

Chapter 21

ADVENTIVE
(NON-NATIVE)
INSECTS:
IMPORTANCE TO
SCIENCE AND
SOCIETY

Alfred G. Wheeler, Jr.¹ and E. Richard Hoebeke²

¹Department of Entomology, Soils & Plant Sciences, Clemson University,
Box 340315, 114 Long Hall, Clemson, South Carolina 29634-0315 USA

²Department of Entomology, Cornell University, Ithaca,
New York 14853-2601 USA

Much of invasion biology's conceptual framework rests on Darwinian thought (Williamson 1996, Ludsin and Wolfe 2001). An awareness of immigrant species in North America predates Darwin's work (Inderjit et al. 2005). Before Darwin (1859) published his treatise on the origin of species, entomologists had warned about the establishment of European plant pests in the New World, a concern motivated by a desire to protect agriculture from foreign pests rather than to conserve native biodiversity. George Marsh, however, was aware not only of the presence of immigrant insects in the USA but also other human-induced changes to the environment. His book *Man and Nature* (Marsh 1864) 'revolutionized environmental thought' (Lowenthal 1990) and presaged the disciplines of conservation biology and invasion ecology.

Two classic works inspired interest in adventive species: Elton's (1958) *The Ecology of Invasions by Animals and Plants*, which initiated the science of invasion biology (Parker 2001), and *The Genetics of Colonizing Species* (Baker and Stebbins 1965). The books differ in their emphasis. Elton's book deals mainly with faunal history, population ecology, and conservation. The book Baker and Stebbins edited stresses evolutionary rather than ecological issues and does not address the effects of adventive species on environmental conservation (Davis 2006).

Bates (1956) examined the role of humans as agents in dispersing organisms ranging from microbes to vertebrates. He observed that anthropogenic influences, such as modification of environmental factors and movement of organisms, offer opportunities for experimental studies that could contribute to issues in theoretical ecology and clarify evolutionary mechanisms. Invasion biology assumed prominence during the 1980s (Kolar and Lodge 2001, Davis 2006), receiving impetus from the Scientific Committee on Problems of the Environment of the International Council of Scientific Unions and its early symposia on biological invasions (Macdonald et al. 1986, Mooney and Drake 1986, Drake et al. 1989). Invasion biology now plays a central role in biotic conservation, and invasive species are used as tools for biogeographic, ecological, and evolutionary research (Vitousek et al. 1987, Williamson 1999, Sax et al. 2005, Davis 2006).

An increased mobility of humans and their commodities, coupled with human-induced habitat disturbances, enables plants and animals to breach once insurmountable geographic barriers and become

established in distant lands and waters (Soulé 1990, Mack et al. 2000, Mooney and Cleland 2001). Human colonization has increased the geographic scope, frequency, and taxonomic diversity of biotic dispersal (U.S. Congress 1993, Vitousek et al. 1997, Mack et al. 2000). A global estimate of the number of adventive species, including microbes, approaches a half million (Pimentel et al. 2001). The spread of adventive organisms ranks only behind habitat destruction as the greatest threat to biodiversity (Wilson 1992, Wilcove et al. 1998).

Invasion biology, featured in both scientific and popular writings (Simberloff 2004), is fraught with misconceptions and characterized by polemical writing, emotionalism, and controversy. Debate continues over such issues as the patterns and processes affecting the movement and success of invaders, invasibility of mainland areas compared to islands, ecological consequences of invaders, and relative importance of direct compared to indirect effects on ecosystems. Should biological invasions be viewed generally as part of ecological change, and as enriching, rather than impoverishing biodiversity? Whether all invasions should be considered bad and whether a global decline in biodiversity necessarily is bad (Lodge 1993b) depend, in part, on perspective: scientific, or moral and social (Brown and Sax 2004; cf. Cassey et al. 2005). The extent to which the effects of invaders are tempered over time and current ecological changes resolved through evolution and succession in the new ecosystems also is uncertain (Daehler and Gordon 1997, Morrison 2002, Strayer et al. 2006).

We cannot treat all facets of a field as diverse and complex as invasion biology or all cultural, ethical, historical, management, philosophical, political, psychological, and socioeconomic aspects of the invasive-species problem. We treat adventive insects that are immigrant (not deliberately introduced) or introduced (deliberately so). Our coverage emphasizes North America. Examples deal mainly with human-assisted movement of insects between countries, even though intracountry changes in range are common among immigrant taxa (e.g., the glassywinged sharpshooter (*Homalodisca vitripennis*) and western corn rootworm (*Diabrotica virgifera*) within the USA). Such range extensions can be as detrimental as those between countries (Simberloff 2000, McKinney 2005). We exclude immigrants that arrive on their own by active flight or passive conveyance on convective air currents (Southwood 1960), on strong winds associated with El Niño events (Roque-Albelo and

Causton 1999), or are able to spread as the result of global climate change (Burckhardt and Mühlethaler 2003, Musolin and Fujisaki 2006, Musolin 2007).

TERMINOLOGY

Invasion ecology's status and public appeal is due partly to its emotive and militaristic language, including the words *alien*, *exotic*, and *invader* (Colautti and MacIsaac 2004, Larson 2005, Coates 2006). An emphasis on 'headline invaders' (Davis et al. 2001) also has contributed to the discipline's prominence. Elton (1958) did not define the terms *invader* and *invasion*, which permeate the literature on invasive species (Richardson et al. 2000, Rejmánek et al. 2002). Terms relating to the concept of 'not native' are used interchangeably, even though they are not strictly synonymous (Simberloff 1997, Mack et al. 2000, Sax et al. 2005); nonnative species are designated as adventive, alien, exotic, immigrant, or introduced, sometimes in the same paper (e.g., Sailer 1978, Devine 1998, Clout 1999). *Newcomer*, a more neutral term than *invader*, has gained some recent favor (Coates 2006, Acorn 2007). The term *neozoa* is used mainly in the European literature to refer to nonnative animals intentionally or unintentionally introduced since 1492 (Occhipinti-Ambrogi and Galil 2004, Rabitsch and Essl 2006).

Entomologists have not been as involved as botanists and plant ecologists in trying to clarify terminology. Zimmerman (1948) categorized insects not native to Hawaii as either 'immigrant', unintentionally brought in by humans, or 'introduced', for instance, for biological control. Frank and McCoy (1990) similarly reserved *introduced* for species deliberately introduced, and used *immigrant* for hitchhikers and stowaways, as well as species that disperse under their own power. Atkinson and Peck (1994), however, regarded bark beetles that have colonized southern Florida by natural dispersal – immigrant according to Frank and McCoy's (1990) terminology – as native. It can be impossible to determine if the arrival of even clearly adventive species involved deliberate human intervention (Simberloff 1997). Certain predators and parasitoids introduced for biocontrol were already established, but undetected, as immigrants at the time of their release (Frick 1964, Turnbull 1979, 1980).

We distinguish adventive taxa as either immigrant or introduced (Frank and McCoy 1990, 1995b; Frank 2002), and follow Cowie and Robinson (2003) by using *vector* to refer to the vehicle or mechanism that transports a species and *pathway* for the activity or purpose by which a species is introduced (cf. Carlton and Ruiz 2005). Table 21.1 gives definitions of these and other key terms used herein.

DISTRIBUTIONAL STATUS: NATIVE OR ADVENTIVE?

Immigrant insects typically are associated with disturbed habitats but can be found in relatively pristine communities and in isolated areas (Wheeler 1999, Klimaszewski et al. 2002, Gaston et al. 2003). Whether a species should be considered native or adventive can be problematic (Claassen 1933, Buckland 1988, Whitehead and Wheeler 1990, Woods and Moriarty 2001). An apparent immigrant of restricted geographic range in its area of invasion poses a conservation dilemma if eradication of the potentially ecologically disruptive species is considered; an effort to resolve distributional status should be made before any attempt is made to eliminate what actually might be a rare precinctive ('endemic') species (Deyrup 2007).

Distributional status is particularly difficult to evaluate in the case of vertebrate ectoparasites, pests of stored products, certain ants, cockroaches, and other cosmopolitan insect groups (Buckland et al. 1995, McGlynn 1999, Kenis 2005). By the late eighteenth century, the honeybee (*Apis mellifera*) had become so common in the USA that it appeared to be native to the New World (Sheppard 1989). The distributional status – native or immigrant – of major North American pests (Webster 1892), such as the Hessian fly (*Mayetiola destructor*) (Riley 1888, Pauly 2002), as well as a species officially listed as endangered in the UK (Samways 1994), remains in doubt. Certain insects once thought to be Holarctic likely are immigrant in North America (Turnbull 1979, 1980; Wheeler and Henry 1992). Certain immigrant insects have been thought initially to represent new species (e.g., Thomas et al. 2003) or have been described as new. Thus, a species is not necessarily native to the continent or island from which it was described (Cox and Williams 1981, Green 1984, Gagné 1995). The status of certain insects described from North America can be immigrant, the species being conspecific with

Table 21.1 Some key terms as used in this chapter.

Term	Definition	Comments
Adventive	Not native (adj.)	More neutral term than <i>alien</i> or <i>exotic</i> , encompassing both immigrant and introduced species (Frank and McCoy 1990); in botanical literature, can refer to nonnative species only temporarily established (Novak and Mack 2001)
Immigrant	Nonnative species not deliberately or intentionally introduced (n.); pertaining to species not deliberately introduced (adj.)	Accidentally or unintentionally introduced (Sailer 1978, McNeely et al. 2001); includes species arriving on their own (Frank and McCoy 1990; cf. Atkinson and Peck 1994); 'true immigrants' (<i>sensu</i> Simberloff 2003)
Introduced	Pertaining to nonnative species deliberately or intentionally introduced (adj.)	Sometimes used broadly to refer to all nonnative species (e.g., Simberloff 2003)
Invasive	Pertaining to species that cause socioeconomic or environmental damage or impair human health (adj.)	Variously defined term and subjective, value-based measurement (Hittingh 2001, Ricciardi and Cohen 2007); sometimes applied to any nonnative species
Pathway	Purpose or activity for which adventive species are introduced, either intentionally or unintentionally (n.)	Follows Cowie and Robinson (2003); for alternative uses, see Richardson et al. (2003), Carlton and Ruiz (2005)
Precinctive	Pertaining to a native species known from no other area (adj.)	More restrictive term than indigenous; often misused for endemic (Frank and McCoy 1990)
Vector	Mechanism or vehicle (physical agent) by which adventive species are transported (n.)	Follows Cowie and Robinson (2003), Ruiz and Carlton (2003); 'pathway' often is used to refer to both pathways and vectors (Carlton and Ruiz 2005)

previously described Old World species (Wood 1975, Wheeler and Henry 1992, Booth and Gullan 2006). Certain Eurasian species in North America should be regarded as native to the Pacific Northwest but immigrant in the Northeast (Lindroth 1957, Turnbull 1980, Sailer 1983). An anthocorid bug (*Anthocoris nemoralis*), apparently immigrant in the Northeast, was introduced for biological control in western North America (Horton et al. 2004).

Lindroth (1957) discussed historical, geographic, ecological, biological, and taxonomic criteria useful in evaluating distributional status. His criteria are particularly appropriate for the North Atlantic region (Sadler and Skidmore 1995), including Newfoundland, Canada, which has received numerous western Palearctic insects, often via ships' ballast (Lindroth 1957, Wheeler and Hoebeke 2001, Wheeler et al. 2006). Certain species likely are immigrant in North America even though they do not meet any of Lindroth's (1957) criteria of immigrant status (Turnbull 1979). The ten criteria used to assess the distributional status of a marine crustacean (Chapman and Carlton 1991) are also appropriate for terrestrial insects. The accuracy of criteria used to resolve distributional

status depends on how well the bionomics of the insects in question are known (Turnbull 1980). To address long-standing questions about the origin of certain immigrant pests (Howard 1894), molecular evidence can be used to identify the geographic sources of adventive insects and, in some cases, to detect overlapping or sequential invasions (e.g., Tsutsui et al. 2001, Miller et al. 2005, Austin et al. 2006).

Biogeographers and ecologists often consider a species native if information is insufficient to resolve its distributional status but do so with unwarranted confidence (Carlton 1996). Whitehead and Wheeler (1990) suggested the opposite approach: when in doubt, consider the species adventive ('nonindigenous'). The term *cryptogenic* refers to species that demonstrably are neither native nor adventive (Carlton 1996).

EARLY HISTORY OF ADVENTIVE INSECTS IN NORTH AMERICA

Other organisms accompanied *Homo sapiens* during each major invasion: from Africa, where humans apparently evolved, to Eurasia; thence to Australia,

the Americas, and, eventually, to the far reaches of the Pacific (McNeely 2001b, 2005). Lice might have been the first insects to have been transported (Laird 1984). As early as the ninth century, the Norse colonists were responsible for the establishment of European insects in Greenland (Sadler 1991). Insects likely arrived in the New World with landfall by Columbus, who 'mixed, mingled, jumbled, and homogenized the biota of our planet' (Crosby 1994). Insects probably arrived in North America with the *Mayflower's* landing in 1620 and continued to enter with every ship that brought additional people and supplies from Europe (Sailer 1978, 1983). Earlier, the house fly (*Musca domestica*) might have been brought to tropical latitudes of the Western Hemisphere via canoe or raft by pre-Columbian inhabitants of Central or South America (Legner and McCoy 1966). Outside North America, the Polynesians who colonized Hawaii in prehistoric times might have brought with them a few insects, such as vertebrate ectoparasites, the house fly, and a cockroach (*Balta similis*) (Gagné and Christensen 1985, Beardsley 1991).

Early-arriving insects in the USA and elsewhere mostly were those that could survive a several-month sea voyage under adverse physical conditions: associates of stored products, ectoparasites and blood suckers of humans and their livestock, inhabitants of their excrement, and soil dwellers in dry ballast brought aboard sailing ships (Lindroth 1957, Sailer 1978, Turnbull 1979, Buckland et al. 1995). For many other insect groups, long sea voyages functioned as inadvertent quarantines years before formal quarantines were adopted (Gibbs 1986).

Among early immigrants in the Northeast were the bed bug (*Cimex lectularius*), head (and body) louse (*Pediculus humanus*), and oriental cockroach (*Blatta orientalis*) (Sasscer 1940, Sailer 1978, 1983). Pestiferousness of the stable fly (*Stomoxys calcitrans*) perhaps led to hasty adoption of the Declaration of Independence (Kingsolver et al. 1987). Crop pests generally were not among the early arrivals (Sailer 1978), although archaeological evidence has shown that certain pests were present much earlier than once thought (Bain and LeSage 1998). On the West Coast, where eighteenth-century agriculture was limited to Spanish missions in southern California, various weevils entered with food and seed cereals. Livestock ships brought several species of muscoid flies to California; fur, hide, tallow, and whaling ships allowed additional stored-product insects to enter (Dethier 1976).

Thirteen immigrant insects apparently became established in the USA by 1800 (McGregor et al. 1973), with the total of adventive species about 30 (Sailer 1983); Simberloff's (1986) total of 36 appears to include the mite species noted by Sailer. Numerous other immigrant insects, common in England but not detected in North America until after 1800, probably were present by the eighteenth century (Sasscer 1940, Sailer 1983). Even with establishment of European plant pests such as the codling moth (*Cydia pomonella*), Hessian fly (*Mayetiola destructor*), oystershell scale (*Lepidosaphes ulmi*), and pear sawfly (*Caliroa cerasi*), neither native nor immigrant insects were particularly problematic in the Northeast before 1800 (Dethier 1976, Sailer 1978, 1983). Pest outbreaks did occur, and cessation of burning by the Native Americans favored additional problems from insects (Cronon 1983). Yet, crops in the American colonies mostly were free from the insects that plague modern agriculture (Popham and Hall 1958). The minimal damage from insects was due partly to a lack of extensive and intensive crop production and scarcity of immigrant pests; damage might have been greater because some crop losses went unrecognized (Davis 1952). Drought, however, was the main enemy of colonial farmers (Dethier 1976). Before the nineteenth century, soil exhaustion and limiting socioeconomic conditions also remained more important than insects as deterrents to agriculture (Barnes 1988).

The subsistence-level agriculture of early European settlers, and their cultivation of crops such as corn and squash, did little to disrupt evolutionary relationships between plants and insects (Dethier 1976, Barnes 1988). Increasingly, however, insects emerged as consistent agricultural pests. It is not true, as a politician in a Western state contended, that the USA lacked destructive insects until the country had entomologists (Webster 1892).

Increasing trade with Europe, more rapid means of transportation, planting of additional European crops, and expanding crop acreages favored the arrival and establishment of new insects from Europe. As humans altered ancient relationships between plants and insects, they unwittingly ushered in an era of immigrant pests (Dethier 1976). In roughly 200 years, a 'new ecology' had been created, setting the stage for damage by native insects and the entry of additional European species (Barnes 1988). The slow accumulation of immigrant insects, lasting until about 1860 (Sailer 1978), gave way to a

'continuous, persistent procession' of immigrants (Herrick 1929).

NUMBERS, TAXONOMIC COMPOSITION, AND GEOGRAPHIC ORIGINS OF ADVENTIVE INSECTS

No continent or island is immune to invasion by immigrant organisms. Changes in transport technology and types of commodities transported have affected the predominance of certain groups of insects at different time periods in every world region. Our discussion of the immigrant insect fauna will emphasize the 48 contiguous U.S. states, a principal focus of Sailer's (1978, 1983) seminal work. The specific composition of the U.S. adventive insect fauna is influenced not only by changes in pathways, vectors, and trade routes, but also by the kinds of natural enemies imported for biocontrol, availability of taxonomists who can identify insects in particular families, taxonomic bias in the kinds of insects collected in detection surveys, and changes in quarantine-inspection procedures.

Faunal lists are important but labor intensive and time consuming; thus, few, up-to-date, comprehensive inventories or databases of immigrant insects exist for most world regions. Lists of adventive taxa, however, allow an analysis of the numbers of established species, systematic composition of the most successful groups, and geographic origins, as well as comparisons among biogeographic regions. From data on immigrant insect faunas, we focus on selected countries on different continents, oceanic islands or atolls, and several agriculturally important U.S. states (Table 21.2). The immigrant insect fauna of the USA is one of the best studied and most thoroughly documented (McGregor et al. 1973, Sailer 1978, 1983). Of more than 3500 species of adventive arthropods that reside in the continental USA (Frank and McCoy 1992), more than 2000 insect species are established, representing about 2–3% of the insect fauna (U.S. Congress 1993).

Sailer's (1978, 1983) analysis revealed several major trends among adventive insects in the U.S. fauna. The ubiquitous use of dry ballast during the era of early sailing ships (seventeenth to early nineteenth century) was responsible for an early dominance of Coleoptera. At British ports, beetles and ground-dwelling bugs were common in dry ballast (Lindroth 1957). After the Civil War, Homoptera and Heteroptera arrived with nursery stock and other plant material from western

Europe. Sailer (1978) determined that homopterans contributed the largest number of adventive species, but in his later analysis, hymenopterans, with approximately 390 species (23%), predominated (Sailer 1983). The introduction of numerous parasitic wasps to help control adventive pest arthropods and weeds was thought responsible for the disproportionate increase in hymenopterans. Next in abundance of species were the Coleoptera (372), Homoptera (345), Lepidoptera (134), and Diptera (95). Immigrant arthropods in the USA originate mainly from the western Palearctic (66.2%), followed by the Neotropical (14.3%), and eastern Palearctic and Oriental Regions (13.8%) (Sailer 1983).

Florida has the highest percentage of adventive insects in the conterminous USA (only Hawaii has a higher percentage); about 1000 such species are established, representing about 8% of Florida's insect fauna (Frank and McCoy 1995a). Whereas many of the species entered with commerce (e.g., as stowaways in plant material), others arrived by aerial dispersal from Caribbean islands (Cox 1999). Although Floridian immigrants originate from many world regions, they arrive mainly from the Neotropics and Asia.

Beetles were best represented (~26%) among the 271 species of immigrant insects newly recorded from Florida from 1970 to 1989. Coleoptera were followed by Lepidoptera (~19%), Hymenoptera (~15%), and Homoptera (~13%) (Frank and McCoy 1992). A similar study in Florida for 1986 to 2000 listed 150 adventive insects (Thomas 2006). Unlike Frank and McCoy's (1992) study, Homoptera contributed the largest number of species (~35%), followed by Coleoptera (~26%). The proportion of Coleoptera was similar, but that of Homoptera increased substantially (~13% to ~35%), while that of Lepidoptera declined (~19% to ~3%). From 1970 to 1989 the majority of immigrant species in Florida arrived from the Neotropics (~65%) (Frank and McCoy 1992). In contrast, from 1986 to 2000, the number of Asian immigrants increased substantially (~50%) (Thomas 2006). Between 1994 and 2000, the number of quarantine pest interceptions at Florida ports of entry increased by 162% (Klassen et al. 2002).

Immigrant insects have a long history of crop damage in California, another important agricultural state. Between 1955 and 1988, infestations of 208 immigrant invertebrates were discovered. Homoptera, followed by Coleoptera and Lepidoptera, made up the greatest number of insects; the majority originated

Table 21.2 The adventive insect fauna of selected geographic areas.

Geographic Area	Number of Described Species	Number of Immigrant Species	Percentage of Total Composition	Estimated Rate of Annual Detection	Orders with Most Immigrants (% of Total)	Reference
Conterminous USA	~90,000	>2,000	2–3%	11.0 spp./yr. (1910–1980) 6.2 spp./yr. (1970–1982)	Homoptera (20.5%) Coleoptera (20.3%) Lepidoptera (7.4%)	Hoebcke and Wheeler 1983, Sailer 1983, U.S. Congress 1993, Arnett 2000, Papp 2001
California	~28,000	208	7.4%	6.1 spp./yr. (1955–1988)	Homoptera (33.7%) Coleoptera (12.0%) Lepidoptera (11.5%)	Powell and Hogue 1979, Dowell and Gill 1989
Florida	12,500	945	7.6–10%	12.9 spp./yr. (1971–1991) 7.7 spp./yr. (1970s)	Coleoptera (33%) Lepidoptera (24.9%)	Frank and McCoy 1992, Frank and McCoy 1995b, Frank et al. 1997
Hawaii	7,998	2,598	~32%	12.4 spp./yr. (1912–1935) 14.5 spp./yr. (1937–1961) 18.1 spp./yr. (1962–1976)	Homoptera (16.3%) Thysanoptera (78.9%) Diptera (44.3%) Homoptera (43.4%)	Beardsley 1962, 1979, 1991; Simberloff 1986; Howarth 1990; Nishida 1994; Eldredge and Miller 1995, 1997, 1998; Miller and Eldredge 1996
Austria	~13,740	212	~1.5%	NA ¹	Coleoptera (1.1%)	Rabitsch and Essl 2006
Great Britain	21,833	325	1.5%	4.5 spp./yr. (1970–2004)	Lepidoptera (0.6%) Homoptera (11.5%)	Williamson and Brown 1986, Smith et al. 2005
Italy	NA	162	NA	4.0 spp./yr. (1975–1995)	Coleoptera (2.6%) Homoptera (64%) Coleoptera (12%) Lepidoptera (7%)	Pelizzari and Dalla Montà 1997, Pelizzari et al. 2005
Japan	29,292	284	9.7%	4.0 spp./yr. (1945–1995)	Coleoptera (32.0%) Homoptera (27.8%)	Kiritani 1998, 2001; Morimoto and Kiritani 1995
Galápagos Islands	~2,013	463	23%	20.7 spp./yr. (1996–2004)	Lepidoptera (12.3%) Homoptera (25.5%)	Peck et al. 1998, Causton et al. 2006
New Zealand (Coleoptera only)	5,579	356	6.4%	1.4 spp./yr. (1950–1987) 1.7 spp./yr. (1988–1997)	Coleoptera (24.0%) Diptera (14.3%) NA	Klimaszewski and Watt 1997
Tristan da Cunha Islands	152	84 ²	55.3%	NA	Hemiptera (86.7%) Coleoptera (46.5%) Lepidoptera (45.5%)	Holdgate 1960, 1965

¹ Not available.

² Includes immigrant ('alien') species and those of doubtful status.

from other regions of North America, followed by the Pacific Region and Europe. Since 1980, the immigration rate from Asia, Australia, Europe, and the Pacific Region increased, especially in Diptera, Hymenoptera, and Homoptera (Dowell and Gill 1989). R.V. Dowell (California Department of Food and Agriculture, Sacramento; cited by Metcalf 1995) compiled a partial list of adventive insects (460 species) established in California between 1600 and 1994.

Hawaii is the most invaded region of the USA because of its particular geography, climate, and history. Approximately 350–400 insects ('original immigrants') colonized the islands before human settlement, probably arriving by ocean or air currents (U.S. Congress 1993). Commerce with the outside world followed the European discovery of the Hawaiian Islands, which allowed additional immigrant insects to enter. Nearly 4600 adventive species have become established, more than half (>2500) of which are arthropods (Nishida 1994, Miller and Eldredge 1996, Eldredge and Miller 1998). More than 98% of pest arthropods are immigrant (Beardsley 1993), and 28% of all Hawaiian insects are adventive (Simberloff 1986), including the entire aphid and ant faunas (Holway et al. 2002, Krushelnycky et al. 2005, Mondor et al. 2007). The rate of establishment of adventive species remains high: an average of 18 new insect species annually from 1937 to 1987 (Beardsley 1979). Since 1965, about 500 immigrant arthropods have become established in the Hawaiian Islands, an annual rate of about 20 species (Beardsley 1979, 1991). With many immigrant pests having become established in Hawaii over the past century, classical biocontrol has been much used (Funasaki et al. 1988).

Canada also is home to numerous adventive insects, with the immigrants of British Columbia, Newfoundland, and Nova Scotia best known. Turnbull (1980) listed 155 immigrant insects in Canada, including human ectoparasites and species associated with dwellings, stored products, cultivated crops and forest trees, and domesticated animals. The Canadian fauna also includes more than 300 species introduced for biological control (Turnbull 1980). The Coleoptera and Hemiptera are reasonably well known in Canada, with recent checklists available for both groups. Of the nearly 7500 coleopteran species recorded in Canada (including Alaska), 469 are considered immigrant ('introduced') in North America (6.2% of the total) (Bousquet 1991). More than 300 species of adventive

Hemiptera have been documented in Canada (and Alaska), representing approximately 7.7% of the nearly 3900 species (Maw et al. 2000); 81 adventive heteropterans, mainly from the western Palearctic, are known from Canada (Scudder and Footitt 2006).

Gillespie's (2001) review of adventive insects detected in British Columbia from the late 1950s to 2000 included information on immigrant lepidopterans such as the codling moth (*Cydia pomonella*), gypsy moth (*Lymantria dispar*), oriental fruit moth (*Grapholita molesta*), and winter moth (*Operophtera brumata*). Among the 48 immigrant lepidopterans are 19 species of Tortricidae (Gillespie and Gillespie 1982). The adventive fauna of British Columbia also includes 42 leafhopper (cicadellid) species (9%) (Maw et al. 2000), 32 plant bug (mirid) species (9%) (Scudder and Footitt 2006), and 10 orthopteroid species (8%) (Scudder and Kevan 1984).

The immigrant fauna of Newfoundland and Nova Scotia has received considerable attention (e.g., Brown 1940, 1950, 1967, Lindroth 1957, Morris 1983). Recent collecting has yielded numerous additional immigrants (e.g., Hoebeke and Wheeler 1996, Majka and Klimaszewski 2004, Wheeler and Hoebeke 2005, Wheeler et al. 2006).

Of 325 adventive invertebrate plant pests that became established in Great Britain from 1787 to 2004, nearly half the species (48.6%) have been recorded since 1970 (Smith et al. 2005). Homopterans (37.1%) and lepidopterans (31.3%) dominate. Of the adventive plant pests, 19% originated from Europe; since 1970, 35.6% of the species originated from continental Europe, 20.3% from North America, and 13.6% from Asia.

At least 500 adventive animal species (~1% of entire fauna) have become established in Austria since 1492 (Essl and Rabitsch 2002, Rabitsch and Essl 2006). The majority (60%) are insects, with Coleoptera and Lepidoptera best represented. About 30% of the Coleoptera are Palearctic (mostly Mediterranean), 23% Oriental, 18% Neotropical, and 7% Nearctic. Nearly 33% of the Lepidoptera originated from the Palearctic, 22% from the Nearctic, 19% from the Oriental, and 10% from the Neotropical Region. The Asian longhorned beetle (*Anoplophora glabripennis*; from China) and western corn rootworm (*Diabrotica virgifera*; from North America) are notable coleopterans detected since 2000.

Insects are the most numerous of all adventive organisms in Switzerland; at least 306 species have become

established via human activities (Kenis 2005). Much of this fauna is Mediterranean, although large numbers of tropical or subtropical insects are found in greenhouses (thrips and whiteflies) or are associated with stored products (beetles and moths). Adventive Coleoptera comprise more than 120 species (~40% of the total adventive insect fauna), including the North American Colorado potato beetle (*Leptinotarsa decemlineata*) and western corn rootworm. Fewer than 20 species of adventive Diptera are established in Switzerland (Kenis 2005).

Of insects documented for the Japanese islands, 239 species (0.8%) were considered adventive by Morimoto and Kiritani (1995), but Kiritani (1998) noted that 260 adventives ('exotic species') had been 'introduced' since 1868. Kiritani and Yamamura (2003) increased the number of adventive insect species known from Japan to 415. Coleoptera (31.2%), Homoptera (25.8%), Hymenoptera (11.2%), and Lepidoptera (12.3%) have the largest number of adventive species. Approximately 76% of the immigrant insects are considered pests, whereas only 8% of native Japanese insects are pestiferous (Morimoto and Kiritani 1995). Although the southern islands represent only 1.2% of Japan's land area, about 40% of all immigrant species first became established in these islands (Kiritani 1998).

More than 2000 invertebrate species (mostly insects) in New Zealand are adventive (Brockerhoff and Bain 2000). The ant fauna consists of 28 immigrant and 11 native species (Ward et al. 2006). Several important pests of exotic trees have become widely established (Scott 1984, Charles 1998); additional, potentially important, species are routinely intercepted at ports of entry (Bain 1977, Keall 1981, Ridley et al. 2000). More than 350 adventive beetle species are known from New Zealand (Klimaszewski and Watt 1997). A recent survey for adventive beetles that attack trees or shrubs in New Zealand yielded 51 immigrants in 12 families, most of which were of Australian (58%) and European (25%) origin (Brockerhoff and Bain 2000). Hoare (2001) reported 27 lepidopteran species new to New Zealand since 1988; the majority (67%) represented migrants from Australia, whereas certain others arrived via commerce with Asia or Europe.

The extent of the Australian insect fauna and number of adventive species is unknown (New 1994). Although the Australian Academy of Science estimated that more than 2000 adventive species are established, the

actual number might be much greater (Low 2002). More than half the insect orders include an adventive component (New 1994). In the Aphididae, about 80% of some 150 species are immigrant (New 2005b). Adventive insects are most diverse and have had greatest impact in areas most strongly influenced by European settlement ('cultural steppe') (Matthews and Kitching 1984, New 1994).

Analyses and lists of the adventive insects in other countries, islands, and regions include those for Central Europe (Kowarik 2003), France (Martinez and Malausa 1999), Germany (Geiter et al. 2002), Israel (Bytinski-Salz 1966, Roll et al. 2007), Italy (Pellizzari and Dalla Montà 1997, Pellizzari et al. 2005), Kenya (Kedera and Kuria 2003), the Netherlands (van Lenteren et al. 1987), Serbia and Montenegro (Glavendekić et al. 2005), southern oceanic islands (Chown et al. 1998), Spain (Perez Moreno 1999), Tristan da Cunha (Holdgate 1960), and Venezuela (MARN 2001). The U.S. Department of Agriculture's National Agricultural Library created the National Invasive Species Information Center in 2005; its Web site (<http://www.invasivespeciesinfo.gov/about.shtml>) provides access to sites that contain data on immigrant insects of additional countries and regions.

EFFECTS OF ADVENTIVE INSECTS

Early concerns about the consequences of immigrant insects in the USA involved agriculture and losses to crop production. Direct effects from ectoparasitic and blood-sucking insects would have been apparent to the colonists, but they likely gave no thought to whether the offending species were native. Arthropod-borne diseases were endemic in the colonies from New England to Georgia (Duffy 1953, McNeill 1976, Adler and Wills 2003), and an outbreak of yellow fever in Philadelphia in 1793 was attributed to trade with the West Indies (Inderjit et al. 2005). However, the demonstration that mosquitoes and certain other arthropods transmit the causal organisms of major human diseases was not forthcoming until the late nineteenth or early twentieth century (Mullen and Durden 2002).

Every organism that colonizes a new area can affect native communities and ecosystems (Smith 1933, Lodge 1993a). Most immigrant insects, other than several widespread species of mosquitoes, are

terrestrial. Additional immigrant aquatic groups include chironomid midges (Hribar et al. 2008), corixid bugs (Polhemus and Rutter 1997, Polhemus and Golia 2006, Rabitsch 2008), and perhaps a black fly in the Galápagos (Roque-Abelo and Causton 1999).

Not all adventive species produce quick and dramatic effects on native ecosystems (Richardson 2005). Many immigrant insects produce minimal or no observable effects (Williamson 1996, Majka et al. 2006) and may never become problematic; they seemingly become integrated into novel communities as benign or innocuous members of the fauna (Turnbull 1967, Sailer 1978). Although certain immigrants undergo rapid spread, for example, the leucaena psyllid (*Heteropsylla cubana*) (Beardsley 1991) and erythrina gall wasp (*Quadrastichus erythrinae*) (Li et al. 2006), others remain localized. An oak leaf-mining moth (*Phyllonorycter messaniella*) has spread little in Australia since being detected in 1976 and remained innocuous with only occasional outbreaks (New 1994). Two immigrant web-spinners (Embiidina) in Australia (New 1994), immigrant beetles in Switzerland in decaying plant material and litter (Kenis 2005), scavenging microlepidopteran in the western USA (Powell 1964), and most immigrant psocopterans in North America (Mockford 1993) likely will remain innocuous and obscure. Some immigrants of cryptic habits remain rarely collected years after their detection, for example, two Palearctic heteropterans in North America: a lace bug (*Kalama tricornis*) (Parshley 1916, Bailey 1951) and leptopodid (*Patapius spinosus*) (Usinger 1941, Lattin 2002). Three immigrant heteropterans (rhyparochromid lygaeoids) that feed on fallen seeds likely would have been predicted to be little-known additions to the fauna of western North America. Instead, these immigrant bugs attracted media attention when they invaded homes, libraries, schools, and businesses, creating anxiety, affecting local economies, and necessitating control measures (Henry and Adamski 1998, Henry 2004). An immigrant thrips (*Cartothrips* sp.) in California (Arnaud 1983) would have been expected to remain an obscure faunal addition, but it has been said (without evidence, except that it probably feeds on fungi in decaying vegetation) to have potential for affecting ecosystem processes such as decomposition and nutrient cycling (Mooney et al. 1986). Labeling most adventive insects as 'innocuous', however, should be done with caution because their potential for adverse effects might never have been investigated (National Research Council 2002). Studies

of immigrant herbivores typically involve their effects on economically important plants rather than possible injury to native species (e.g., Messing et al. 2007). In addition, extended lag times between establishment and explosive population growth are relatively common (Carey 1996, Crooks and Soulé 1999, Loope and Howarth 2003), and competitive exclusion on continental land masses might not take place for long periods (New 1993).

The environmental effects of invasive species sometimes are thought to have received substantial attention only in the twentieth century, mainly after Elton's (1958) book appeared. Yet, Marsh's (1864) book, stressing global anthropogenic disturbances, often is overlooked by current conservationists and invasion biologists. In discussing civilization's effects on the insect fauna of Ohio, Webster (1897) noted vegetational changes such as the reduction of forested areas, apparent disappearance of some native insects, and establishment of European insects. He did not, however, suggest that adventive insects cause environmental changes. We now know that diverse systems are as vulnerable to invasion as those of low diversity, perhaps more so (Levine 2000, D'Antonio et al. 2001; cf. Altieri and Nicholls 2002 with respect to agroecosystems); that in some cases, invasive species drive global environmental change (Didham et al. 2005; cf. MacDougall and Turkington 2005); and that biotic mixing can involve the introduction of alien alleles and genotypes (Petit 2004).

According to the 'tens rule' (Williamson 1996, Williamson and Fitter 1996), about 10% of the invaders become established, and about 10% of the established species become pests. The rule, despite its statistical regularity, involves considerable variability (Williamson and Fitter 1996, White 1998); it should be considered a working hypothesis (Ehler 1998) and perhaps disregarded for predictive purposes (Suarez et al. 2005). Immigrant insects can become pestiferous at rates almost ten times higher than for native species (Kiritani 2001). Despite impending homogenization of our biota, immigrants are not uniformly dispersed and, as might be predicted, show less cosmopolitanism than plant pathogens (Ezcurra et al. 1978). Even so, immigrant species essentially are everywhere: national parks, nature reserves, and relatively pristine communities (Macdonald et al. 1989, Cole et al. 1992, Pyšek et al. 2003), as well as boreal areas (Simberloff 2004) and Antarctica (Block et al. 1984, Frenot et al. 2005). Fewer

immigrant insects have become established in remote areas than along major trade routes and in other areas subject to human disturbance, as is true generally for invasive species (Sala et al. 2000, McNeely 2005; cf. Gaston et al. 2003). Urban areas serve as foci of entry for invaders (Frankie et al. 1982, McNeely 1999). Immigrants, including insects (Wheeler and Hoebeke 2001, Majka and Klimaszewski 2004), often are concentrated around shipping and other transport hubs (U.S. Congress 1993, Floerl and Inglis 2005).

The ecological effects of adventive species tend to be severe on old, isolated oceanic islands (Vitousek 1988, Coblenz 1990; cf. Simberloff 1995). The economic effects of such species can be particularly devastating to developing nations (Vitousek et al. 1996). Countries that experience the greatest effects from invasive species are heavily tied into systems of global trade (Dalmazzone 2000, McNeely 2006). Invasive species generally have had greater impact in the USA than in continental Europe, where traditionally they have been regarded as a less serious threat (Williamson 1999). Europe, though largely an exporter of species, has experienced recent increases in immigrant species (Pellizzari and Dalla Montà 1997, Essl and Rabitsch 2004, Kenis 2005). More attention, therefore, is being devoted to the problem (Scott 2001, Reinhardt et al. 2003). In addition to the USA (U.S. Congress 1993), countries such as Australia, New Zealand, and South Africa have been substantially affected (Macdonald et al. 1986, McNeely 1999, Pimentel 2002). By 2100, adverse effects from invasive species are expected to be most severe in Mediterranean ecosystems and southern temperate forests (Sala et al. 2000).

The various consequences of invasive species create what Barnard and Waage (2004) termed a 'national, regional, and global development problem'. In contrast to most other human-induced environmental disturbances – pollution and inappropriate use of resources such as poor farming or the draining of wetlands – the invasive species problem is harder to ameliorate and often ecologically permanent (Coblenz 1990). Mooney (2005) created 13 categories for the harmful effects of invasive species, some relevant mainly or solely to plants; at least 6, however, relate to insects: animal disease promoters, crop decimators, forest destroyers, destroyers of homes and gardens, species eliminators, and modifiers of evolution. Whereas invasion biologists and conservationists generally agree that the consequences of invasive species are substantial, they disagree on how best to measure the impact of

invaders (Parker et al. 1999, National Research Council 2002).

We discuss beneficial and detrimental effects of adventive insects here; because of contradictory effects and conflicts of interest, both positive and negative aspects are mentioned for certain species. Although the numerous species thought to have neutral consequences might better be categorized as 'effects unknown' (U.S. Congress 1993), we do not include Unknown as a category.

Adventive insects can be viewed differently in different regions and considered either positive or negative, depending on an observer's perspective. For example, a North American planthopper (*Metcalfa pruinosa*) immigrant in Europe has become a plant pest, but honeybees collect its honeydew in producing a honey that Italian apiarists market as 'Metcalfa honey' (Wilson and Lucchi 2007). Our perceptions of adventive species can be fluid, modified as the result of environmental change, subsequent introductions (U.S. Congress 1993, Simberloff et al. 1997), or as the status of natural enemies introduced for biocontrol changes with changing values (Syrett 2002). The arrival of immigrant fig wasps allowed certain fig species to become weedy in New Zealand and elsewhere (McKey 1989, Kearns et al. 1998). Two immigrant seed wasps detected in Florida in the 1980s, one associated with Brazilian pepper (*Schinus terebinthifolius*) and the other with laurel fig (*Ficus microcarpa*), would have been considered detrimental when these plants were valued as ornamentals but can be viewed as beneficial now that both plants are considered weeds (Nadel et al. 1992, Frank et al. 1997). The presence in Florida of other *Ficus*-associated insects reveals the complexity of evaluating the status of adventive species. The Cuban laurel thrips (*Gynaikothrips ficorum*), upon detection considered a pest of ornamental figs, now is regarded as a beneficial natural enemy of *F. microcarpa*. Another immigrant fig insect, an anthocorid bug (*Montandoniola moraguesi*), until recently would have been viewed as beneficial because it preys on laurel thrips. With reversal in the fig's status, the anthocorid has become an unwanted enemy of a thrips that inflicts severe foliar damage to an undesirable tree (Bennett 1995). In Hawaii, the anthocorid's status changed from a predator introduced to control the Cuban laurel thrips to one that impaired the effectiveness of a thrips introduced for weed biocontrol (Reimer 1988).

Beneficial

Insects are crucial to human existence and ecosystem functions (Waldbauer 2003). The ecological services provided in the USA by mostly native insects is estimated to be nearly \$60 billion annually (Losey and Vaughan 2006). Comparable data on adventive species are unavailable, but such insects also contribute important ecological services. Here, we mention immigrant insects involved in several scientific advances and other ways that immigrants might be considered beneficial.

The products of certain insects, such as cochineal, shellac, and silk, are well known and have been used where the insects are not native (Glover 1867, Metcalf and Metcalf 1993, New 1994). For example, the cochineal industry helped save the Canary Islands from starvation after the grape phylloxera (*Daktulosphaira vitifoliae*) devastated the islands' vineyards in the late nineteenth century (Cloudsley-Thompson 1976). Importation of insect galls as drugs and for dyeing and tanning was once important (Fagan 1918). Insects are valuable recyclers of nutrients. Dung beetles (Scarabaeidae) have been introduced into Australia to alleviate problems from slowly decomposing cattle dung. Native scarabs, adapted to feed on the drier dung of precinctive marsupials, feed only to a limited extent on moist cattle dung (Waterhouse 1974, New 1994). African dung beetles also have been introduced into the USA to assist native scarabs (Hoebeke and Beucke 1997). Classical biological control of arthropods and weeds has enjoyed long-term successes (McFadyen 1998, Gurr et al. 2000, Waterhouse and Sands 2001). The use of introduced natural enemies can help reduce pesticide contamination and maintain and manage ecosystem processes (National Research Council 2002, Hoddle 2003, 2004).

Biological control can also help reduce threats from pests of conservation or environmental concern and has been used to conserve endemic plants threatened by immigrant insects (Van Driesche 1994, cf. Samways 1997, Louda and Stiling 2004). Several notable campaigns have been carried out despite the difficulty of obtaining financial support (Frank 1998). More than 50 species of parasitoids and predators were introduced into Bermuda from 1946 to 1951 to help reduce infestations of two diaspidid scale insects (mainly *Carulaspis minima*) that were eliminating Bermudian cedar (*Juniperus bermudiana*). This attempt, the first major bio-control project undertaken expressly for conservation, failed to prevent the death of about 99% of the cedar

forests (Challinor and Wingate 1971, Samways 1994). In the 1990s, a lady beetle (*Hyperaspis pantherina*) introduced into the South Atlantic island of St. Helena saved a precinctive gumwood tree (*Commidendrum robustum*) from extinction by an immigrant ensign scale (*Orthezia insignis*) (Fowler 2004, Wittenberg and Cock 2005).

Adventive insects sometimes can be viewed as ecologically desirable additions to a fauna, such as carabid beetles in impoverished arctic communities (Williamson 1996). In western Canada, immigrant synanthropic carabids were regarded as enriching the fauna; they appear not to threaten native Carabidae because only one native species is strictly synanthropic (Spence and Spence 1988). Immigrant natural enemies arriving with, or separately from, immigrant pests provide fortuitous, though often ineffective, biocontrol (DeBach 1974, Colazza et al. 1996, Nechols 2003). An aquatic moth (*Parapoynx diminutalis*), evaluated for possible use against an aquatic weed (*Hydrilla verticillata*), soon after was detected in Florida as an immigrant (Delfosse et al. 1976). An immigrant parasitoid (*Prospaltella perniciosi*) might provide effective control of the San Jose scale (*Quadraspidiosus perniciosus*) in the USA (Sailer 1972).

Immigrant insects, such as the blow fly (*Chrysomya rufifacies*) in Hawaii, are useful in forensic entomology for establishing postmortem intervals (Goff et al. 1986). Immigrant insects also play a major role in pollination. The alfalfa leafcutter bee (*Megachile rotundata*) is a useful pollinator of alfalfa in the USA (Cane 2003) but is overshadowed in importance by the honeybee, introduced in the early seventeenth century (Sheppard 1989, Horn 2005). Its value to crop pollination is estimated to be \$15 to 19 billion annually (Levin 1983, Morse and Calderone 2000), with annual U.S. production of raw honey valued at \$150 to 200 million (Flottum 2006, U.S. Department of Agriculture NASS 2006). Societal benefits from the honeybee also include its potential use in monitoring air pollution and hazardous wastes (Shimanuki 1992).

Insects, although important as human food in many parts of the world, are little used in Europe and North America. An increased consumption of insects could promote biodiversity preservation and sustainable agriculture (DeFoliart 1997, Paoletti 2005). In the USA, at least two introduced insects, a belostomatid (*Lethocerus indicus*) and the silkworm (*Bombyx mori*), are sold in Asian food shops (Pemberton 1988, DeFoliart 1999).

Immigrant insects, such as the yellow mealworm (*Tenebrio molitor*), are sold in bait and pet shops as

food for insects, birds, and fish (Berenbaum 1989). In nature, adventive species can facilitate native species by providing trophic subsidies (Rodriguez 2006). Immigrant insects provide food for birds, mammals, amphibians, reptiles, and insects, including endangered species (Majka and Shaffer 2008). In the northeastern USA, a European weevil (*Barypeithes pellucidus*) contributes substantially to the diet of a native salamander (*Plethodon cinereus*); other predators, including birds, small mammals, snakes, and invertebrates, also prey on the weevil (Maerz et al. 2005). An immigrant leafhopper (*Opsius stactagalus*) of the adventive saltcedar (*Tamarix ramosissima*) provides food for native birds and riparian herpetofauna in southwestern states (Stevens and Ayers 2002). North American birds prey on egg masses of the introduced gypsy moth (*Lymantria dispar*) (Glen 2004).

Although the prominence of *Drosophila melanogaster* as a research organism does not depend on its immigrant status, the fly has been studied on continents where it is not native. Now almost cosmopolitan, it originally was restricted to the Old World tropics and subtropics (Patterson and Stone 1952). Its arrival in the USA appears undocumented, but it must have been present long before Thomas H. Morgan began his classic studies in genetics in 1909. Experimental work on this immigrant fly has led to four Nobel Prizes (Berenbaum 1997), and it became the third eukaryote whose genome was fully sequenced (DeSalle 2005). An Old World congener (*D. subobscura*) now established in North and South America (Beckenbach and Prevosti 1986) is being used to enhance our understanding of the predictability and rate of evolution in the wild (Huey et al. 2005). Other adventive insects that have advanced our understanding of ecology, evolution, genetics, and physiology include flour beetles (*Tribolium castaneum*, *T. confusum*) (Sokoloff 1966, Price 1984), a blood-feeding reduviid (*Rhodnius prolixus*) (Wigglesworth 1984), and the yellow mealworm (Schuurman 1937, Costantino and Desharnais 1991). The Madagascan hissing cockroach (*Gromphadorhina portentosa*), which also is used as an experimental animal (Guerra and Mason 2005), is featured in classrooms and insect zoos to introduce children to the pleasures of entomology and pique their interest in insects (Gordon 1996, Rivers 2006); in Florida, it once was a popular pet (Thomas 1995, Simberloff 2003). The popularity of adventive insects as pets can enhance the public's appreciation of insects, but they should be imported legally and not pose a conservation

concern (New 2005a). Regardless of how the monarch (*Danaus plexippus*) arrived in Australia, New Zealand, and smaller islands in the Pacific – direct flight, long-distance movement with tropical storms, hitchhiking on ships, or introduction with infested host plants (Zalucki and Clarke 2004) – this butterfly doubtlessly has delighted nature lovers outside North America. The value of insects to human society – in art, decoration, fashion, language, music, spiritual reflection, story, and symbol (Kellert 1996) – might include additional adventive species.

Sterile insect technique, a new principle in population suppression and 'technological milestone in the history of applied entomology' (Perkins 1978), was developed to eradicate the screwworm (*Cochliomyia hominivorax*) from the southern USA (Knipling 1955, Klassen and Curtis 2005). Other immigrants, such as the European corn borer (*Ostrinia nubilalis*) and Hessian fly (*M. destructor*), played key roles in the development of resistant crop varieties in the USA (Painter 1951, Kogan 1982); others, such as the cereal leaf beetle (*Oulema melanopus*), contributed to the modeling of population dynamics and pattern of spread (Kogan 1982, Andow et al. 1990). Identification and synthesis of sex-attractant pheromones of lepidopterans immigrant in North America, including the codling moth (*Cydia pomonella*), European corn borer, and oriental fruit moth (*Grapholita molesta*), helped elucidate chemical communication in insects (Roelofs et al. 1969, 1971, Cardé and Baker 1984) and, in the case of the European corn borer, shed light on evolution of the Insecta (Roelofs et al. 2002). Science and society also have been served by using pheromones of immigrant lepidopterans to monitor pest densities and disrupt mating as an alternative to pesticidal control (Cardé and Baker 1984, Cardé and Minks 1995, Weseloh 2003). Characterization and synthesis of the sex pheromone of the German cockroach (*Blattella germanica*) provided a means for its monitoring and control (Nojima et al. 2005).

Benefits derived from adventive insects can be extended to the red imported fire ant (*Solenopsis invicta*). It not only can be a useful predator under certain conditions (Reagan 1986, Tschinkel 2006, cf. Eubanks et al. 2002) and provided insights into the evolution of social organization in insects (Ross and Keller 1995) but also helped shape the career of Edward O. Wilson, indirectly promoting studies in insect biodiversity. Wilson's discovery of the ant at Mobile, Alabama, when he was only 13, represented the earliest U.S. record of the species and his first scientific observation.

At 19, he took a leave of absence from the University of Alabama to study the fire ant's spread and impact. This work for the state conservation department was the first professional position (Wilson 1994) for a biologist who would popularize biodiversity studies and become a leading scientist of the twentieth century.

Detrimental

Invasive species produce adverse socioeconomic, environmental (ecological), and health effects. The problem can be viewed as involving economic as much as ecological issues (Evans 2003). Economic costs can be direct, involving exclusion, eradication, control, and mitigation; or indirect, involving human health or alteration of communities and ecosystems (Perrings et al. 2005, McNeely 2001a). Indirect economic costs, which include ecosystem services (Charles and Dukes 2007), are more difficult to calculate, often are not considered, and can overwhelm direct costs (Ranjan 2006). Seldom considered are both the economic and environmental costs of using pesticides to control (or manage) immigrant pests. Invasive species sometimes act synergistically, their collective effects being greater than those of the species considered individually (Howarth 1985, Simberloff 1997). The red imported fire ant (*Solenopsis invicta*) might facilitate the success of an immigrant mealybug (*Antonina graminis*) that uses the ant's honeydew (Helms and Vinson 2002, 2003). Synergistic effects can make it easier for more species to invade ('invasional meltdown'; Simberloff and Von Holle 1999).

Detecting ecological impacts of invasive species and quantifying their effects on population dynamics of native species are difficult, perhaps more so in the case of insects because of their small size and complex, subtle indirect effects – those involving more than two species (Strauss 1991, White et al. 2006). Indirect effects of adventive insects can include unintended cascading effects unlikely to be predicted by risk analysis or revealed during prerelease screening of biocontrol agents. Quantitative estimates of the probability of indirect effects cannot be made (Simberloff and Alexander 1998). Unintended consequences that affect biodiversity fall within the 'externalities' of economists (McNeely 1999, Perrings et al. 2000).

Harm from invasive insects sometimes is considered only in terms of economic losses to agriculture, forestry, or horticulture: crop damage plus control

costs. Costs of control may include only those borne by governments, with costs of private control omitted (U.S. Congress 1993). The calculation of losses may fail to consider that they are dynamic, changing from year to year and by regions (Schwartz and Klassen 1981). Crop losses, coupled with far-reaching societal impacts, can be severe when an invasive insect threatens an industry: for example, grape phylloxera (*Daktulosphaira vitifoliae*) and wine production in Europe (Pouget 1990, Campbell 2005), San Jose scale (*Quadraspidiosus perniciosus*) and deciduous fruit culture in California (Iranzo et al. 2003), and sugarcane delphacid (*Perkinsiella saccharicida*) and sugar production in Hawaii (DeBach 1974).

Economics in relation to invasive insects encompasses more than is treated in most entomological publications, for example, research and management costs (McLeod 2004). Consideration of the consequences of immigrant insects in the USA also should include the federal government's procedures for their exclusion, which can entail substantial annual costs within the country and in the countries of origin (Wallner 1996). How the costs of preventing the introduction of an immigrant species compare with those that would have been caused by that species had it become established represent a 'great unknown' (Cox 1999).

Aggregate costs of invasive species, including insects, seldom have been estimated on a national scale (Reinhardt et al. 2003, Essl and Rabitsch 2004, Colautti et al. 2006). The costs estimated by U.S. Congress (1993) and Pimentel et al. (2001, 2005) are cited frequently. Annual damage to U.S. crops by invasive insects is nearly \$16 billion (Pimentel et al. 2001). Because Pimentel et al. (2000, 2001) dealt only with a subset of effects from invasive species, they might have understated the problem (Lodge and Shrader-Frechette 2003; cf. Theodoropoulos 2003, p. 116).

Historical data on crop losses from insects in the USA include Walsh's (1868) estimate of \$300 million. If immigrant insects are assumed to have caused 40% of the losses, as Pimentel et al. (2001) did, losses in 1868 would have been about \$120 million (~\$4 billion in 2005 dollars based on Consumer Price Index). Sasscer (1940) estimated annual losses from insects (including costs for maintaining research and quarantine facilities, loss of markets due to quarantines, and processing costs from insect damage) to be about \$3 billion annually, with at least half resulting from immigrant species (~20 billion in 2005 dollars).

Estimated losses from immigrants in other countries are Australia: AU\$4.7 billion from insects from 1971 to 1995; British Isles: US\$960 million annually from arthropods; New Zealand: NZ\$437 million annually in crop damage plus control costs for invertebrates, mainly insects; and South Africa: US\$1 billion each year in crop damage plus control costs for arthropods (Pimentel 2002).

Economic losses from individual species can be huge (Table 21.3). In 1927, the U.S. Congress appropriated an unprecedented \$10 million to conduct a clean-up campaign to check further spread of the European corn borer (*Ostrinia nubilalis*) (Worthley 1928). For pests not as well established as the corn borer, actual and predicted costs of eradication, as well as predicted losses, are impressive. Unsuccessful campaigns to eradicate the red imported fire ant from the southeastern USA cost more than \$200 million (Buhs 2004). When the ant was detected in California in 1997, eradication costs were estimated at about \$4 billion to almost \$10 billion (Jetter et al. 2002). Eradication programs often are controversial and unsuccessful; undesirable

consequences include adverse effects on human health, death of wildlife, and reduction of arthropod natural enemies leading to secondary-pest outbreaks (Dreistadt et al. 1990, Buhs 2004). Eradication, however, can provide great financial benefits (Klassen 1989, LeVeen 1989, Myers and Hosking 2002). Annual costs associated with the anticipated arrival of the Russian wheat aphid (*Diuraphis noxia*) in Australia might be as high as several million dollars (New 1994). Full costs to the U.S. bee industry from invasion by the African honeybee (*Apis mellifera scutellata*) are not yet known (Schneider et al. 2004), but prior to its arrival, were estimated at \$26 million to \$58 million for beekeeping and another \$93 million for crop losses due to reduced pollination (Winston 1992).

Losses from the Asian longhorned borer (*Anoplophora glabripennis*) in nine at-risk U.S. cities could range from \$72 million to \$2.3 billion and, if every urban area in the conterminous states became totally infested, might reach nearly \$670 billion (Nowak et al. 2001). The emerald ash borer (*Agrilus planipennis*) poses nearly a \$300 billion threat to U.S. timberlands (Muirhead

Table 21.3 Some economic losses from invasive insects.

Species	Description of Loss ¹	Locality	Reference
Alfalfa weevil (<i>Hypera postica</i>)	\$500 million, 1990	USA	Simberloff 2003
Asian papaya fruit fly (<i>Bactrocera papayae</i>)	AU\$100 million, 1990s	Queensland, Australia	Clarke et al. 2005
Boll weevil (<i>Anthonomus grandis</i>)	\$15 billion, cumulatively since 1893	USA	Cox 1999, Myers and Hosking 2002
Codling moth (<i>C. pomonella</i>)	\$10–15 million annually	USA	Gossard 1909
European corn borer (<i>O. nubilalis</i>)	\$350 million, 1949	USA	Haeussler 1952
Formosan subterranean termite (<i>Coptotermes formosanus</i>)	\$1 billion annually	USA	Pimentel et al. 2000
Hessian fly (<i>Mayetiola destructor</i>)	\$40 million annually	USA	Gossard 1909
Mediterranean fruit fly (<i>Ceratitis capitata</i>)	\$100 million, eradication 1982–1983; losses to economy exceed projected \$1.4 billion	California, USA	Kim 1983, Kiritani 2001
Melon fly, Oriental fruit fly (<i>Bactrocera cucurbitae</i> , <i>B. dorsalis</i>)	\$250 million, eradication	Japan	Kiritani 2001
Mole crickets, <i>Scapteriscus</i> spp.	>77 million annually, including control costs	Southeastern USA	Frank 1998
Pink hibiscus mealybug (<i>Maconellicoccus hirsutus</i>)	\$125 million annually	Trinidad and Tobago	Ranjan 2006
Russian wheat aphid (<i>Diuraphis noxia</i>)	\$500–900 million, through 1990s	USA	Footitt et al. 2006
Sheep blow fly (<i>L. cuprina</i>)	AU\$100 million annually	Australia	New 1994
Small hive beetle (<i>Aethina tumida</i>)	\$3 million, 1998	USA	Hood 2004

¹All losses are in U.S. dollars unless otherwise noted; costs have not necessarily been documented by economists.

et al. 2006). Canada could be severely affected by the Asian longhorned borer, as well as the emerald ash borer and brown spruce longhorn beetle (*Tetropium fuscum*) (Colautti et al. 2006). An analysis indicating that the Asian longhorned borer's introduction into Europe would pose a significant threat was in press (MacLeod et al. 2002) when the beetle was detected in Austria (Tomiczek and Krehan 2001).

Immigrant herbivores become problematic by feeding on economically important plants, but they also have indirect effects, such as the transmission of viruses and other phytopathogens. The role of the European elm bark beetle (*Scolytus multistriatus*) in spreading Dutch elm disease in North America is well known (Sinclair and Lyon 2005). With millions of disease-susceptible American elms (*Ulmus americana*) having been planted and a competent immigrant vector already established (a native bark beetle is a less efficient vector (Sinclair 1978b)), conditions were favorable for disease outbreak when the fungal pathogen arrived from Europe. By the mid-1970s, about 56% of urban American elms had died (Owen and Lownsbery 1989). Dutch elm disease has had the greatest societal impact of all insect-related tree diseases of urban areas (Campana 1983); cumulative economic losses have amounted to billions of dollars (Sinclair 1978a). Though often considered an urban problem, this disease also affects plant and animal composition in forests (Sinclair 1978a, Campana 1983). The banded elm bark beetle (*S. chevyrewi*), detected recently in western states, could exacerbate problems from Dutch elm disease in North America (Negrón et al. 2005). A serious problem of eastern North American forests is beech bark disease, which involves American beech (*Fagus grandifolia*), a Palearctic scale insect (*Cryptococcus fagisuga*) detected in Nova Scotia about 1890 (Ehrlich 1934), and nectria fungi (formerly *Nectria* spp. but now placed in other genera (Rossmann et al. 1999)). Feeding by the scale insect allows fungi that are unable to infect intact bark to invade injured areas. The disease not only kills beech trees, thereby altering the composition of eastern forests and reducing their commercial and recreational use, but likely also adversely affects birds, small mammals, and arthropods (Sinclair and Lyon 2005, Storer et al. 2005).

Other immigrant insects that transmit phytopathogens are agriculturally and horticulturally important. An example is a Nearctic leafhopper (*Scaphoideus titanus*) that apparently was shipped with grapevine material to the Palearctic Region; it serves

as the principal vector of a phytoplasma disease (flavescence dorée) of cultivated grapes in Europe (Lessio and Alma 2004, Bressan et al. 2005). A recent (2000) immigrant, the soybean aphid (*Aphis glycines*), quickly became the most important insect pest of U.S. soybean production (Rodas and O'Neil 2006); this Asian native transmits (or is suspected to transmit) several plant viruses in North America (Heimpel et al. 2004, Damsteegt et al. 2005). Another Old World aphid (*Toxoptera citricida*) transmits the virus that causes citrus tristeza. The disease, though present in Venezuela by 1960, did not threaten the citrus industry until the aphid arrived. By the mid-1980s, the disease had devastated the country's citrus culture (Lee and Rocha-Peña 1992). Whiteflies of the *Bemisia tabaci* species complex, transported with commerce throughout much of the world (Oliveira et al. 2001, Perring 2001), transmit several geminiviruses (Czosnek et al. 2001). In the 1980s, the western flower thrips (*Frankliniella occidentalis*), native to the southwestern USA, assumed near cosmopolitan distribution from global trade in greenhouse plants. Emerging as the main vector of the tospovirus that causes tomato spotted wilt, it induced disease epidemics (Ullman et al. 1997, Morse and Hoddle 2006).

Immigrant insects also transmit pathogens to native uneconomic plants. A recently detected Asian ambrosia beetle (*Xyleborus glabratus*) transmits a fungus responsible for extensive mortality of native red bay (*Persea borbonia*) trees in the southeastern USA (Haack 2006, Mayfield 2006). Immigrant aphids may vector viruses of native Hawaiian plants, including precinctive species (Messing et al. 2007).

Immigrant insects of veterinary importance serve as vectors of disease organisms and otherwise affect productivity or harm domestic and companion animals. Annual losses from long-established species affecting livestock in the USA include nearly \$1 billion (Castiglioni and Bicudo 2005) for the horn fly (*Haematobia irritans*) (losses are nearly \$70 million in Canada (Colautti et al. 2006)). The stable fly (*Stomoxys calcitrans*), long a pest of cattle in midwestern U.S. feedlots, now affects range cattle. When pest numbers are high, daily decreases in weight gain can be nearly 0.5 lb per head (Hogsette 2003, Campbell 2006). The stable fly and other synanthropic Diptera are nuisance insects that affect the U.S. tourist industry (Merritt et al. 1983). In Australia, annual loss of production and treatment costs for the sheep blow fly (*Lucilia cuprina*), an immigrant ectoparasite responsible for cutaneous myiasis

(flystrike) of sheep (Levot 1995), amount to more than AU\$160 million (McLeod 1995).

Costs associated with the loss of wildlife as the result of immigrant insects are more difficult to express monetarily than those for domestic animals. Avian malaria, though present in Hawaii, did not seriously affect the native avifauna until a competent vector was in place. Following the establishment of a mosquito (*Culex quinquefasciatus*) in lowland areas of Maui by the early nineteenth century, malaria and avian pox became epidemic, which led to many native birds, especially honeycreepers, becoming endangered or extinct (Warner 1968, Jarvi et al. 2001; cf. van Riper et al. 1986). Disease resistance, however, might be evolving in certain Hawaiian forest birds (Woodworth et al. 2005, Strauss et al. 2006). An immigrant muscid fly (*Philornis downsi*) recently was detected on the Galápagos archipelago. This obligate ectoparasite of birds apparently has killed nestlings on the islands and could threaten Darwin's finches (Fessl and Tebbich 2002).

Costs associated with human diseases transmitted by immigrant insects can be estimated (Gratz et al. 2000), as was done in Australia for dengue infections after the yellow fever mosquito (*Aedes aegypti*) became established (Canyon et al. 2002). The impact of invasive insects on human health, however, cannot be expressed adequately in monetary terms. At least five immigrant insects associated with vector-borne diseases helped shape South Carolina's culture and history (Adler and Wills 2003).

Medical effects from invasive insects include mild skin reactions (pruritus, urticaria) from contact with browntail moth or gypsymoth larvae (Allen et al. 1991, Mullen 2002); reactions from exposure to allergens of immigrant cockroaches (Peterson and Shurdut 1999); and life-threatening envenomation and hypersensitive reactions from adventive hymenopterans such as the honeybee, red imported fire ant, and other ant species (Akre and Reed 2002, Klotz et al. 2005, Nelder et al. 2006). Effects on humans are catastrophic when immigrant insects serve as vectors of diseases that cause massive population die-offs (Cartwright 1972, Vitousek et al. 1997). In fourteenth-century Europe, following introductions of the black rat (*Rattus rattus*) and oriental rat flea (*Xenopsylla cheopis*), about 25 million people were killed by plague in a pandemic often called the Black Death (Cartwright 1972, Cloudsley-Thompson 1976, Laird 1989). A mid-seventeenth-century immigrant to the Western

Hemisphere was the yellow fever mosquito (*Aedes aegypti*), which arrived in the Caribbean with ships bearing Africans for the slave trade and became a notorious vector of viruses that cause dengue and yellow fever (Bryan 1999). Throughout human history, immigrant insects have transmitted agents responsible for major diseases (Cloudsley-Thompson 1976, Lounibos 2002).

With the advent of air travel in the 1920s, airplanes became important transporters of mosquitoes that could serve as disease vectors in new areas (Gratz et al. 2000). Disease outbreaks most often result from independent introductions of vector species and pathogens (Juliano and Lounibos 2005). Mosquito species arriving by ship are more likely to become established than those moved by aircraft (Lounibos 2002).

The establishment of an immigrant mosquito (*Anopheles gambiae* s.l.) in Brazil during the 1930s led to epidemic malaria, imposing great socioeconomic burden on the country (Killeen et al. 2002, Levine et al. 2004). Eradication of the mosquito from northeastern Brazil, rapid and unexpected, ended the severe epidemics (Davis and Garcia 1989). A relatively recent global invader, the Asian tiger mosquito (*Aedes albopictus*), can transmit dengue virus and certain other viral agents of encephalitis (Gratz 2004). Native to the Orient, it has become established on five continents since the late 1970s (Adler and Wills 2003, Aranda et al. 2006). In some regions, the Asian tiger mosquito has displaced an immigrant congener, *A. aegypti* (Juliano 1998, Reitz and Trumble 2002, Juliano et al. 2004), although continental U.S. populations of the latter species had been declining prior to the arrival of *A. albopictus* (Rai 1991). An East Asian mosquito (*Ochlerotatus japonicus*) was first collected in the Western Hemisphere in 1998 in the northeastern USA (Peyton et al. 1999). This public-health threat has spread to the southeastern states (Reeves and Korecki 2004), west coast (Sames and Pehling 2005), and southern Canada (Darsie and Ward 2005), and has become established in Hawaii (Larish and Savage 2005) and continental Europe (Medlock et al. 2005). It is a competent laboratory vector of West Nile virus (and potential vector of others), and the virus has been detected in field-collected specimens (Andreadis et al. 2001, Turell et al. 2001).

The world might be entering another (fourth) transition in the history of human diseases, one characterized by ecological change rather than contact among human populations (Baskin 1999). Insects moved in

commerce promise to play crucial roles in additional changes in the patterns of vector-borne diseases.

The toll of vector-borne diseases, in addition to loss of life, impaired health, and socioeconomic consequences, includes environmental effects such as the draining and oiling of U.S. wetlands to reduce mosquito populations and malaria (Adler and Wills 2003). Similarly, wetlands in other countries have long been drained, but the restoration of wetlands or construction of new ones has become more common with realization of the need to conserve biodiversity (Schäfer et al. 2004).

In contrast to long-standing interests in calculating economic losses due to invasive species, ecological costs only recently have begun to be assessed (With 2002). The environmental effects of immigrant insects are difficult to estimate (Simberloff 1996, Binggeli 2003) and perhaps are being overlooked (Kenis 2005), due, in part, to an overemphasis on extinction in the popular press (U.S. Congress 1993). Yet, only a 'small minority' of adventive species appears to be affecting native species (Simberloff and Von Holle 1999). Of 81 adventive heteropterans recorded from Canada, only one species might be causing environmental harm (Scudder and Footitt 2006). Despite their diversity, insects are said not to show 'high potential' for causing environmental harm (Wittenberg 2005). Though adventive insects probably damage the environment less than pathogens, plants, and mammals do (Simberloff 2003), the direct and indirect ecological effects of immigrant insects on eastern North American forests (Liebhold et al. 1995, Cox 1999) alone seem sufficient to negate Wittenberg's (2005) statement. Moreover, immigrant oak-associated herbivores, while not economically important, could adversely affect western oak (*Quercus garryana*) meadows in British Columbia (Gillespie 2001). Simberloff's (2003) comment, therefore, seems more appropriate: 'Relative to the numbers of species introduced, insects rarely cause enormous ecological (as opposed to economic) damage'.

Insects seem not to alter fire regimes as do some invasive plants (D'Antonio and Vitousek 1992, D'Antonio 2000), although an immigrant cerambycid (*Phoracantha semipunctata*) might create a fire hazard in California by killing eucalyptus trees (Dowell and Gill 1989). As underlying mechanisms for adverse effects, ranging from individual to ecosystem levels, competition and predation generally are considered more important than hybridization in insects (Rhymer and Simberloff 1996, National Research Council 2002), with interference competition more easily

demonstrated than resource competition (Simberloff 1997, 2000). Hybridization and introgression, though apparently uncommon in insects (Dowling and Secor 1997), occur in certain species of *Drosophila* (Mallet 2005) and subspecies of the honeybee (Sheppard 1989, Schneider et al. 2006) and between the red imported fire ant (*Solenopsis invicta*) and an immigrant congener (*S. richteri*) in a portion of their U.S. range (Tschinkel 2006). Establishment of the Asian gypsy moth in North America and its possible hybridization with the European form are cause for concern (Cox 2004). Hybridization and genetic disruption between an immigrant and an endemic tiger beetle (*Cicindela* spp.) might be taking place in the Galápagos (Causton et al. 2006). Moreover, multiple immigrations of pest insects enhance genetic diversity (Tschinkel 2006) and potentially create more virulent biotypes (Lattin and Oman 1983, Whitehead and Wheeler 1990).

Environmental effects attributed to invasive insects often are based on anecdotal rather than quantified data; inferences on species interactions may fail to consider alternative hypotheses for explaining the observations (Simberloff 1981). Populations of several native coccinellid beetles appear to have declined after the adventive coccinellids *Coccinella septempunctata* and *Harmonia axyridis* became established in North America (e.g., Wheeler and Hoebeke 1995, Michaud 2002). Declines in native species correlated with the establishment of immigrants do not establish causation (Williamson 1996, Simberloff 1997), and other factors might be involved in the decrease in lady beetle densities (Wheeler and Hoebeke 1995, Day and Tatman 2006). Assessing the proximate and ultimate causes of declines in imperiled native species, which are likely subject to multiple threats, is difficult, as is evaluating the threats and their relative importance (Gurevitch and Padilla 2004). As Tschinkel (2006) emphasized, few studies in which competitive displacement by immigrant ants is claimed actually were designed to measure such an effect. The examples of the environmental effects of adventive insects we give later vary in scientific rigor.

Eurasian phytophagous insects in North America tend to colonize the same genera (and often the same species) they do in the Old World and might not have been able to become established without the presence of their native (or closely related hosts) in the New World (Mattson et al. 1994, Niemelä and Mattson 1996, Frank 2002). Species of *Eucalyptus*, planted in North America since the 1800s, were available

for late-twentieth-century colonization by specialized immigrant herbivores (Paine and Millar 2002). Certain immigrants have been found in the Nearctic Region only on Palearctic hosts. Examples include several plant bugs (Miridae) and jumping plant lice (Psyllidae) on European ash (*Fraxinus excelsior*) (Wheeler and Henry 1992, Wheeler and Hoebeke 2004), a psyllid (*Livilla variegata*) on ornamental laburnums (*Laburnum* spp.) (Wheeler and Hoebeke 2005), and a lace bug (*Dictyla echi*) on viper's bugloss (*Echium vulgare*) (Wheeler and Hoebeke 2004). Two Palearctic seed bugs are restricted in North America to cosmopolitan and pantropical cattails (*Typha* spp.) (Wheeler 2002). Even if these specialized phytophages expand their host ranges in North America, they are unlikely to cause environmental harm. In other cases, Eurasian plants serve as alternative hosts of recently established immigrant insects that become crop pests, for instance, the Russian wheat aphid (*Diuraphis noxia*) (Kindler and Springer 1989).

Other immigrant phytophages also are not benign faunal additions. Direct feeding by insects immigrant in Hawaii imperils plants of special concern (Howarth 1985). In the Galápagos Islands, the cottony cushion scale (*Icerya purchasi*) killed endangered plants and, in turn, apparently caused local extirpation of certain host-specific lepidopterans (Causton et al. 2006). A Mexican weevil (*Metamasius callizona*) detected in Florida in 1989 feeds on introduced ornamental bromeliads and kills native epiphytic bromeliads (*Tillandsia* spp.) that are protected by law. Destruction of native bromeliads also destroys the invertebrate inhabitants of water impounded in leaf axils (phytotelmata) on the plants (Frank and Thomas 1994, Frank and Fish 2008).

Immigrant phytophages can threaten not only novel host plants but also their naïve natural enemies. The glassywinged sharpshooter (*Homalodisca vitripennis*), detected in French Polynesia in 1999, developed atypically large populations but did not adversely affect the new hosts on which it fed or affect them indirectly by transmitting the bacterium *Xylella fastidiosa*. Instead, the effects of the leafhopper's arrival were seen at higher trophic levels: a lethal intoxication of its spider predators. The cause of mortality is unknown but might involve the leafhopper's bacterial endosymbionts. By using lethal allelochemicals against spiders, *H. vitripennis* might alter the structure and species composition of food webs in the South Pacific (Suttle and Hoddle 2006).

Ants are among the more spectacular of invasive organisms (Moller 1996); several hundred species have been or are being moved in global trade (McGlynn 1999, Suarez et al. 2005, Ward et al. 2006). Those moving readily in commerce – the so-called tramp species (Passera 1994) – afford opportunities for behavioral, ecological, and evolutionary studies relevant to conservation and agriculture. Immigrant ants not only can reduce biodiversity but also can disrupt the biological control of plant pests (Coppler et al. 2007) and disassemble native ant communities (Sanders et al. 2003). Immigrant ants' competitive displacement of native species often is reported, but, at best, is hard to document (e.g., Krushelnycky et al. 2005). The effects of immigrant ants on ant-plant mutualisms warrant more study (Holway et al. 2002, Ness and Bronstein 2004). Ants' mutualistic tending of homopterans such as aphids and scale insects can protect pest species, increasing their densities and damage and deterring predation by natural enemies (Kaplan and Eubanks 2002, Hill et al. 2003, Jahn et al. 2003). Immigrant ants, in turn, sometimes are replaced by later-arriving ant species (Simberloff 1981, Moller 1996), a phenomenon seen among immigrants in other insect groups and among biocontrol agents (Ehler and Hall 1982, Reitz and Trumble 2002, Snyder and Evans 2006; cf. Keller 1984).

The red imported fire ant (*Solenopsis invicta*) adversely affects various invertebrate and vertebrate groups (Porter and Savignano 1990, Vinson 1994, 1997). The recent review of the causes and consequences of ant invasions (Holway et al. 2002), review of the effects of the red imported fire ant on biodiversity (Wojcik et al. 2001, Allen et al. 2004), and critique of purported ecological effects from this fire ant (Tschinkel 2006) provide information and references beyond those we mention here.

Immigrant ants can affect seed dispersal and pollination, processes critical to plant reproductive success. By removing seeds, red imported fire ants are potential threats to spring herbs (e.g., *Trillium* spp.) in deciduous forests of the southeastern USA (Zettler et al. 2001). In the Cape fynbos flora of South Africa, the Argentine ant (*Linepithema humile*) has displaced native ants associated with certain precinctive proteaceous plants (myrmecochores) whose seeds are ant dispersed. Argentine ants are slower to discover the seeds, move them only short distances, and eat the elaiosomes without burying the seeds in subterranean nests, as native ants do. Exposed seeds are vulnerable to predation

and desiccation. Plant community composition might change as a result of reduced seedling recruitment (Bond and Slingsby 1984, Gilomee 1986). Because the two native ant species displaced by Argentine ants are more effective dispersers of large-seeded Proteaceae than are the two coexisting native species, the fynbos shrubland community might shift toward smaller-seeded species (Christian 2001). Displacement of native ants in Australia involves interference competition by Argentine ants (Rowles and O'Dowd 2007). Argentine ants also deter insect visitation to flowers of certain fynbos proteas (*Protea nitida*) (Visser et al. 1996), reduce fruit and seed set of a euphorbiaceous shrub (*Euphorbia characias*) in Spain (Blancafort and Gómez 2005) and generally threaten myrmecochory in the Mediterranean biome (Gómez and Oliveras 2003), and pose a threat to precinctive plants in Hawaii by reducing their pollinators and plant reproduction (Loope and Medeiros 1994, 1995, Cox 1999). The longlegged or yellow crazy ant (*Anoplolepis gracilipes*) has had severe direct and indirect effects on Christmas Island, killing an estimated 10–15 million red crabs (*Gecarcoidea natalis*) and eliminating populations of this keystone species that regulates seedling recruitment, composition of seedling species, litter breakdown, and density of litter invertebrates. The crab's elimination has long-term implications for forest composition and structure. The ant's mutualism with honeydew-producing homopterans further disrupts the rainforest ecosystem (O'Dowd et al. 2003, Green et al. 2004). Detected in the Seychelles islands in the 1960s, *A. gracilipes* also has begun to affect biodiversity on Bird Island in the Seychelles, following its discovery in the 1980s (Gerlach 2004). Other immigrant ants (Williams 1994) cause adverse environmental effects, including the bigheaded ant (*Pheidole megacephala*) in Hawaii (Jahn and Beardsley 1994, Asquith 1995) and other Pacific islands (Wetterer 2007), and the little fire ant (*Wasmannia auropunctata*) in the Galápagos (Lubin 1984).

Nonsocial bees immigrant in North America have not adversely affected native bees (Cane 2003). The introduced honeybee, a social species, by competing for floral resources with native bees and disrupting the pollination of native plants (e.g., Gross and Mackay 1998, Spira 2001, Dupont et al. 2004), might affect native ecosystems. Though harmful effects on native flower visitors have been attributed to honeybees, better experimental data and longer studies generally are needed to support the claims (Butz Huryn 1997, Kearns et al. 1998, Goulson

2003). As principal pollinators of invasive plants, honeybees can also enhance fruit set, thus facilitating invasiveness (Goulson and Derwent 2004). Caution should be exercised before introducing social bees that have become invasive elsewhere, for example, a bumble bee (*Bombus terrestris*) into mainland Australia, when it is highly invasive on the Australian island of Tasmania (Hingston 2006). Immigrant wasps and yellowjackets have been implicated in detrimental ecological effects. Examples include the western yellowjacket (*Vespula pensylvanica*) in Hawaii, which preys on native arthropods, reducing their densities and threatening arthropods of Maui's native ecosystems (Gambino et al. 1990, Asquith 1995); two yellowjackets (*V. germanica*, *V. vulgaris*) in beech (*Nothofagus*) forests in New Zealand, where they restructure invertebrate communities through predation and competition and compete with the precinctive kaka parrot (*Nestor meridionalis*) by harvesting honeydew from margarodid scale insects (*Ultracoelostoma* spp.), thereby limiting the birds' reproductive success (Beggs and Wilson 1991, Beggs et al. 1998, Beggs and Rees 1999); and a paper wasp (*Polistes versicolor*), which feeds mainly on lepidopteran larvae in the Galápagos and competes for food with native vertebrates such as finches (Causton et al. 2006).

Forest insects continue to be carried to all major continents (Ciesla 1993, Britton and Sun 2002, Haack 2006). Adventive insects that alter forest ecosystems in eastern North America are immigrants except for the European gypsy moth, which was introduced into Massachusetts with the hope of crossing the moth with native silkworms to produce a disease-resistant strain for a U.S. silk industry (Spear 2005). Gypsy moth defoliation of oaks (*Quercus* spp.) and its suppression by applications of the insecticide *Bacillus thuringiensis* have changed forest stand composition; increased nest predation of songbirds; decreased mast (acorn) production, resulting in declines of small mammals and changes in foraging patterns of bear and deer; and decreased lepidopteran populations (Liebhold et al. 1995, Wallner 1996). Cascading effects of this eruptive pest encompass interactions among mast production, mice, deer, and ticks that, in turn, affect the incidence of Lyme disease (Elkinton et al. 1996, Jones et al. 1998, Liebhold et al. 2000). The gypsy moth's sociological impact – on esthetic quality and recreational and residential values – might be even greater than its environmental effects (Liebhold et al. 1995).

An immigrant aphidoid, the balsam woolly adelgid (*Adelges piceae*), affects balsam fir (*Abies balsamea*) forests in the Northeast and has nearly eliminated old-growth Fraser fir (*A. fraseri*) in the spruce–fir ecosystem of the southern Appalachians (Jenkins 2003, Potter et al. 2005). The hemlock woolly adelgid (*A. tsugae*) spread from landscape plantings to native stands of eastern hemlock (*T. canadensis*) in the late 1980s (Hain 2005). This immigrant has caused significant mortality in New England forests, shifting nutrient cycling, composition, and structure and imperiling species that are important culturally, economically, and ecologically (Jenkins et al. 1999, Small et al. 2005, Stadler et al. 2005). The effects of hemlock's decline might extend to long-term effects in headwater stream ecosystems (Snyder et al. 2005). *Adelges tsugae* threatens eastern hemlock and Carolina hemlock (*T. caroliniana*) in the southern Appalachians (Graham et al. 2005).

Although introduced pollinators have not caused substantial ecological harm, scarab beetles released to help remove cattle dung might compete with native beetles (Thomas 2002). In Hawaii, the beetles are eaten by mongooses (*Herpestes javanicus*), perhaps allowing these generalist carnivores to maintain larger-than-normal densities (Howarth 1985). The ill-advised biocontrol release of the mongoose to suppress rat populations in Hawaii, and this carnivore's adverse effects on native birds, is well documented (van Riper and Scott 2001).

That invasion biology and classical biological control are linked has been pointed out by numerous workers (e.g., Ehler 1998, Strong and Pemberton 2000, Fagan et al. 2002). Biological control was once considered to lack environmental risk (DeBach 1974), and as recently as the early 1980s was not discussed among numerous causes of decline in insect populations (Pyle et al. 1981). Evidence for adverse effects of natural enemies, however, had long been available (Howarth 2000) and concern over their unforeseen effects had been expressed at least since the 1890s (Perkins 1897, Spear 2005, p. 260).

During the 1980s, biocontrol began to be criticized by conservationists for its irreversibility and possible adverse effects on nontarget plants and insects (Howarth 1983, 1985). Adverse effects in some cases had been anticipated but considered unimportant because the most vulnerable native plants lacked economic value (McFadyen 1998, Seier 2005). A concern for organisms of no immediate or known human benefit 'provoked a revolution in the field of

biological control that has continued . . . and has yet to be resolved' (Lockwood 2000).

Follett and Duan (2000) reviewed the problem of unintended effects from both biocontrol and conservationist perspectives. Indirect ecological effects of biocontrol were the focus of another edited book (Wajnberg et al. 2001). Louda et al. (2003) gave case histories of problematic biocontrol projects: three dealing with herbivores used to suppress weeds and seven with parasitoids or predators used against other insects. Negative ecological effects of parasitoids generally have been less than for predators (Onstad and McManus 1996). Among the conclusions of Louda et al. (2003) was that North American redistribution of an inadvertently established (immigrant) weevil (*Larinus planus*) to control Canada thistle (*Cirsium arvense*) is having major nontarget impact on a native thistle (*C. undulatum* var. *tracyi*). Effects from releases of a flower-head weevil (*Rhinocyllus conicus*) against carduine thistles were considered severe, especially in relation to densities of the native Platte thistle (*Cirsium canescens*) in western states. *Cactoblastis cactorum*, a pyralid moth released against prickly pear (*Opuntia* spp.) in the West Indies, might enhance the risk of extinction of a rare cactus (*O. corallicola*) in Florida. The moth arrived in Florida via immigration or introduction (Frank et al. 1997, Johnson and Stiling 1998), eventually threatening cacti native to the southwestern states and Mexico (Bloem et al. 2005). Louda et al. (2003) concluded that the tachinid *Compsilura concinnata* used against the gypsy moth could have long-term effects on Nearctic silk moths and might cause local extirpation, and that parasitoids released to control the southern green stink bug (*Nezara viridula*) in Hawaii might be accelerating a decline of koa bug (*Coleotichus blackburniae*) populations that could result in extinction.

Certain nontarget effects from well-screened insects used in biocontrol can be considered trivial from a population perspective (Messing and Wright 2006). 'Spillovers' onto nearby nontarget plants that are associated with weed biocontrol agents at high population densities do not represent host shifts (Blossey et al. 2001); the injury can be considered nontarget feeding rather than impact (van Lenteren et al. 2006). The slight foliar injury on a native willow (*Salix interior*) by adults of leaf beetles (*Galerucella* spp.) used against purple loosestrife (*Lythrum salicaria*) in North America actually had been predicted during prerelease testing and should be regarded as 'verification of science done well' (Wiedenmann 2005).

Most biocontrol projects for insect (Lynch and Thomas 2000, van Lenteren 2006) and weed (Fowler et al. 2000, Gould and DeLoach 2002) suppression are thought to produce slight or inconsequential effects on nontarget organisms, although postrelease monitoring for adverse effects typically has not been done or has been minimal (McFadyen 1998, Hajek 2004). Host-specific species traditionally have been chosen for weed control because of the threat that released herbivores pose to crop plants (Waage 2001, Hajek 2004). Host-range testing of biocontrol agents used against insects has been less rigorous than for weeds (Van Driesche and Hoddle 2000, van Lenteren et al. 2006) and can be constrained by an inadequate ecological and taxonomic knowledge of native insects (Barratt et al. 2003). Behavioral factors can complicate tests for nontarget hosts among insects used in arthropod biocontrol (Messing and Wright 2006), and the complex effects of generalist predators on other species of a community – beneficial or detrimental – are unpredictable (Snyder and Evans 2006). Although predators and parasitoids were not initially subject to as thorough host-range testing as weed agents, the use of generalist parasitoids and predators now is less common (Sands and Van Driesche 2003, Hajek 2004).

Inundative biological control, involving the mass rearing and release of natural enemies, has shown fewer adverse ecological effects than classical biocontrol. Permanent establishment of natural enemies to achieve long-term pest management is not the goal of inundation. Even though inundative biocontrol lacks the irreversibility of classical biocontrol, its use still can produce negative effects on nontarget species and ecosystems. Guidelines have been developed to minimize such risks (van Lenteren et al. 2003).

Biological control, properly conducted and carefully regulated, can be an ally of agriculture and conservation (Hajek 2004, Hoddle 2004, Messing and Wright 2006; cf. Louda and Stiling 2004). Adventive organisms used in classical biological control still add to biotic homogenization (e.g., Louda et al. 1997). Such agents are intentional biotic contaminants (Samways 1988, 1997) whose release has moral implications (Lockwood 2001). Released agents can spread to adjacent regions and neighboring countries (Fowler et al. 2000, Henneman and Memmott 2001, Louda and Stiling 2004). Predicting the impact of candidate biocontrol agents on target species remains problematic (Hopper 2001, Lonsdale et al. 2001). Roitberg

(2000) suggested that biocontrol practitioners incorporate concepts of evolutionary ecology, advocating collaboration with evolutionary biologists who study behavioral plasticity so that variables most likely to determine whether candidate natural enemies would harm nontarget hosts might be identified. Even rigorous host-specificity tests of biocontrol agents (and pest-risk analyses of adventive species) cannot be expected to predict all unintended effects that might disrupt communities and ecosystems (Pemberton 2000, Hoddle 2003). Almost nothing is known about the microsporidia that biocontrol agents of weeds might carry and their potential adverse effects (Samways 1997). Indirect effects essentially are unavoidable in multispecies communities (Holt and Hochberg 2001). Because of documented direct and indirect (including cascading) effects on nontarget organisms, a cautious approach to biocontrol is warranted (Howarth 1991, Follett and Duan 2000, Wajnberg et al. 2001). Classical biological control is a complex discipline that evokes controversy (Osborne and Cuda 2003). Even careful consideration of perceived benefits and risks of a proposed project will not satisfy all those who might be affected: biocontrol specialists, conservationists, regulatory officials, policymakers, and general public.

The stochastic nature of biological systems is exemplified by the recent discovery of human-health implications arising from a seemingly straightforward biocontrol project: release of seed-head flies (*Urophora* spp.) to suppress spotted knapweed (*Centaurea biebersteinii* (= *maculosa* of authors)) in rangelands of western North America. The flies, released in the 1970s, proliferated but did not curtail spread of the weed. Ineffective biocontrol agents such as *Urophora* (Myers 2000) can become abundant and pose greater risks of nontarget effects than agents that effectively control target organisms (Holt and Hochberg 2001). Although the tephritids have not directly harmed nontarget plants (the host-specific flies have remained on target), their larvae provide a winter food source for deer mice (*Peromyscus maniculatus*) when little other food is available. The mice climb knapweed stalks to forage above the snow cover. Food subsidies thus have allowed densities of deer mice, the primary reservoirs of Sin Nombre hantavirus, to increase as much as threefold. Blood samples from mice showed that seropositive individuals were three times more numerous when flies were present. Elevated densities of seropositive mice might alter hantavirus ecology, increasing the risk of virus infections in humans (Pearson and Callaway 2006).

Spectacular early successes in biological control – suppression of cottony cushion scale in California with importation of the vedalia beetle (*Rodolia cardinalis*) from Australia (Caltagirone and Douth (1989) and prickly pear cactus (*Opuntia* spp.) by various insects (DeLoach 1997) – gave way to realism: that similar successes would not come as easily. Dunlap (1980) noted that L.O. Howard referred to introducing insects into a new environment as being ‘infinitely more complicated than we supposed 20 years ago’ (Howard 1930). More than 75 years later, Howard’s comment, referring specifically to parasitoids, applies generally to the uncertain behavior of adventive insects in novel environments (e.g., Henry and Wells 2007).

SYSTEMATICS, BIODIVERSITY, AND ADVENTIVE SPECIES

Systematics and taxonomy are fundamental to the study, communication, and identification of agriculturally important pest species (Miller and Rossman 1995). Misidentifications can result in serious miscalculations concerning life-history studies, pest-risk assessments, and biocontrol strategies, as evidenced by species of the moth genus *Copitarsia* (Simmonds and Pogue 2004, Venette and Gould 2006). Numerous pest problems have been solved through a systematic knowledge of organisms that affect agricultural and forest ecosystems (Miller and Rossman 1995, Rossman and Miller 1996). The elucidation of the biology of a pest species for control purposes can be achieved only through accurate identification by taxonomists (Wilson 2000).

The availability of an adequate ‘biosystematic service’ (Knutson 1989) is needed to deal with the problem of immigrant insects (Dick 1966, Oman 1968). Relatively few nations have biosystematic service centers, and those that do often lack specialists for certain economically important groups. Such gaps in taxonomic coverage (Oman 1968, Wheeler and Nixon 1979) impede the execution of plant-regulatory functions and enforcement of quarantine laws (Knutson 1989, New 1994), although the availability of port identifiers (Shannon 1983) helps compensate for a lack of taxonomic specialists in particular groups. A limited understanding of taxonomy and lack of specialists can lead to catastrophic socioeconomic losses, as happened with Dutch elm disease in North America (Britton and Sun 2002). Accurate identification facilitates determination of an invader’s origin, allowing

appropriate areas to be searched for natural enemies that might suppress pest densities by classical biological control (Sabrosky 1955, Delucchi et al. 1976, Danks 1988). Thorough systematic knowledge also is critical to assure accurate identification of natural enemies released by researchers and those sold commercially (e.g., Henry and Wells 2007).

Better support for taxonomy and systematics (Knutson 1989, New 1994) would enhance our ability to identify newly established species that threaten agriculture, forestry, human health, and the environment and determine their areas of origin. It also would enhance our ability to identify insects intercepted in commerce and assist regulatory agencies in determining whether the species are likely to be harmful or innocuous.

CONCLUDING THOUGHTS

Invasive species might soon supplant habitat loss and fragmentation as the principal threats to native biodiversity (Crooks and Soulé 1999) and undoubtedly will continue to provide ‘wonder and surprise’ (Simberloff 1981) to ecologists who study them. Adventive insects will continue to be redistributed globally given the development of new transportation technologies and emphasis on free trade, coupled with inevitable increases in human migration and tourism. Programs of regulatory enforcement are unlikely to keep pace with increases in global commerce due to liberalization of trade (Jenkins 1996). The use of DNA barcoding eventually may allow immigrant insects to be identified rapidly and accurately. Climate change might affect the abundance, distribution, and phenology of adventive insects (Cannon 1998). The public will remain generally unaware that losses in invertebrate diversity can be detrimental to human well-being (Kellert 1995). Even though it is generally acknowledged that invading insects can affect ecosystem structure and function, more rigorous scientific data are needed to assess their detrimental effects on native biodiversity, as is the case for invasive species in general (Brown and Sax 2007).

As the numbers of immigrant insects continue to increase, so too will opportunities for introducing parasitic and predatory insects to help suppress agricultural pests among the newly established species. Because of the idiosyncratic nature of adventive insects (including biocontrol agents) in new environments, even the most objective and quantitative risk assessments for excluding potential pests, or development of new pest-risk

assessment tools, cannot predict with certainty where adventive species might become established or their economic effects, let alone their complex and subtle environmental interactions and consequences. A guilty-until-proven-innocent approach to pest exclusion and use of 'white lists' (e.g., McNeely et al. 2001), however, would represent useful change from current regulatory policy (Ruesink et al. 1995, Simberloff et al. 1997, Simberloff 2005). Messing and Wright (2006) recommended that U.S. policies regulating the introduction of biocontrol agents be made similar to those employed by Australia and New Zealand.

Changes to our first line of defense – attempts at exclusion or prevention of establishment – likely will come slowly. As Van Driesche and Van Driesche (2001) pointed out, Americans tend to view prevention as an unpalatable concept. Attempts to exclude immigrant species conflict with society's emphasis on free trade and travel (Kiritani 2001, Low 2001). Not only will additional immigrant insects continue to become established in the USA and elsewhere, but some species once considered innocuous faunal additions will be revealed as harmful. This prediction follows from the realization that relatively few immigrant insects have received attention from researchers, and with lag times sometimes being protracted, adverse ecological effects can take years to develop and even longer to be detected. Global warming likely will lead to northward spread of immigrant pests in temperate regions (Knight and Wimshurst 2005). Immigrants infused with new genetic material via subsequent introductions may continue to adapt to new environments. Pestiferous immigrants no longer thought to represent a threat might resurge as a result of changes in agricultural practices, climate, and environment.

The invasive species problem is 'a complex social and ethical quandary rather than solely a biological one' (Larson 2007). Invasive species cannot be prevented, but the problem can be minimized if attempts at amelioration are viewed as the 'art and science of managing people' (Reaser 2001). We agree that human dimensions of the problem deserve more attention and that effective solutions depend heavily on policymakers appreciating connections between invasive species and global trade, transport, and tourism (McNeely 2001b, 2006). Numerous suggestions for alleviating the invasive-species problem have been made (e.g., Lodge et al. 2006, Nentwig 2007). Recommendations include an obvious need to develop reliable predictive theories of biological invasions; to

be more aware of species that have become invasive elsewhere; and to foster greater international collaboration and cooperation (Clout and De Poorter 2005, Bateman et al. 2007), with continued development of online information networks and less emphasis on political boundaries (McNeely 2001c, McNeely et al. 2001, De Poorter and Clout 2005, Simpson et al. 2006). Greater collaboration among biologists, economists, geographers, psychologists, and sociologists will be particularly crucial in addressing problems (McNeely 2006). Among more innovative suggestions is the development of approaches that would subsidize native species until they are able to adapt to altered environments and coexist with invaders (Schlaepfer et al. 2005). As is the case for most other aspects of invasion biology, researchers, conservationists, policymakers, and the public disagree on how best to deal with adventive organisms. Disparate views have long characterized discussions of adventive species. Before the USA enacted plant-regulatory legislation, a leading federal official once advocated a laissez-faire approach to immigrant insects (Marlatt 1899), which elicited a storm of protest (Wheeler and Nixon 1979). More recently, 'blanket opposition' to adventive organisms has been predicted to become 'more expensive, more irrational, and finally counterproductive as the trickle becomes a flood' (Soulé 1990).

Progress toward documenting the extent of the invasive-species problem and devising solutions has been made in recent years. The Scientific Committee on Problems of the Environment (SCOPE) was a founding partner in the Global Invasive Species Program (GISP). Created in 1997, GISP seeks solutions through new approaches and tools (Mooney 1999, McNeely et al. 2001, Barnard and Waage 2004). Noteworthy U.S. initiatives include creation in 1999 of a National Invasive Species Council. Historical data such as interception records of regulatory agencies (e.g., Worner 2002, McCullough et al. 2006, Ward et al. 2006) are being evaluated to address the lack of information on failed introductions (other than biocontrol agents), a deficiency that Simberloff (1986) pointed out. Other positive signs are increased emphasis on the role of taxonomy in the early detection of immigrants, such as regional workshops for enhancing the identification skills of diagnosticians at land-grant universities and identifiers at U.S. ports of entry (Hodges and Wisler 2005). We also note recent collaboration of the Carnegie Museum of Natural History, traditionally a research institution, with federal and state

agencies involved in new-pest detection. This linkage supplements the museum's budget while providing timely identifications of insects taken in traps or surveys in or near ports of entry.

Of the four principal means of dealing with invasive species – exclusion, detection, eradication, and control or management – we feel that detection warrants greater attention. J.W. Beardsley regularly looked for new immigrant insects in Hawaii from 1960 to 1990 (Loope and Howarth 2003). More entomologists familiar with local faunas, and hence more likely to recognize insects that seem out of place (Lutz 1941, p. 6; Hoebeke and Wheeler 1983), are conducting detection surveys. Our own fieldwork in the vicinity of port cities in New England and the Atlantic provinces of Canada (e.g., Hoebeke and Wheeler 1996, Wheeler and Hoebeke 2005), and that by Christopher Majka and colleagues in Atlantic Canada (e.g., Majka and Klimaszewski 2004), attest to the value of detective work in areas vulnerable to entry by immigrant insects. With early detection of immigrants (detecting incipient invasions at low-density populations generally is difficult), more rapid response is possible (Burgess 1959, Oman 1968, Reynolds et al. 1982) and eradication (also usually difficult to achieve) and classical biological control (Ehler 1998) are more likely to succeed. The advantage of early detection, coupled with public involvement (Dick 1966), was demonstrated in Auckland, New Zealand, in 1996; a private citizen gave government scientists a distinctive caterpillar that proved to be the Asian whitespotted tussock moth (*Orgyia thyellina*). This potential pest, though apparently established for more than 1 year, was eradicated (Clout and Lowe 2000). Contact with a local U.S. Department of Agriculture office by a Chicago resident who suspected he had a specimen of the Asian longhorned beetle (*Anoplophora glabripennis*) proved crucial to the city's eradication efforts against the pest (Lingafelter and Hoebeke 2002, Antipin and Dilley 2004).

A review of recent literature on immigrant insects in British Columbia revealed a trend toward reporting the first records of adventives in trade magazines and in-house publications rather than in scientific journals. Outlets for reporting immigrants new to the province might have changed during the 1990s because of inability to pay publication costs for papers in scientific journals, the view that with increasing biotic homogenization the presence of species new to a fauna no longer warrant documentation in journal articles,

a lack of taxonomic specialists capable of identifying immigrant species, and too few entomologists remaining in British Columbia to address new threats to agriculture, forestry, and public health (Gillespie 2001). Britton and Sun (2002) acknowledged that Internet sites can omit relevant references and often are ephemeral. We, therefore, encourage publishing the detection of immigrants in mainstream journals, with accompanying summaries of bionomics in the area where species are native, as well as taxonomic information to facilitate recognition in their new faunas. The availability of at least the approximate time of arrival is important in understanding the long-term effects of invaders (Strayer et al. 2006). We also feel it is useful to follow the spread of immigrants and to document range extensions; such historical records are invaluable in allowing future workers to reconstruct immigration events. Knowledge of the new ranges of transferred species can even enhance our biological understanding of invasive organisms (McGlynn 1999).

A global computerized database of immigrant pests has been envisioned for more than 15 years to complement the Western Hemisphere (formerly North American) Immigrant Arthropod Database (WHIAD), administered by the U.S. Department of Agriculture (Knutson et al. 1990, Kim 1991). Other world regions would benefit from a master list of all adventive species, which would help in inventorying Earth's biota, serve as a database for assessing biotic changes, and facilitate dissemination of information on invasive species (Wonham 2003). Schmitz and Simberloff (2001) proposed a U.S. database administered by a National Center for Biological Invasions. Taking advantage of existing capacities and partnerships (WHIAD was not mentioned), the center would place the administration of rules and regulations pertaining to invasive species under a central agency linked to a major university (perhaps the Institute for Biological Invasions, University of Tennessee, which Simberloff directs; or the Center for Invasive Species Research, University of California, Riverside). Loosely modeled after the Centers for Disease Control and Prevention (Schmitz and Simberloff 2001), the center would be of immeasurable value in dealing promptly and effectively with invasive species.

Creation of a National Center for Biological Invasions might forestall homogenization of the U.S. biota and further erosion in quality of life. Societal effects of immigrants can include loss in the amenity value of ecosystems and reduction in ecotourism, owing to

sameness among biotic communities (McLeod 2004, Olden et al. 2005). The harmful effects of immigrant insects might also include development of a biophobic public reluctant to venture outdoors (Soulé 1990) because of the possibility of inhaling small immigrant insects such as whiteflies, and threats from imported fire ants and African honeybees (Vinson 1997, Paine et al. 2003) or mosquito-transmitted diseases. In the event of bioterrorism involving the release of pathogens or other harmful organisms in the USA (Pratt 2004), a rapid and effective response to the threat would be more likely if a national center for invasive species were in place. We feel that congressional action on Schmitz and Simberloff's (2001) proposal, perhaps more than any other initiative, would increase public understanding of the problem, stimulate interest in studying invasive species, improve current programs of pest exclusion and detection, and ensure prompt responses to new invaders. A U.S. center for bioinvasions also could serve as a model for other nations as they try to protect native biodiversity and preserve society's 'sense of place and quality of life' (Olden et al. 2005).

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