthia dilectella Zeller	Yponomeutidae	External chewer	*Juniperus*	Maitland Emmet et al. 1996
Argyresthia trifasciata Stgr.	Yponomeutidae	External chewer	*Juniperus*	Gomboc 2003
Argyresthia thuiella Packard*	Yponomeutidae	Leafminer	Cupressaceae	van Frankenhuizen 1974
Janeetiella siskyiou Felt*	Cecidomyiidae	Cone feeder	*Chamaecyparis*	De Meijere 1935
Cryptomeria japonica				
Hylobius abietis L.	Curculionidae	Root feeder	Conifers	Dominik 1972
Hylotrupes bajulus (L.)	Cerambycidae	Xylophagous	Conifers	Dominik 1972
***Thuja* spp.**				
Cinara cupressi (Buckton)	Aphididae	Sap sucker	Cupressaceae	Winter 1989
Cinara thujafilina (Del Guercio)	Aphididae	Sap sucker	Cupressaceae	Binazzi 1978
Acmaeodera bipunctata (Olivier)	Buprestidae	Xylophagous	*Pinus*	Hellrig 1978
Palmar festiva (L.)	Buprestidae	Xylophagous	*Juniperus*	Hellrig 1978
Hylotrupes bajulus (L.)	Cerambycidae	Xylophagous	Conifers	Dominik 1972
Leptura rubra (L.)	Cerambycidae	Xylophagous	Conifers	Dominik 1972
Phymatodes glabratus (Charp.)	Cerambycidae	Xylophagous	Cupressaceae	Schwenke 1982
Lineaspis striata (Newstead)	Coccidae	Sap sucker	Cupressaceae	Ülgentürk et al. 2004
Parthenolecanium fletcheri	Coccidae	Sap sucker	Conifers, angiosperms	Golan 2003
Planococcus vovae (Nassonov)	Coccidae	Sap sucker	Cupressaceae	Golan and Jaskiewicz 2002
Cossus sp.	Cossidae	Xylophagous	Conifers	Dominik 1972
Hylobius sp.	Curculionidae	Root feeder	Conifers	Dominik 1972
Otiorhynchus ovatus (L.)	Curculionidae	External chewer	Conifers	Schwenke 1982
Otiorhynchus singularis (L.)	Curculionidae	Xylophagous, shoot borer	Conifers, angiosperms	Schwenke 1982
Otiorhynchus sulcatus (F.)	Curculionidae	Root feeder	Conifers	van Tol et al. 2001
Carulaspis carueli (Signoret)	Diaspididae	Sap sucker	Cupressaceae	Ülgentürk et al. 2004
Carulaspis minima Targioni	Diaspididae	Sap sucker	Cupressaceae	Ülgentürk and Çanakcioğlu 2004
Diaspis visci (Schrank)	Diaspididae	Sap sucker	Conifers	Hrubik 1973
Pachypasa otus (Drury)	Lasiocampidae	External chewer	Cupressaceae	de Freina and Witt 1987
Pachypasa limosa (Serres)	Lasiocampidae	External chewer	Cupressaceae	de Freina and Witt 1987
Calopus serraticornis L.	Oedemeridae	Xylophagous	Conifers	Dominik 1972
Cryphalus piceae (Ratzeburg)	Scolytidae	Xylophagous	Conifers	Schwenke 1982
Phloeosinus aubei Perris	Scolytidae	Xylophagous, shoot borer	Cupressaceae	Schwenke 1982
Phloeosinus rudis Blandford	Scolytidae	Xylophagous, shoot borer	Cupressaceae	Schwenke 1982
Phloeosinus thujae (Perris)	Scolytidae	Xylophagous, shoot borer	Cupressaceae	Hrubik 1973
Xyleborus dispar F.	Scolytidae	Xylophagous	Conifers, angiosperms	Schwenke 1982
Xyleborus saxeseni (Ratzeburg)	Scolytidae	Xylophagous	Conifers	Dominik 1972
Argyresthia trifasciata Stgr.	Yponomeutidae	Leafminer	Cupressaceae	Gomboc 2003
Argyresthia thuiella Packard*	Yponomeutidae	Leafminer	Cupressaceae	van Frankenhuizen 1974

*Exotic arthropod species introduced in Europe.