

How can alien species inventories and interception data help us prevent insect invasions?

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Abstract

Information relevant to invasion processes and invasive alien insect species management in Central Europe was extracted from two databases: a compilation of two inventories of alien insects in Austria and Switzerland, and a list of interceptions of non-indigenous plant pests in Europe gathered by the European and Mediterranean Plant Protection Organisation (EPPO) for the period 1995–2004. For one-third of the insects established in Switzerland and Austria, the region of origin is unclear. Others come mainly from North America, Asia and the Mediterranean region. Among the intercepted insects, 40% were associated with commodities from Asia, 32% from Europe and only 2% from North America. Sternorrhyncha, Coleoptera and Psocoptera were particularly well represented in the alien fauna compared to the native fauna. In the interception database, Sternorrhyncha were also well represented but Diptera accounted for the highest number of records. Sap feeders and detritivores were the dominant feeding niches in the alien insect fauna. In contrast, external defoliators, stem borers, gall makers, root feeders, predators and parasitoids were underrepresented. Nearly 40% of the alien insects in Switzerland and Austria live only indoors. Another 15% live outdoors but exclusively or predominantly on exotic plants. Less than 20% are found mainly in 'natural' environments. The majority of introductions of alien insects in Europe are associated with the international trade in ornamental plants. An economic impact was found for 40% of the alien insects in Switzerland and Austria, whereas none is known to have an ecological impact. The implications of these observations for further studies and the management of alien species in Europe are discussed.

Keywords: invasive alien species, non-indigenous insects, pathways of introduction, economic impact, environmental impact, origin of alien species, feeding niche of alien species

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Introduction

Invasive alien species are recognized as one of the leading threats to biodiversity. The ways in which non-native species affect native species and ecosystems are numerous and usually irreversible (Parker *et al.*, 1999). Non-indigenous species also impose enormous costs on agriculture, forestry and human health (Pimentel *et al.*, 2002b). Rapidly accelerating human trade, tourism, transport and travel over the past century have dramatically enhanced the spread of invasive species, allowing them to surmount geographic barriers. Since this tendency is likely to increase (Levine & D'Antonio, 2003), national and international strategies are required to assess the full scope of the threat of invasive alien species and to deal with it effectively.

Insects represent the majority of living organisms and, hence, form a large part of the alien species problem. In many regions, such as North America, Australasia and South Africa, exotic insect pests are considered as important as native pests, if not more so (Pimentel, 2002b). Traditionally, problems have been less severe in Europe (Niemelä & Mattson, 1996). However, in recent years, several pests of economic importance have invaded Europe, inducing more interest in the issue of alien insects. For example, the western corn rootworm, *Diabrotica virgifera virgifera* LeConte, is seriously threatening European maize production (Baufelt & Enzian, 2005); and the horse-chestnut leaf miner, *Cameraria ohridella* Deschka and Dimic, an insect of unknown origin, is causing much public concern because of its spectacular damage to urban trees in Central Europe (Freise & Heitland, 2004).

Management of alien species invasion requires a good knowledge of invasion processes, i.e. pathways of introduction, establishment processes, species traits and habitat characteristics that favour invasion (Williamson, 1996; Wittenberg & Cock, 2001). It also requires a precise assessment of economic and ecological hazards caused by the alien species in order to improve risk assessments, define tolerance thresholds and evaluate the benefits of control measures to be weighted against costs of control (Parker *et al.*, 1999). Invasion processes in invertebrates and pathogens are rather different from those observed in other invasive organisms such as plants and vertebrates and, thus, require different strategies and research priorities. Firstly, the introduction of invertebrates is usually accidental, biological control agents being an exception (Causton *et al.*, 2006). The introduction phase is rarely observed and pathways of introduction are poorly known (National Research Council, 2002). Secondly, when established in a new region, an insect quickly spreads to invade new regions and habitats. In general, there is no obvious 'lag phase', as is often seen in plant invasions (e.g. Lonsdale, 1993); and when a lag phase is observed, it is usually of short duration (Memmott *et al.*, 2005; Drake & Lodge, 2006). Consequently, an alien insect is usually discovered when it is already firmly established, spreading and causing damage. An invasion process is usually studied *a posteriori*, and management methods focus on the control of already invasive, or damaging, populations; whereas, ideally, management efforts should be directed to the first stages of the invasion processes by preventing introduction or developing early eradication programmes (Puth & Post, 2005).

Nevertheless, *a posteriori* studies of already established alien insects are useful to assess which taxonomic or

bioecological groups of alien species are better invaders or more harmful to the economy or environment and which ecosystems or habitats are more at risk (Mondor *et al.*, 2007). Pathways and vectors of introduction can often be guessed from the biology of the insect, supported by interception data from national phytosanitary services. Such information allows the development or improvement of invasion risk assessment methods for species, ecosystems or pathways (Wittenberg & Cock, 2001).

Some European countries have recently established national lists of non-indigenous organisms, including insects, as part of a national strategy to address invasive alien species (e.g. Essl & Rabitsch, 2002: for Austria; Geiter *et al.*, 2002: for Germany; Hill *et al.*, 2005: for UK; Šefrová & Laštůvka, 2005: for the Czech Republic; Wittenberg, 2005: for Switzerland). The objectives of the present study were to extract, from a combination of the Swiss and Austrian lists, information relevant to invasion processes and invasive alien species management in Central Europe. In particular, we assessed insect species traits that correlate with the ability to invade and determined which habitats have been particularly susceptible to invasion. We also identified the most likely pathways or vectors for insect introductions and compared the results with a dataset of interceptions of non-indigenous insects in Europe, collected by national services of inspection and quarantine. Finally, we evaluated the actual and potential economic and environmental hazards linked to insect invasions in Central Europe and propose recommendations for management and conservation.

Material and methods

Datasets

A dataset of 341 non-indigenous insects of Austria and Switzerland has been built, based on recent lists for Austria (Essl & Rabitsch, 2002) and Switzerland (Kenis, 2005). The criteria for including an insect species in the dataset were those used to build the Swiss list (Kenis, 2005): (i) it is believed to be non-indigenous in Austria and Switzerland; (ii) there is proof, or at least a high probability, that the insect has been introduced into Europe by human activities (or into Austria and Switzerland for insects of European origin); and (iii) it is permanently established in Austria and Switzerland, i.e. it is self-reproducing and would maintain populations even without new introductions (this includes also insects that survive only in heated environments such as houses, stores, greenhouses, compost heaps, etc.). The Austrian list (Essl & Rabitsch, 2002) also includes non-established species and, thus, only the insects that match the criteria mentioned above were incorporated in our dataset. Archaeozoans, originally included in the Swiss list but not in the Austrian list, were included in our analyses. A few non-indigenous insects have been added to the Austrian list since its publication, and data for some groups not treated therein (e.g. Diptera, Psocoptera, Anoplura) were added from Fauna Europaea (2005).

Another dataset was built from data on the interceptions of non-indigenous plant pest insects in Europe made by the national services of inspection and quarantine for the period 1995–2004. These data were regularly reported as notifications of non-compliance (detection of regulated pests) by the European and Mediterranean Plant Protection Organisation (EPPO) and were recently synthesized by two of the authors

(Roques & Auger-Rozenberg, 2006). It does not include all insects intercepted but focuses primarily on alien insects that are on the quarantine list of the EPPO or on insect groups that are potentially dangerous for plant health. This database contains 6743 interceptions of non-indigenous insects from 28 European countries, involving 13,558 individual specimens and 285 species identified to the species level of which 255 can be considered non-European. A sizable amount of intercepted alien insects were identified at genus or family level only. From these, 19 genera were added to our dataset because no species of these genera had been identified to the species level and, thus, these genera represent additional species. Hence, the list of intercepted insects comprises a total of 274 species.

To test the hypothesis that the taxonomic distribution of the non-indigenous insect fauna in Switzerland and Austria is similar to the native European fauna, we used Fauna Europaea (2005) as reference for the insect fauna in Europe. To test the hypothesis that the taxonomic distribution of the non-indigenous insect fauna of North American origin in Switzerland and Austria is similar to the native North American fauna, we used the data presented by Simberloff (1986).

Area of origin of the insects

The area of origin of each alien insect established in Austria or Switzerland was classified by one of the following regions: North America; Central and South America; Asia (except Mediterranean area, but including Continental Asian Turkey); Africa (except Mediterranean area); Eastern Europe; Southern Europe and Mediterranean region (including Northern Africa and Middle East); Pacific region (Australia, New Zealand and other Pacific islands); or unknown. When the insect was thought to originate from two of these regions, the closest region to Central Europe was chosen. A similar classification was used for the interception data, but the origin was that of the commodity on which the insect was found rather than that of the origin of the species.

Feeding niche

Each insect of the dataset was categorized into one of the following feeding niches: external defoliators (including leaf rollers and webbers); sap feeders; leaf miners; gall makers; casebearers; wood borers; root borers/feeders; seed borers/feeders; stem borers (including twigs, buds and flowerhead borers); fruit borers; parasitoids; predators; ectoparasites; detritivores (including saprophages, coprophages and mycetophages); or omnivores. Insects whose larvae and adults occupy a different feeding niche were classified by the feeding niche of the larval stage. When the larva passes through two feeding niches, we chose the feeding niche in which it spends the longest time. Insects for which the biology is not known were assigned to the 'most-likely' feeding niche, i.e. that occupied by taxonomically closely related species.

An identical feeding niche classification was built for the European insects listed in Fauna Europaea (2005), which comprises about 93,000 insect species. In this case, the approximate proportion of each feeding niche was estimated by assigning each insect of the list to the feeding niche encountered in its family or sub-family. For species-rich families and sub-families showing two or more feeding

niches, an approximate proportion of each feeding niche was used, based on proportions calculated from regional or national checklists (e.g. for diverse Coleoptera families and sub-families, we used Freude *et al.* (1965–1983)). We then tested the hypothesis that the proportion of the feeding niches in the non-indigenous insect fauna is similar to that of the native fauna.

Environment, host plant and EUNIS habitat

The following types of environments and host plants were used to classify the insects: stored products (including non-food products such as fabrics, but not wood products); domestic (i.e. living only in heated buildings, but not on stored products and not on living plants in greenhouses); greenhouses; outdoors on indigenous host plant; outdoors on non-indigenous host plant; outdoors on decaying matters (including compost heaps); aquatic; and ectoparasite on vertebrates. Predators and parasitoids were categorized into the environment of their main prey/hosts. Insects living in different environments were classified in the one where they are most commonly found in Austria and Switzerland. Insects that are found frequently on both indigenous and exotic plants were classified in the category 'indigenous host plant'.

In addition, each insect was categorized into one of the major habitat classes of the EUNIS classification (EEA, 2005) present in Austria and Switzerland: C, inland surface waters; D, mires bogs and fens; E, grasslands and lands dominated by forbs, mosses or lichens; F, heathland, scrub and tundra; G, woodland, forest and other wooded land; H, inland unvegetated or sparsely vegetated habitats; I, regularly or recently cultivated agricultural, horticultural and domestic habitats; or J, constructed, industrial and other artificial habitats. When an insect is known to occur in two or more habitat classes, the habitat in which it has been most frequently reported was chosen.

Pathways and vectors of introduction

For each insect, a pathway or vector of introduction into Europe (for non-European insects) or into Austria or Switzerland (for European insects) was allocated. Since, in most cases, the exact pathway is not known, the most likely vector was deduced by considering their preferred habitats, lifestyle or food plant. The categories used were: host plant; wood material; stored products; biological control agents; host animal; others; and multiple/unknown. Insects with two or more possible pathways or vectors were categorized as 'multiple/unknown pathway'. The proportion of these estimated pathways and vectors was compared with those of the interception dataset. The commodities associated with interceptions were classified into the following categories: ornamental trade (aquarium plants, bonsai trees, cut flowers, plants for planting, seeds); plant products for consumption (fruits, stored products, vegetables); and wood and its derivatives (wood, bark, wood packing material).

Economic and ecological impacts

An insect was categorized as having an economic impact when we found at least one web page from Austrian, Switzerland or a neighbouring country describing damage and suggesting control methods. Similarly, an insect was

Table 1. A selection of alien insect species recorded only in Switzerland or only in Austria.

Recorded only in Switzerland	Recorded only in Austria
<i>Aedes albopictus</i> (Skuse) [Dipt.: Culicidae]	<i>Anoplophora glabripennis</i> (Motschulsky) [Col.: Cerambycidae]
<i>Cacyreus marshalli</i> (Butler) [Lep.: Lycaenidae]	<i>Antheraea yamamai</i> Guerin-Men. [Lep.: Saturniidae]
<i>Corythucha arcuata</i> (Say) [Hem.: Tingidae]	<i>Diuraphis noxia</i> (Kurdjumov) [Hem.: Aphidae]
<i>Orientus ishidae</i> (Matsumura) [Hem.: Cicadellidae]	<i>Lignyodes bischoffi</i> (Blatchley) [Col.: Curculionidae]
<i>Pulvinaria regalis</i> Canard [Hem.: Coccidae]	<i>Macropsis elaeagni</i> Emeljanov [Hem.: Cicadellidae]
<i>Rhagoletis completa</i> Cresson [Dipt.: Tephritidae]	<i>Phyllonorycter issikii</i> (Kumata) [Lep.: Gracillariidae]
<i>Rodolia cardinalis</i> (Mulsant) [Col.: Coccinellidae]	<i>Sceliphron caementarium</i> (Drury) [Hym.: Sphecidae]

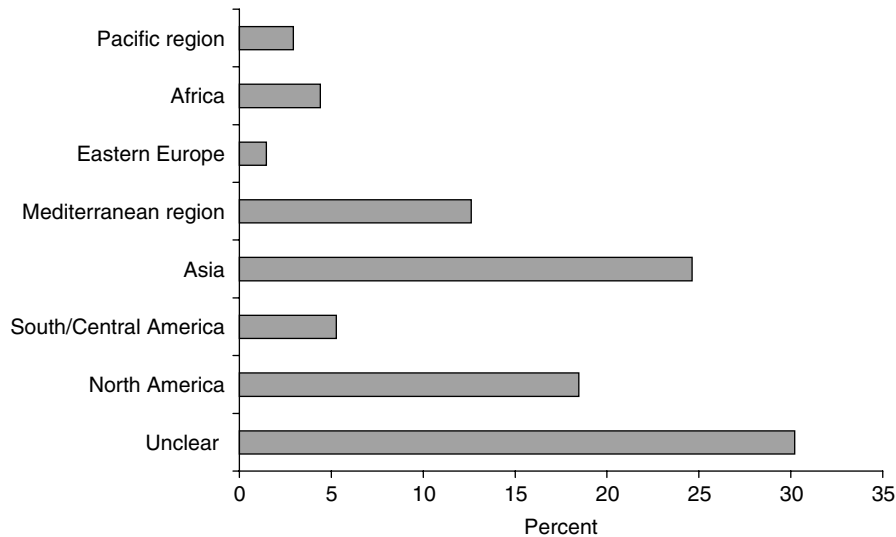


Fig. 1. Proportional representation of the areas of origin of the 341 non-indigenous insects established in Austria and Switzerland.

considered as having an ecological impact when a publication or a web page from the same geographic region was found describing an environmental hazard associated with this insect.

Results and discussion

Comparison between the Austrian and the Swiss databases

Despite their proximity and similarity in size, geography, climate, environment and number of international ports of entry, Switzerland and Austria have rather different alien insect faunas. Of the 341 species of the combined database, approximately one-third of the species (35%) are known only for Switzerland (90 species) or only for Austria (30 species). A significant proportion of species are recent invaders, and their presence in the other country is expected for the near future. Table 1 shows a selection of alien insects that are presently recorded from one of the two countries only. Another factor that may explain the variation between the two countries is the difference in taxonomic expertise in the two countries. Some groups are better known in Switzerland (e.g. Diptera, Psocoptera, Sternorrhyncha), whereas others are particularly well covered in Austria (e.g. Lepidoptera, part of Coleoptera).

Origin of alien insects in Switzerland and Austria

For nearly one-third of the alien insects in Austria and Switzerland, the region of origin is unclear. In some cases, such as the horse-chestnut leaf miner, *Cameraria ohridella*, the insect appeared in Europe without having been described elsewhere; and the only data on its population ecology, parasitism and dispersal biology lead to the conclusion that it probably originated from another continent (Kenis *et al.*, 2005). However, most insects classified as of 'unknown origin' are species whose distribution is cosmopolitan and for which there is no agreement regarding their area of origin. This is particularly the case for the numerous stored-product pests and some ectoparasites on animal pets that presently occur on most continents.

The majority of the alien insects, for which the area of origin is known, came from Asia and North America (fig. 1), two continents that include regions climatically and ecologically similar to Central Europe. A sizeable number of alien insects came from the Mediterranean region, probably on their host plants imported to Central Europe as crop planting material or products or as ornamentals. In recent years, Southern European species, e.g. moths and dragonflies, have been increasingly observed in Austria and Switzerland. Many of them are thought to migrate naturally, probably because of global warming, and are thus not included in the list (Kenis, 2005).

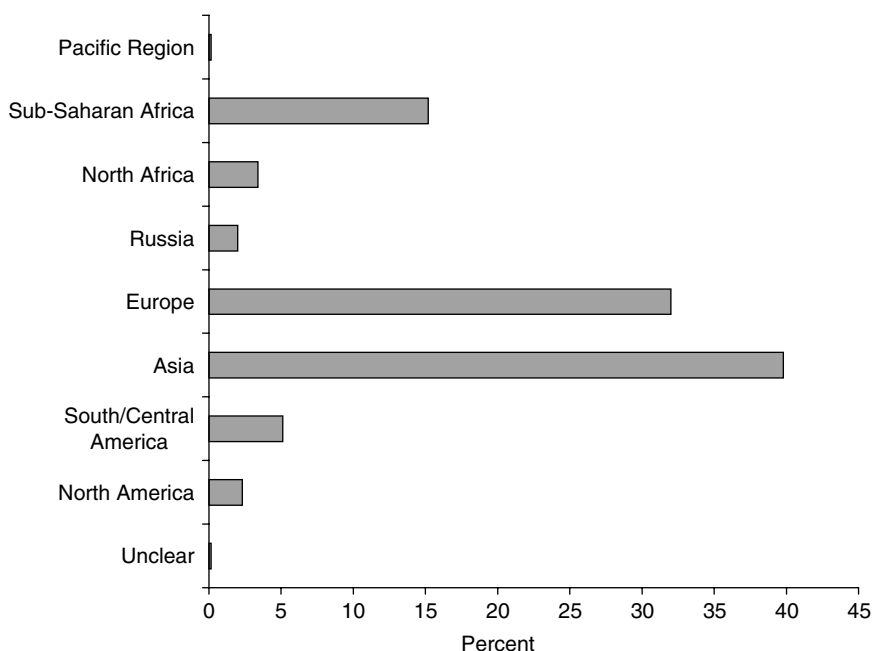


Fig. 2. Proportional representation of the origin of the commodities on which non-indigenous insects were intercepted by the national phytosanitary services in Europe during the period 1995–2004.

Among the alien insects intercepted by European phytosanitary services, many were found on commodities from Asia (39.8%) and other European regions (32.0%). Surprisingly few were found on commodities from North America (2.3%) (fig. 2), although North American insects account for 18% of the alien insect fauna in Switzerland and Austria (fig. 1). This discrepancy between interception data and the origin of established insects may be explained by the climatic similarity between Europe and North America that allow smaller numbers of North American species and individuals to establish more easily in Europe than tropical species. In addition, the interception data being based on recent records only (1995–2004), the apparent difference with the alien fauna dataset may also reflect changes in foreign trade in recent years, increasing exchange being made with more 'exotic' regions, particularly Asia for ornamental plants. Since the interception data nearly exclusively concerned plant pests, it is not surprising to find many interception records on Asian commodities. In their analysis of alien plant pests established in Great Britain, Smith *et al.* (2005) also noted that Asia supplied a relatively high number of recent introductions. Similarly, Haack (2001, 2006) noted that the most recent establishments and interceptions of bark- and wood-boring Coleoptera in North America were of Asian origin. Furthermore, it cannot be ruled out that the low occurrence of insects in North American imports may be due to better sanitary practices in North America than in other regions.

Taxonomic groups

Figure 3 shows the taxonomic composition of the alien insects in Austria and Switzerland, which significantly differs from the composition of the native insect fauna in Europe (goodness of fit χ^2 test; $\chi^2=568.50$, $P<0.001$; the

12 smallest orders of fig. 3 being pooled together to avoid low expected frequencies). Three insect orders and sub-orders are particularly overrepresented in the alien fauna compared to the native fauna: Coleoptera, Sternorrhyncha and Psocoptera. In contrast, Diptera and Hymenoptera are underrepresented. A comparison between the alien insects of North American origin in Switzerland and Austria and the native insect fauna in North America shows the same pattern (goodness of fit χ^2 test; $\chi^2=111.69$, $P<0.001$; the 12 smallest orders of fig. 4 being pooled together to avoid low expected frequencies), with American Sternorrhyncha having been more successful in invading Europe than other insect groups (fig. 4). Alien insects in the USA show the same pattern, except that alien Hymenoptera are proportionally much more abundant in North America, partly because of the large number of exotic parasitoids introduced into North America for biological control purposes (Simberloff, 1986). Nevertheless, there are also many more alien herbivorous Hymenoptera, particularly sawflies, in North America than in Europe (Mattson *et al.*, 1994). This overrepresentation of Coleoptera and Sternorrhyncha may be explained by the fact that beetles are easily transported in, or with, stored products whereas aphids, scale insects and whiteflies are often carried inconspicuously with their host plant.

The interception data show a somewhat different pattern (fig. 5). Sternorrhyncha were also frequently intercepted but, surprisingly, Diptera accounted for the highest number of interceptions. Two-thirds of these were agromyzid leaf miners and the remaining one-third were mainly fruit flies of the Tephritidae family. However, the number of species intercepted per order led to a larger representation of Sternorrhyncha and Coleoptera, whose respective proportions were similar to those observed in the established alien fauna. Moreover, interception data are strongly biased

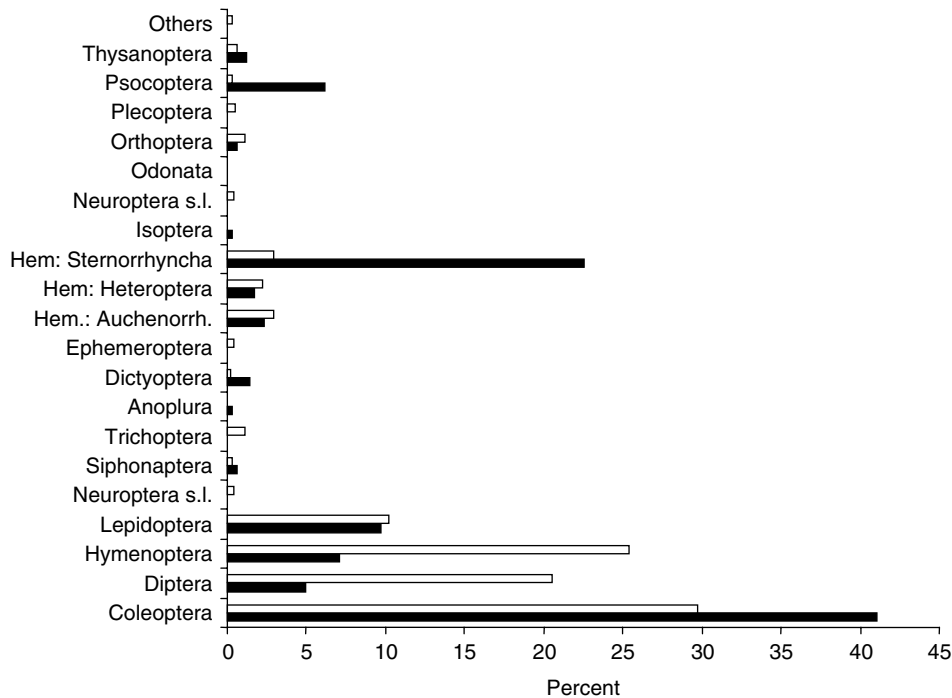


Fig. 3. Proportions of insect orders and sub-orders in the 341 non-indigenous insect species in Austria and Switzerland (black bars) compared to the European insect fauna (source: Fauna Europaea, 2005) (white bars). Orders that were not treated in the Austrian and Swiss lists (e.g. all Apterygota, Mallophaga) were excluded from the analysis. 'Others' include small orders (<0.4%) for which no non-indigenous species are known from Austria and Switzerland, i.e. Dermaptera, Mecoptera, Odonata, Phasmatodea, Strepsiptera.

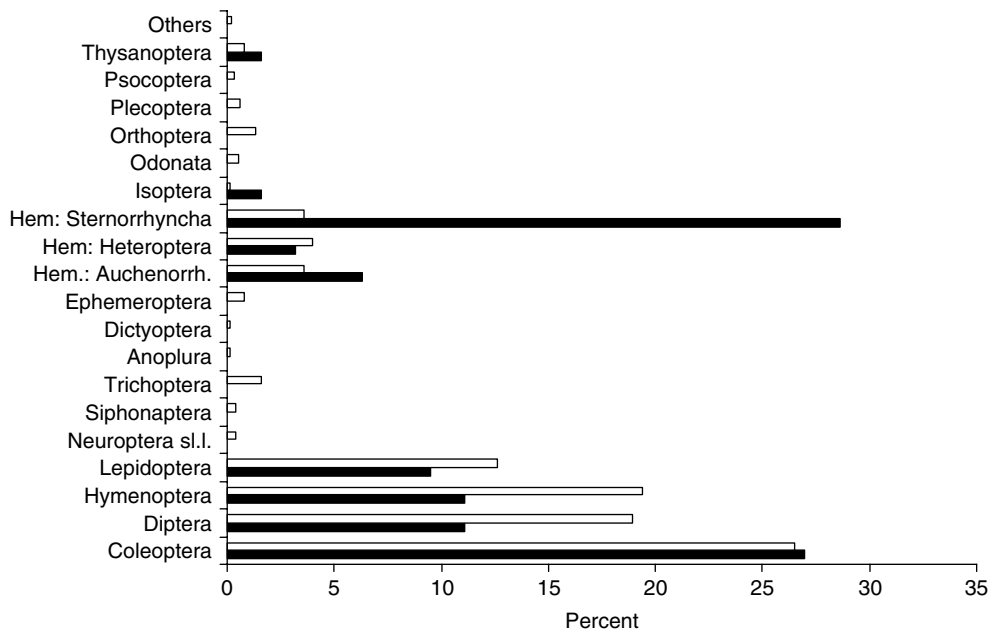


Fig. 4. Proportions of insect orders and sub-orders in the 341 non-indigenous insect species in Austria and Switzerland originating from North America (black bars) compared to the North American insect fauna (Simberloff, 1986) (white bars). Orders that were not treated in the Swiss and Austrian lists (e.g. all Apterygota, Mallophaga) were excluded from the analysis. 'Others' include small orders (<0.4%) for which no non-indigenous species are known from Switzerland and Austria, i.e. Dermaptera, Mecoptera, Phasmatodea, Strepsiptera.

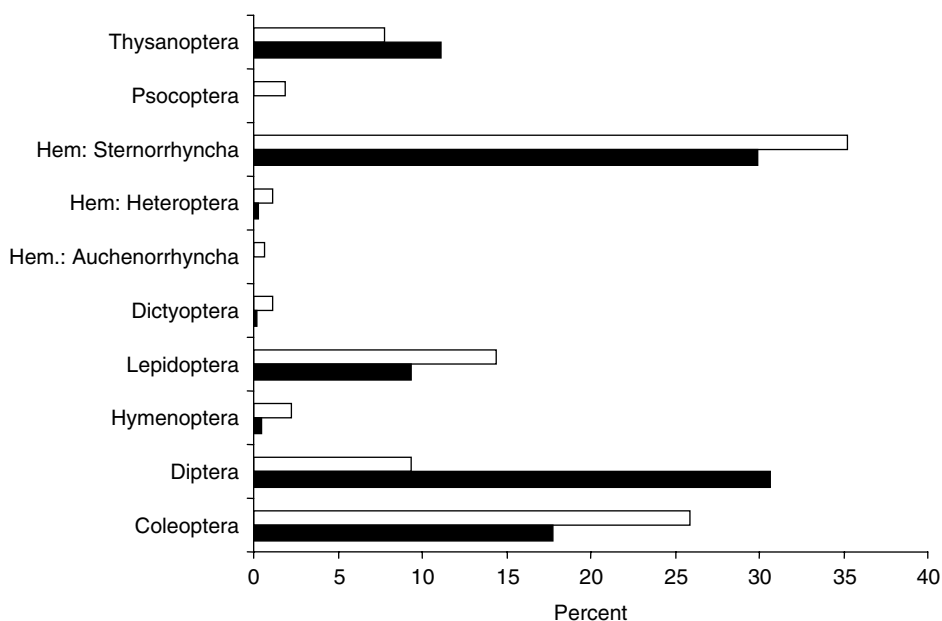


Fig. 5. Proportion of insect orders and sub-orders in the non-indigenous insects intercepted by the national phytosanitary services in Europe during the period 1995–2004. Black bars, number of interceptions; white bars, number of species intercepted.

by the fact that surveys concentrate on plant pests. For example, Hymenoptera, the vast majority of which are parasitoids, predators or nectar/pollen feeders, are hardly represented in the interception data. Nevertheless, many plant pests intercepted by phytosanitary services probably contained hymenopteran parasitoids that have the potential to become established and invasive.

Feeding niche

The proportion of feeding niches in the alien fauna is significantly different from that of the European fauna (goodness of fit χ^2 test, $\chi^2 = 366.57$, $P < 0.001$). Sap feeders and detritivores are clearly the dominant feeding niches in the alien insect fauna of Austria and Switzerland. Their proportion in the alien fauna is much higher than in the European fauna (fig. 6). The majority of the sap feeders are Sternorrhyncha, followed by other Hemiptera and Thysanoptera. Small sap feeders are unnoticeably carried from one region to another attached to seedlings, cut flowers, vegetables, etc. Detritivores are well represented in the alien list because many stored-product pests belong to this category. Other guilds that are proportionally more represented in the alien fauna than in the European fauna are wood borers, fruit borers, seed feeders/borers and omnivores. In contrast, external defoliators, root feeders/borers, stem borers, gall makers, predators and parasitoids seem to travel or establish less successfully. The number of parasitoids is most probably underestimated in our dataset. The frequency of parasitoids in insect faunas varies from 8.5–25% according to different estimations (Godfray, 1994). Hence, in Austria and Switzerland, only 11 alien parasitoid species (3% of the dataset) are recorded as probably established. All were released in Europe as biological control agents. The absence of naturally introduced and established parasitoids may suggest that these insects do not establish

new populations easily. However, it almost certainly also reflects their cryptic life-history and the taxonomic difficulties related to this group. New indigenous parasitoid species are still described every year in Europe. Many species are recorded from two or more continents, and it is probable that several of these species invaded Europe from Asia or North America recently.

Environment, host plant and EUNIS habitat

Figure 7 shows that nearly 40% of the alien insects in Austria and Switzerland live only indoors, in houses, stores, greenhouses, etc. Another 15% live outdoors but exclusively or predominantly on exotic plants. Following the EUNIS classification, less than 20% of the alien insects live in a 'natural environment', the majority of them occurring in regularly or recently cultivated agricultural, horticultural and domestic habitats, or in constructed, industrial and other artificial habitats (fig. 8). Among those insects that occur in 'natural environments', the vast majority are found in forest habitats, which includes plantations. It is a common observation that simple, disturbed, human habitats are more readily invaded by insects and other invaders than complex, undisturbed, natural habitats. Elton (1958) attributes this phenomenon to the 'biotic resistance', i.e. natural enemies and competitors that are more prevalent in natural habitats than in disturbed habitats. Simberloff (1986) suggests two other, more simple, hypotheses to which we adhere. Firstly, disturbed, man-made habitats (i.e. agricultural and domestic habitats) are more important to humans and, thus, are studied more carefully than natural habitats. As a result, new establishments are more likely to be detected. Secondly, insects linked to human environments and activities (e.g. pests) are more likely to be carried by human transports into a new region than insects living in natural areas. The second hypothesis is confirmed by interception data that invariably

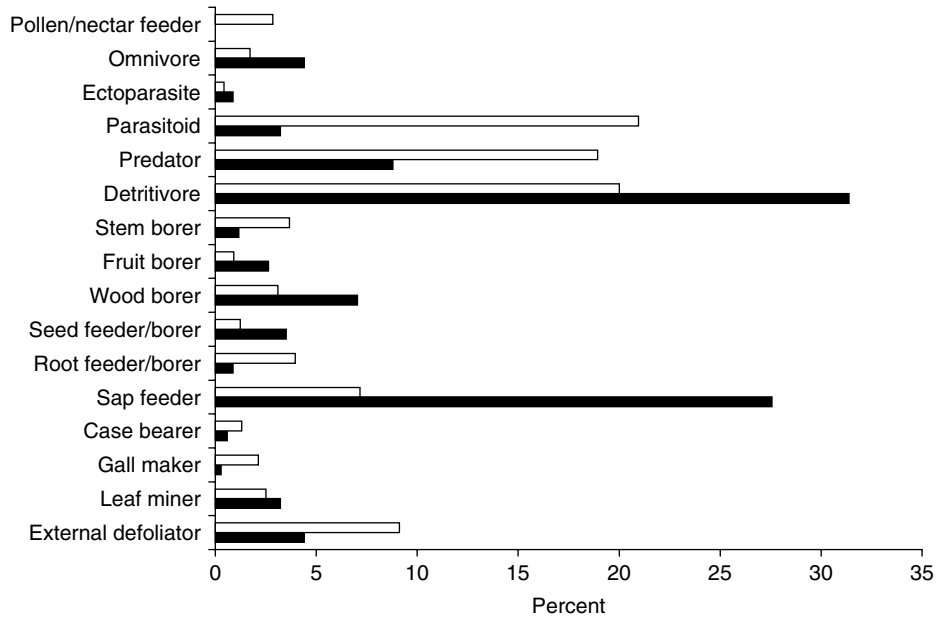


Fig. 6. Proportional representation of the feeding niches of the 341 non-indigenous insects in Austria and Switzerland (black bars) and of the European insect fauna (white bars).

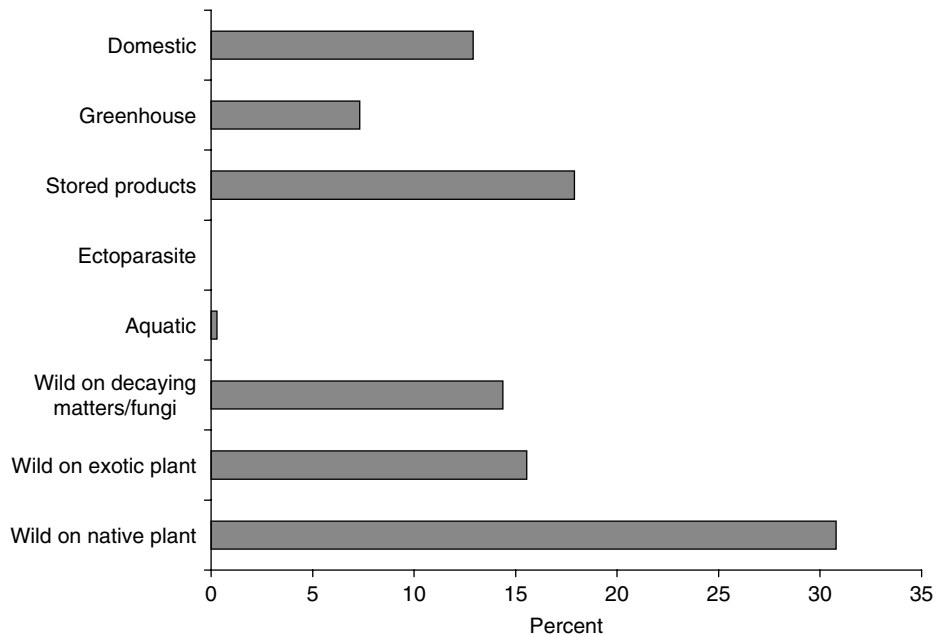


Fig. 7. Proportional representation of the environments and host plants of the 341 non-indigenous insects in Austria and Switzerland.

contain far more agricultural and domestic pests than insects linked exclusively to natural habitats. The first hypothesis should be tested by extensive and specific surveys for alien species in natural habitats.

Pathways and vectors of introduction

Among the 341 alien insects established in Austria and Switzerland, the exact pathway of introduction is known with confidence for only the 12 biological control agents

deliberately released in Europe. However, for nearly 80% of the alien insect species, a likely vector, usually a commodity, could be deduced or assumed based on their biology, plant or animal host, etc. (fig. 9). The main vectors of introduction were, in decreasing order, host plants (accounting for nearly half of the introductions), stored products and wood material. Of those insects that were probably introduced with their host plant (wood excluded), at least 40% undoubtedly came on ornamentals and 20% on vegetables and fruits. From insects assumed to have arrived

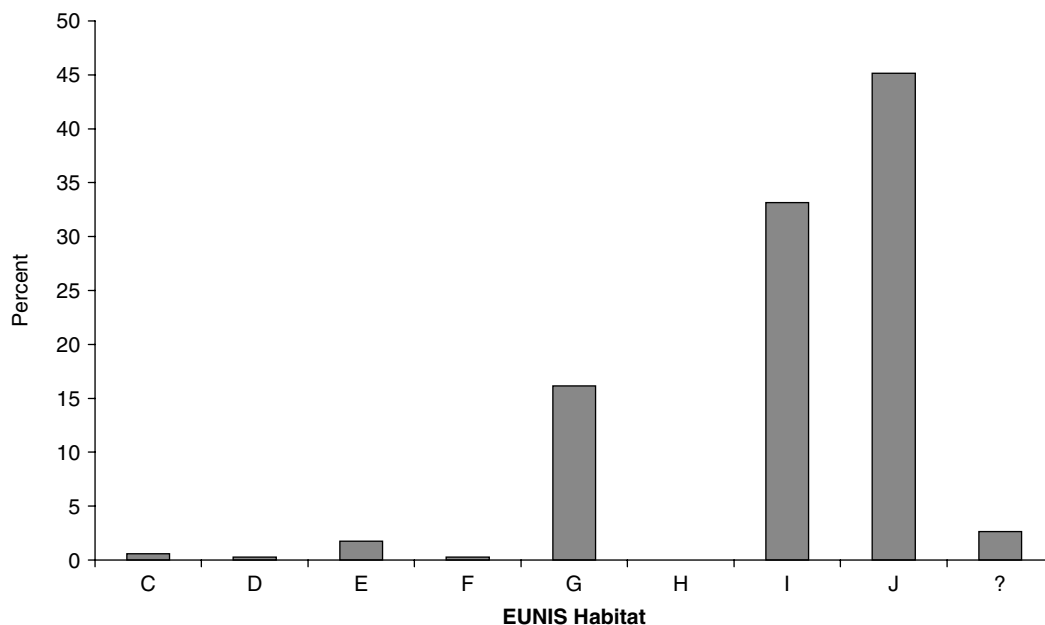


Fig. 8. Proportional representation of the main habitat classes (EUNIS classification) of the 341 non-indigenous insects in Austria and Switzerland. C, inland surface waters; D, mires bogs and fens; E, grasslands and lands dominated by forbs, mosses or lichens; F, heathland, scrub and tundra; G, woodland, forest and other wooded land; H, inland unvegetated or sparsely vegetated habitats; I, regularly or recently cultivated agricultural, horticultural and domestic habitats; J, constructed, industrial and other artificial habitats; ?, habitat unclear.

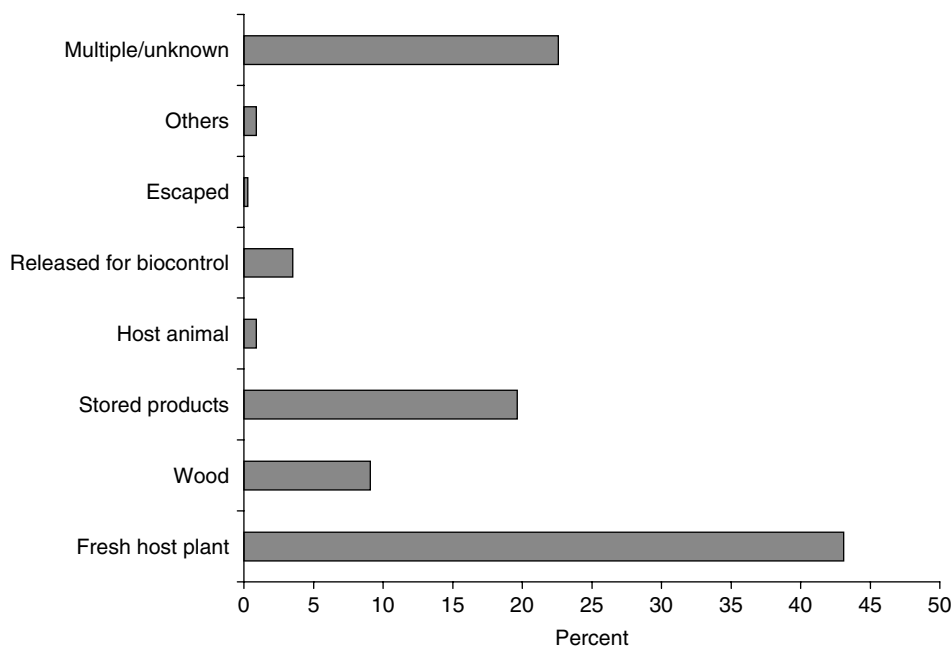


Fig. 9. Proportional representation of the most likely pathways and vectors of introduction for the 341 non-established insects in Austria and Switzerland. Fresh host plant refers to live or freshly cut host plants.

with wood material, about two-thirds are associated with wood (logs, processed lumber or fresh wood packaging) and one-third with old wood material (e.g. furniture). The relative proportion of vectors assessed from the establishment data and the importance of the ornamental

plant trade as pathway is confirmed by the interception data (table 2). Cut flowers, seedlings (nearly exclusively for ornamental purposes), bonsai trees, seeds and aquarium plants represented 52.7% of the commodities on which insects were intercepted. Nearly 30% of the insects were

Table 2. Relative importance of pathways and commodities associated with insect interceptions in Europe during 1995–2004.

Pathway	Commodity	No. Interceptions	% Interceptions
Ornamental trade	Aquarium plants	305	4.5
	Bonsai trees	281	4.2
	Cut Flowers	1939	28.8
	Plants for planting	1003	14.9
	Seeds	20	0.3
Food products	Fruits	753	11.2
	Stored products	610	9.0
	Vegetables	1343	19.9
Wood and derivates	Wood/Bark	190	2.8
	Wood Package	293	4.3
Miscellaneous	Unclear	6	0.1
Total		6743	100

intercepted on cut flowers, which is about the same proportion found on fresh food (vegetables and fruits). The relative efforts put on inspection of these different commodities is not known; however, considering that the food trade is far more extensive than the ornamental trade, one can assume that proportionally many more alien insects were found on ornamentals than on vegetables and fruits. Interestingly, more insects were intercepted on wood packaging (4.3%) and bonsai trees (4.2%) than on logs, processed lumber and bark (2.8%) ($\chi^2 = 22.08$, $P < 0.01$ and $\chi^2 = 19.40$, $P < 0.001$, respectively). The origin of the commodity on which insects were intercepted strongly varies with the type of commodity. Asia seems to be the major source for insects on bonsai trees (96.7%) and wood packaging (76.9%), whereas 47.9% of the insects intercepted on fresh wood and bark came from Russia.

Economic and ecological impact

For 124 alien insects established in Austria or Switzerland (40% of all species), data on economic damage are available from Austria, Switzerland or a neighbouring country. In contrast, the rate of native insects reaching pest status in temperate countries is probably much lower than 5% (our estimates derived from numbers given in Pimentel (2002) and Pimentel *et al.* (2002a, 2002b)). Although alien insects represent only about 1% of the insect fauna in Austria (Rabitsch & Essl, 2006) and 1.7% in continental United States (Simberloff, 1986), it is usually estimated that between 30 and 45% of the insect pests in agriculture and forestry worldwide are of alien origin (Pimentel *et al.*, 2002a, 2002b). The higher rate of pest species among non-indigenous faunas compared to indigenous faunas may be explained by three factors that are not mutually exclusive. Firstly, alien insects causing economic damage are more likely and more rapidly discovered than insects that are economically harmless. Thus, it is very likely that many alien insects, established in Austria or Switzerland in natural habitats, are yet to be discovered (Kenis, 2005). Secondly, insects are more likely to become pests as introduced aliens than in their region of origin. Many alien insects having economic impact are in fact of little, or of no, importance in their region of origin, where they are controlled by natural enemies and host resistance derived from co-evolutionary history (e.g. Löhr *et al.*, 1990; McClure & Cheah, 1999). Thirdly, pests are

more likely to invade new areas because they are more abundant, their habitats are increasing in size and connectivity, and they feed on economically important plants or goods (Kenis, 2005). This is particularly the case with stored-product insects that have become pests in many regions and are regularly transported with the commodities in which they live.

To our knowledge, no study has been carried out to investigate the ecological impact of alien insect species in Austria and Switzerland, and only limited data are available for Europe in general. A few alien insect species present in Austria or Switzerland cause ecological concerns in other regions. The ladybird, *Harmonia axyridis* (Pallas), originally from eastern Asia, is believed to out-compete and displace native aphidophagous species by predation and competition for food in North America (Koch, 2003). This species has been recently recorded in the wild in Europe, including Switzerland, where it is expected to cause similar damage (Klausnitzer, 2004; Majerus *et al.*, 2006). The argentine ant, *Linepithema humile* (Mayr), is a serious environmental pest in many regions in the world. It has been causing changes in invertebrate and plant communities in the Mediterranean region by predation and displacement of native species (Gómez & Oliveras, 2003). It has been occasionally reported in Switzerland, where it reaches its ecological and climatic limit and will probably never cause damage.

Species comparison between establishment and interception lists

The most frequently intercepted alien insect species are already established in Europe, if not in the wild, at least in greenhouses and other heated environments, e.g. *Bemisia tabaci* (Gennadius) (Hem.: Aleyrodidae, 1502 interceptions); *Liriomyza huidobrensis* (Blanchard) (Dipt.: Agromyzidae, 658); *Helicoverpa armigera* (Hübner) (Lep.: Noctuidae, 447); *Frankliniella occidentalis* (Pergande) (Thysan.: Thripidae, 222). However, several other species are very frequently intercepted and are not yet established in Europe, e.g. *Tinocallis takachihoensis* Higushi (Hem.: Aphidae, 62 records) or Asian *Monochamus* spp. (Col.: Cerambycidae, 65). On the other hand, many species that are already established in Europe have been very rarely or never intercepted. An interesting case is the recent introduction and spread of the western

corn rootworm, *Diabrotica virgifera virgifera*. A recent study showed that the different established populations in Europe originate from different introductions (Miller *et al.*, 2005), yet our interception list contains only one record for *D. v. virgifera*. Altogether, out of the 341 alien insect species in Switzerland and Austria, only 34 (10.0%) were intercepted by phytosanitary services. On the other hand, only 34 out of the 274 (12.4%) non-European alien species intercepted are known to be established in Switzerland or Austria. Similarly, only 42 intercepted species are found in the list of 381 (11.0%) alien insects established in the Czech Republic (Šefrová & Laštůvka, 2005).

It is not clear why some species are frequently intercepted but never become established, while others are rarely or never intercepted but become established. There are probably numerous factors linked to the species biology and ecology (e.g. climate matching, life cycle, host plant availability, taxonomic isolation of host plants, etc.) or to pathway characteristics (e.g. phytosanitary regulations better implemented for some pathways). It must be noted that more than half of the intercepted species are of tropical or subtropical origin, which decreases the probability of establishment in the wild in most of Europe.

Another major constraint to investigate establishment successes is the lack of reliable, rigorous interception data. It may simply be that insects that are established but never intercepted are often introduced but not intercepted on the right pathways at the right moment using the right method. Work *et al.* (2005) estimated that even rigorous inspections probably detected only 19–50% of the imported species, depending on the pathway. In addition, interception surveys focus mainly on quarantine plant pests and targeted commodities (Haack, 2006). Insects belonging to economically unimportant groups are not searched for or not identified, and only species under quarantine can be denied entry when found at ports of entry. Furthermore, non-indigenous insects that are already widely established in Europe are removed from quarantine lists.

Implications for further studies and management strategies against alien insects

Evaluation of species traits and habitat characteristics that make insects and habitats prone to invasion is a rewarding step towards understanding insect invasion processes, as shown for plant or vertebrate invasions (Williamson, 1996; Alpert *et al.*, 2000; Kolar & Lodge, 2001). Such studies, unfortunately, are limited by lack of knowledge of the biology and ecology of most insects, their distribution (especially in natural habitats) and their pathways of introduction. Nevertheless, we were able to determine general patterns characterising invading insects and invaded habitats. For example, our study clearly showed that sap sucking Sternorrhyncha feeding on ornamental plants are more likely to be introduced into a new region than, e.g. Lepidoptera defoliators or Coleoptera root feeders living in natural habitats. However, it is not clear whether such generalizations are of much help in building strategies for the prevention and management of invasive insects. Exceptions are definitively too important to be neglected. For example, the two most damaging alien insects to outdoor agriculture in Europe, the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and the western corn rootworm, *Diabrotica virgifera virgifera*, are both exceptional. Firstly, they

are the only alien representatives of the species-rich family Chrysomelidae, which does not seem to include successful invaders in general. Secondly, they belong to two feeding niches, 'external defoliators' and 'root feeders', for which we have found relatively few alien species. Thirdly, a clear pathway of introduction could not be identified for either of these two insects. Finally, they originate from Mexico and Central America, regions that have not provided many other outdoor-living invaders in Europe. Furthermore, many of the most damaging alien insects are not pests in their region of origin. The two examples cited above were known before their introduction to Europe because they had reached pest status when they invaded the USA and Canada. However, other invasive species, such as the horse-chestnut leaf miner, *Cameraria ohridella*, the silver fir woolly aphid, *Dreyfusia nordmanniana* Eckstein, and the eastern subterranean termite, *Reticulitermes flavipes* Kollar, were unknown before reaching Europe.

These examples unambiguously show that, with invasive alien insects, economic and/or ecological threats arise from different geographic, taxonomic and ecological directions, as observed with other taxa (e.g. Levine *et al.*, 2003). The unpredictability of insect introductions and invasiveness, and the fact that the introduction of alien insects is usually accidental and often detected only long after their establishment, put doubts on the usefulness of species-based risk assessments for invasive alien insects (Simberloff, 2005). Standard protocols for species-based risk assessment are most suitable for alien organisms introduced deliberately, and for which an assessment is needed before the probable establishment in the wild, e.g. ornamental plants, fishes, biological control agents, etc. (National Research Council, 2002; Louda *et al.*, 2003) In contrast, strategies against invasive alien insects should focus on specific pathways and awareness building of the relevant authorities (Simberloff *et al.*, 2005). There are few published examples of risk assessments for insects aimed at specific pathways. Notable exceptions are the risk assessment procedures developed by the US Department of Agriculture to evaluate the risk of importing unprocessed larch from Russia and pine from New Zealand and Mexico (e.g. Tkacz, 2002), but these were also calculated on a species-based analysis by combining risks of introducing each particular species that may be transported through these pathways. A better goal would be to define approaches to identify and compare all key pathways and commodities, determine risks associated with each, and sever or restrict the riskiest (Simberloff, 2005). However, until now, too little has been known about the pathways of introduction for alien insects to produce risk assessments for key pathways. Interception data in Europe and elsewhere are usually strongly biased according to detection priorities, which depend on pest or commodities of current concern (Haack, 2001, 2006). In addition, there are large discrepancies among countries, ports of entries, etc. Furthermore, insects are not always determined to species level. In the EPPO interception list, 69.8 and 88.1% of the insects were determined to species or genus level, respectively, because interception efforts focused mainly on insects of quarantine significance. However, in more systematic interception surveys the percentage of insects identified to species level is usually much lower (e.g. 23% in Work *et al.*, 2005; 35% in Haack, 2006). More importantly, interception data only record positive data, whereas to fully analyse pathways and rates of introduction, negative interceptions

also need to be recorded. More studies should focus on specific pathways, using a scientific approach that will produce statistically robust data, such as that of Work *et al.* (2005). They used statistically-robust data collected by USDA APHIS at US ports of entry as part of the Agricultural Quarantine Inspection Monitoring Protocol (AQUIM: Venette *et al.*, 2002) to estimate arrival rates of non-indigenous insects via four cargo pathways: air cargo, refrigerated and non-refrigerated maritime cargo and US-Mexico border cargo. They determined the risks of invasion associated with each of these pathways and were able to evaluate the effectiveness of current efforts to monitor arrival of alien species. We strongly encourage the development of similar investigations on pathways of introduction in Europe.

Despite important limits and bias, our analyses of pathways and vectors of introduction were useful in identifying important patterns. In particular, they clearly showed that host plants, especially ornamentals, are the most important vector for the introduction of alien insects into Europe. More than half of the interceptions of alien insects into Europe were made on cut flowers, seedlings, potted plants or bonsai trees. Our results on the most likely pathways for introductions of established insects in Austria and Switzerland also emphasized the role of ornamental plants as vectors. Similarly, Smith *et al.* (2005) found that all but one of the significant invertebrate plant pests established in Great Britain after 1970 were on ornamentals. Work *et al.* (2005) showed that 69% of the insect interceptions in air cargo were on cut flowers; whereas, in the US-Mexico border cargo, 75% of the insect interceptions were associated with ornamental palms. Interestingly, the ornamental trade is also responsible for the introduction and establishment of the majority of the most serious invasive plants in Europe (Pyšek *et al.*, 2002) and elsewhere (Reichard & White, 2001). Similarly, many of the most invasive vertebrates in Europe, such as the grey squirrel, *Sciurus carolinensis*, and the ruddy duck, *Oxyura jamaicensis*, were initially introduced for aesthetic purposes (Wittenberg, 2005). Ornamental plants are by no means essential commodities for human welfare. Therefore, their intercontinental trade should be more regulated. Instead, priority should be given to locally grown indigenous plants. The importance of minor ornamental trades in the introduction of invasive species is exemplified by the trade in bonsai trees. Nearly twice as many pest insects are intercepted on bonsai trees as on timber. Insects intercepted on bonsai trees include many aphids, such as *Cinara* spp., *Tinocallis viridis* (Takahashi) and *T. takachihoensis*, and scales, such as *Saissetia neglecta* DeLotto, but also long-horned beetles of the genus *Anoplophora*. The bonsai trade is known to be responsible for the introduction of at least one major tree pest in France, Italy and the USA in recent years, the citrus long-horned beetle, *Anoplophora chinensis* (Förster) (Hérard *et al.*, 2005; Haack, 2006).

This survey also showed that there is little information on the ecological impact of invasive insects in Europe. In other parts of the world, quite a few invasive insects are known to cause serious damage to the environment, but the impact is most often noticed when 'valuable' plant or animal species or entire ecosystems are affected, such as the hemlock and balsam woolly adelgids, *Adelges tsugae* and *A. piceae*, destroying forest ecosystems in North America, or the red fire ant, *Solenopsis invicta*, and the Formosan termite, *Coptotermes formosanus*, causing structural damage to

various ecosystems in Southern USA (Pimentel *et al.*, 2002a). There is a need for studies to properly assess the ecological impact of invasive alien insects and take the appropriate conservation measures. In this paper, we showed that only a minority of the alien insects in Central Europe live in natural habitats and, consequently, have the potential to be detrimental to natural ecosystems. However, it is not clear whether these data reflect a balanced view or just a lack of entomological and ecological investigations in natural habitats compared to human habitats.

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References

- Alpert, P., Bone, E. & Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3, 52–66.
- Baufeld, P. & Enzian, S. (2005) Maize growing, maize high-risk areas and potential yield losses due to western corn rootworm (*Diabrotica virgifera virgifera*) damage in selected European countries. pp. 285–302 in Vidal, S., Kuhlmann, U. & Edwards, C.R. (Eds) *Western Corn Rootworm: Ecology and Management*. Wallingford, CAB International.
- Causton, C.E., Peck, S.B., Sinclair, B.J., Roque-Albelo, L., Hodgson, C.J. & Landry, B. (2006) Alien insects: threats and implications for conservation of Galápagos Islands. *Annals of the Entomological Society of America* 99, 121–143.
- Drake, J.M. & Lodge, D.M. (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. *Biological Invasions* 8, 365–375.
- EEA (2005) EUNIS Habitat Classification. <http://eunis.eea.eu.int/habitats.jsp>. Cited 20 July 2006.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. 181 pp. London, Methuen.
- Essl, F. & Rabitsch, W. (Eds) (2002) *Neobiota in Österreich*. Wien, Umweltbundesamt.
- Fauna Europaea (2005) <http://www.faunaeur.org>. Cited 20 July 2006
- Freise, J.F. & Heitland, W. (2004) Bionomics of the horse-chestnut leaf miner *Cameraria ohridella* Deschka and Dimic 1986, a pest on *Aesculus hippocastanum* in Europe (Insecta: Lepidoptera: Gracillariidae). *Senckenbergiana Biologica* 84, 1–20.
- Freude, H., Harde, K.W. & Lohse, G.A. (1965–1983) *Die Käfer Mitteleuropas, Band 1–11*. Krefeld, Germany, Goeke and Evers.
- Geiter, O., Homma, S. & Kinzelbach, R. (2002) *Bestandsaufnahme und Bewertung von Noezoen in Deutschland*. Umweltforschungsplan des Bundesministeriums für Umwelt, Naturschutz und Reaktorsicherheit. Forschungsbericht 296 89 901/1 UBA-FB 000215.

- Godfray, H.C.J.** (1994) *Parasitoids. Behavioral and Evolutionary Ecology*. 471 pp. Princeton University Press, Princeton, USA.
- Gómez, C. & Olivera, J.** (2003) Can the Argentine ant (*Linepithema humile* Mayr) replace native ants in myrmecochory? *Acta Oecologica* **24**, 47–53.
- Haack, R.A.** (2001) Intercepted Scolytidae (Coleoptera) at U.S. ports of entry: 1985–2000. *Integrated Pest Management Reviews* **6**, 253–282.
- Haack, R.A.** (2006) Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* **36**, 269–288.
- Hérard, F., Jollivet, C. & Reynaud, P.** (2005) Gestion des foyers de capricornes asiatiques: en France, Autriche, Allemagne et Italie, l'éradication est lancée. *Phytoma – La Défense des Végétaux* **583**, 22–26.
- Hill, M., Baker, R., Broad, G., Chandler, P.J., Copp, G.H., Ellis, J., Jones, D., Hoyland, C., Laing, I., Longshaw, M., Moore, N., Parrot, D., Pearman, D., Preston, C., Smith, R.M. & Waters, R.** (2005) *Audit of Non-Native Species in England*. English Nature Research Report 662, Northminster House, Peterborough, UK.
- Kenis, M.** (2005) Insects-Insecta. pp. 131–212 in Wittenberg, R. (Ed.) *An inventory of alien species and their threat to biodiversity and economy in Switzerland*. CABI Bioscience Switzerland Centre. Centre report to the Swiss Agency for Environment, Forests and Landscape.
- Kenis, M., Tomov, R., Svatos, A., Schlinsog, P., Lopez Vaamonde, C., Heitland, W., Grabenweger, G., Girardoz, S., Freise, J. & Avtzis, N.** (2005) The horse-chestnut leaf miner in Europe. Prospects and Constraints for biological control. pp. 77–90 in *Proceedings of the Second International Symposium on Biological Control of Arthropods*. Morgantown, WV, USA, Forest Health Technology Enterprise Team, 12–16 September 2005, Davos, Switzerland.
- Klausnitzer, B.** (2004) *Harmonia axyridis* (Pallas, 1773) in Basel-Stadt (Coleoptera, Coccinellidae). *Mitteilungen der Entomologischen Gesellschaft Basel* **54**, 115–122.
- Koch, R.L.** (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science* **3**, 32. Available online: insectscience.org/3.32.
- Kolar, C.S. & Lodge, D.M.** (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**, 199–204.
- Levine, J.M. & D'Antonio, C.M.** (2003) Forecasting biological invasions with increasing international trade. *Conservation Biology* **17**, 322–326.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S.** (2003) Mechanisms underlying the impact of exotic plant invasions. *Philosophical Transactions of the Royal Society of London* **270**, 775–781.
- Löhr, B., Varela, A.M. & Santos, B.** (1990) Exploration for natural enemies of the cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae), in South America for the biological control of this introduced pest in Africa. *Bulletin of Entomological Research* **80**, 417–421.
- Lonsdale, W.M.** (1993) Rates of spread on an invading species – *Mimosa pigra* in northern Australia. *Journal of Ecology* **81**, 513–521.
- Louda, S.M., Arnett, A.E., Rand, T.A. & Russell, F.L.** (2003) Invasiveness of some biological control insects and adequacy of their ecological risk assessment and regulation. *Conservation Biology* **17**, 322–326.
- Majerus, M.E.N., Strawson, V. & Roy, H.E.** (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecological Entomology* **31**, 207–215.
- Mattson, W.J., Niemelä, P., Millers, I. & Inguanzo, Y.** (1994) *Immigrant phytophagous insects on woody plants in the United States and Canada: an annotated list*. General Technical Report NC-169. St. Paul (MN), US Department of Agriculture.
- McClure, M.S. & Cheah, C.A.S.** (1999) Reshaping the ecology of invading populations of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Sdelgidae), in Eastern North America. *Biological Invasions* **1**, 247–254.
- Memmott, J., Craze, P.G., Harman, H.M., Syrett, P. & Fowler, S.V.** (2005) The effect of propagule size on the invasion of an alien insect. *Journal of Animal Ecology* **74**, 50–62.
- Miller, N., Estoup, A., Toepfer, S., Bourguet, D., Lapchin, L., Derridj, S., Kim, K.S., Reynaud, P., Furlan, L. & Guillemaud, T.** (2005) Multiple transatlantic introductions of the western corn rootworm. *Science* **310**, 992.
- Mondor, E.B., Tremblay, M.N. & Messing, R.H.** (2007) Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands. *Biological Invasions* **9**, 87–100.
- National Research Council (United States)** (2002) *Predicting invasions of non-indigenous plants and plant pests*. Washington DC, National Academy Press.
- Niemelä, P. & Mattson, W.J.** (1996) Invasion of North America Forest by European phytophagous insects. *Bioscience* **46**, 741–753.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L.** (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**, 3–19.
- Pimentel, D.** (2002) Non-native invasive species of arthropods and plant pathogens in the British Isles. pp. 151–158 in Pimentel, D. (Ed.) *Biological Invasions. Economic and Environmental costs of Alien Plants, Animal and Microbe Species*. Boca Raton, USA, CRC Press.
- Pimentel, D., Lach, L., Zuniga, R. & Morrison, D.** (2002a) Environmental and economic costs associated with non-indigenous species in the United States. pp. 285–306 in Pimentel, D. (Ed.) *Biological Invasions. Economic and Environmental costs of Alien Plants, Animal and Microbe Species*. Boca Raton, USA, CRC Press.
- Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T.** (2002b) Economic and environmental threats of alien plant, animal and microbe invasions. pp. 307–330 in Pimentel, D. (Ed.) *Biological Invasions. Economic and Environmental costs of Alien Plants, Animal and Microbe Species*. Boca Raton, USA, CRC Press.
- Pyšek, P., Sádlo, J. & Mandák, B.** (2002) Catalogue of alien plants of the Czech Republic. *Preslia* **74**, 97–186.
- Puth, L.M. & Post, D.M.** (2005) Studying invasion: have we missed the boat? *Ecology Letters* **8**, 715–721.
- Rabitsch, W. & Essl, F.** (2006) Biological invasions in Austria: Patterns and case studies. *Biological Invasions* **8**, 295–308.
- Reichard, S.H. & White, P.** (2001) Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* **51**, 103–113.

- Roques, A. & Auger-Rozenberg, M.A.** (2006) Tentative analysis of the interceptions of nonindigenous organisms in Europe during 1995–2004. *EPPO Bulletin* **36**, 490–496.
- Šefrová, H. & Laštůvka, Z.** (2005) Catalogue of alien animal species in the Czech Republic. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* **53**, 151–170.
- Simberloff, D.** (1986) Introduced insects: a biogeographic and systematic perspective. pp. 3–26 in Mooney, H.A. & Drake, J.A. (Eds) *Ecology of Biological Invasions of North America and Hawaii*. New York, Springer-Verlag.
- Simberloff, D.** (2005) The politics of assessing risk for biological invasions: the USA as a case study. *Trends in Ecology and Evolution* **20**, 216–222.
- Simberloff, D., Parker, I.M. & Windle, P.N.** (2005) Introduced species policy, management and future research needs. *Frontiers in Ecology and the Environment* **3**, 12–20.
- Smith, R.M., Baker, R.H.A., Malumphy, C.P., Hockland, S., Hammon, R.P., Ostojá-Starzewski, J.C. & Collins, D.W.** (2005) Non-native invertebrate plant pests established in Great Britain: an assessment of patterns and trends. *BCPC Symposium Proceedings* **81**, 119–124.
- Tkacz, B.M.** (2002) Pest risks associated with importing wood to the United States. *Canadian Journal of Plant Pathology* **24**, 111–116.
- Venette, R.C., Moon, R.D. & Hutchison, W.D.** (2002) Strategies and statistics of sampling for rare individuals. *Annual Review of Entomology* **47**, 143–174.
- Williamson, M.** (1996) *Biological Invasions*. 244 pp. London, Chapman and Hall.
- Wittenberg, R.** (Ed.) (2005) *An Inventory of Alien Species and their Threat to Biodiversity and Economy in Switzerland*. CABI Bioscience Switzerland Centre. Centre report to the Swiss Agency for Environment, Forests and Landscape.
- Wittenberg, R. & Cock, M.J.W.** (2001) *Invasive Alien Species: A Toolkit of Best Prevention and management Practices*. 228 pp. Wallingford, CAB International.
- Work, T.T., McCullough, D.G., Cavey, J.F. & Komsa, R.** (2005) Arrival rate of nonindigenous species into the United States through foreign trade. *Biological Invasions* **7**, 323–332.

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