INVASIONS BY INSECT VECTORS OF HUMAN DISEASE

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Key Words biogeography, establishment, medical entomology, spread, transport

Abstract Nonindigenous vectors that arrive, establish, and spread in new areas have fomented throughout recorded history epidemics of human diseases such as malaria, yellow fever, typhus, and plague. Although some vagile vectors, such as adults of black flies, biting midges, and tsetse flies, have dispersed into new habitats by flight or wind, human-aided transport is responsible for the arrival and spread of most invasive vectors, such as anthropophilic fleas, lice, kissing bugs, and mosquitoes. From the fifteenth century to the present, successive waves of invasion of the vector mosquitoes *Aedes aegypti*, the *Culex pipiens* Complex, and, most recently, *Aedes albopictus* have been facilitated by worldwide ship transport. Aircraft have been comparatively unimportant for the transport of mosquito invaders. Mosquito species that occupy transportable container habitats, such as water-holding automobile tires, have been especially successful as recent invaders. Propagule pressure, previous success, and adaptations to human habits appear to favor successful invasions by vectors.

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INTRODUCTION AND DEFINITIONS

Most observers would agree that Elton's landmark book, *The Ecology of Invasions by Animals and Plants* (49), established the field of invasion biology as a scientific discipline, particularly in light of the increasing incidence of human-assisted dispersal of nonindigenous species. Research in the 1980s organized by the Scientific Committee on Problems of the Environment, part of the International Council of Scientific Unions, documented the extent of plant and animal invasions in specific geographic areas (e.g., 42, 70, 109, 124) and provided a framework for interpreting why certain species and areas are more susceptible than others to invasion (e.g., 65, 88, 95). In the past decade, increasing awareness of the biotic and economic consequences of invasive species stimulated a proliferation of books on case histories (118), geographic and global perspectives and consequences (32, 44, 125, 187), and theory and practice (182, 219); reports and special issues of journals (23, 93, 110), and a new journal (24) confirm the importance of the new discipline. Although possible impacts of nonindigenous mosquito species have been addressed in some of these compilations (33, 57, 206), invasion biology has largely not intersected with that of medical entomology, despite many historical examples of human-aided dispersal of disease vectors.

The term vector is applied to an organism that transfers a pathogen from one host to another (2). This review is limited to invasions of insect vectors of human diseases, although some pathogens carried by the same blood-sucking insects may affect other vertebrate hosts.

Three essential stages—arrival, establishment, and spread—characterize a biological invasion (219). A recent proposal recommends that nonindigenous invaders should be distinguished from colonizers based on impact (39). Accordingly, only a species with great impact on its new environment should be characterized as invasive. However, the impact criterion is highly subjective and depends on scale and personal values (37). Therefore, a more suitable criterion of an invasive species, besides its novelty in a new environment, is spread, measurable as population growth and distance dispersed (37, 159).
Because of lack of consensus of their use, other terms from the literature, such as alien (35), exotic (66), imported (221), nonnative and colonizer (39), will be avoided. Nonindigenous (151) is applied here to the occurrence of species beyond their native range. This review considers invasive vectors as those that satisfy the biogeographic and spread criteria. Some invasive species are unlikely, based on their biology, to become vectors of human pathogens but are nonetheless included in this review because they are in blood-sucking vector groups, such as mosquitoes, and because changes in their behavior in new habitats are unpredictable. After documenting the extent of vector invasions, I try to integrate some developments of invasion biology, culled from results on nonvector pests, especially plants (219), with observations on invasions of medically important insects. Whereas most previous concerns and implications of invasive species are in areas of biodiversity, conservation, ecosystem disruption, and economic losses (147, 151, 206), invasive vectors affect human health by altering patterns and frequency of disease transmission.

This review is not organized systematically by taxon, geography, or disease, but is rather an eclectic sampling of what is known and interesting about vector invasions. Useful records of vector invasions are not available for many areas of the world, and literature prior to the twentieth century is often anecdotal or inadequate for inferences about invasion processes. For some vector groups or vector-borne diseases covered sparsely or not at all in this review, evidence for invasiveness was weak or poorly documented.

DISEASE OUTBREAKS FOMENTED BY VECTOR INVASIONS

*Aedes aegypti*, Yellow Fever, and Dengue

*Aedes aegypti*, the so-called yellow fever mosquito, is believed to have migrated from West Africa to the New World in the fifteenth through seventeenth centuries aboard slave ships (29). Alternatively or additionally, *Ae. aegypti* may have first invaded Portugal and Spain before reaching the Western Hemisphere on European ships (197). In either case, the evolution of domestic traits in an originally feral species (197) was crucial for enabling *Ae. aegypti* to occupy and flourish in water storage jars in the holds of these sailing vessels.

Yellow fever was absent from urban settlements in the New World until the arrival of *Ae. aegypti*, the only known vector of urban epidemics of this disease (199). The first clearly documented New World epidemic of yellow fever occurred in the Yucatan in 1648 (119), although it is thought to have appeared in Haiti as early as 1495 (30). Throughout the seventeenth through nineteenth centuries, yellow fever ravaged seaports on the Atlantic Coast, as far north as Philadelphia and New York (199). Presumably the yellow fever virus was being reintroduced by passengers, especially African slaves, on these ships.

In tropical and mild temperate regions of the Americas, *Ae. aegypti* became established and spread into the interior, whereas in the northeastern United States,
where this species was unlikely to overwinter, new arrivals on ships may have vectored the yellow fever epidemics. *Ae. aegypti* was reduced in abundance and distribution, but not eliminated, by an intensive eradication scheme in the 1950s and 1960s (190). Currently the species is widespread in the Americas, where reinfestations after the failed eradication scheme are associated with the reemergence of dengue and the appearance of dengue hemorrhagic fever (72). In North America its distribution receded in the 1990s concomitant with the spread of *Aedes albopictus* in the southeastern United States (80, 120, 143, 145a).

In tropical Asia, *Ae. aegypti* is presumed to have arrived and established later, based on the absence of urban dengue in this region until late in the nineteenth century (189). The more recent dispersal of *Ae. aegypti* in the Oriental region is supported by comparatively low genetic diversity in tropical Asian populations of this species (197).

### Epidemic Malaria and Invasive *Anopheles*

The arrival from West Africa in 1930 and establishment and spread into northeastern Brazil of the African malaria vector *Anopheles gambiae* s.l. rivals the introduction of *Ae. aegypti* into the New World for epidemiological impact (191). Larvae or adults of this anopheline are believed to have traveled by air or fast passenger ship from Dakar, Senegal, to Natal, Brazil (153), where the first malaria epidemic attributable to *An. gambiae* s.l. occurred in March–May, 1930. Although malaria was endemic in northeastern Brazil, the native anopheline vectors were inefficient transmitters compared with the highly anthropophilic and endophilic (= house entering) *An. gambiae* s.l. (26, 40).

At the time of its invasion into Brazil (1930–1941), *An. gambiae* was not recognized as a species complex, which consists currently of six closely related named species (62). Of the two members of this complex known as efficient malaria vectors, *An. gambiae* s.s. and *Anopheles arabiensis*, the adaptation of the invader to the dry northeast of Brazil is more consistent with the habits of *An. arabiensis* in the African Sahel region. Intolerance of the Brazilian invader to salt (25) rules out the halophilic species of this complex, *Anopheles merus* and *Anopheles melas*.

Although insecticide treatments eradicated *An. gambiae* s.l. by 1932 in Natal, the invading species escaped and spread outside the city limits (191). In the so-called silent years, the invader spread west, then south (Figure 1), especially along water courses. Then a malaria epidemic that rivaled “the worst outbreaks described in the literature of this disease” (191) occurred in 1938, with mortalities ranging from 10–25%. Such high mortality rates had also occurred on the island of Mauritius in 1866–1867 when accidentally introduced *An. gambiae* s.l. also

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**Figure 1** The arrival and spread, especially along river courses, of *Anopheles gambiae*, in northeastern Brazil in the 1930s and associated malaria epidemics. Information derived from Soper & Wilson (191). Ceará, Rio Grande do Norte, and Paraiba are state names.
fomented malaria epidemics (167). In both Mauritius and Brazil, the invasion of *An. gambiae* s.l. changed malaria transmission from endemic to epidemic.

Field observations indicated that the spread of *An. gambiae* during 1930–1937 occurred primarily by infiltration, i.e., movement from one habitat to another by natural dispersal (191). However, long-distance dispersal in 1939–1940 may have been assisted by car, train, or boat. Preferred larval habitats in this arid region were small temporary pools, borrow pits, and shallow wells (caçimbas) dug for drinking water (25).

Concentrations of this species in discrete areas, especially during the dry season, facilitated the successful massive eradication scheme led by the Rockefeller Foundation, which treated larval habitats with the highly toxic Paris green (191). Coupled with house spraying with pyrethrum, the African invader was eliminated, without DDT, only 19 months after the eradication campaign began (40). As soon as *An. gambiae* s.l. disappeared from northeastern Brazil, malaria incidence dropped precipitously (26).

*Anopheles darlingi*, the most efficient malaria vector native to the New World, is the principal transmitter of this disease in the Central Amazon region (106). Prior to the 1990s, this species was sparsely distributed in the Upper Amazon region of Peru (22) and absent from the Iquitos region as recently as 1991 (137). However, sometime early in the past decade, this species appeared in abundance in the vicinity of Iquitos and became the primary vector of epidemic malaria (51), with more than 130,000 registered cases in 1997 among a population of less than four million persons (5).

Although the mode of range expansion of *An. darlingi* into the Loreto (Iquitos) Region is unknown, one speculation is that larvae were transported by boats with tropical fish, which are cultivated locally for export and sale in the aquarium trade. Artificial ponds excavated for fish culture, so-called piscigranjas, are used as larval habitats by *An. darlingi* in the Iquitos region (106) in addition to the littoral riverine and backwater habitats occupied by this species in its native range (111, 169).

**Bubonic Plague and the Oriental Rat Flea**

The plague bacillus, responsible for the Black Death of the Middle Ages, is transmitted to humans from infected rodents, often rats, by flea bites, usually from the Oriental rat flea *Xenopsylla cheopis* (102). Three pandemics of bubonic plague—from the sixth to eighth centuries AD, during medieval times, and from late-nineteenth into early-twentieth century—are estimated to have killed more than 200 million persons (46). The worldwide pattern of outbreaks in ports during the last pandemic suggests that the disease was probably introduced from infected Norway rats that disembarked from sailing ships or freight vessels accompanied by *X. cheopis* and other flea species (K.L. Gage, personal communication). During that pandemic, plague began in inland China and reached Chinese port cities in 1894, from which at the turn of the century it was disseminated by ships and erupted in epidemic form at major international ports such as San Francisco, Asuncion, Rio de Janeiro, Brisbane, Sydney, and Bombay (46).
Insofar as the cosmopolitan *X. cheopis* was probably already present in these ports, the arrival of infected Oriental rat fleas on ships does not constitute an invasion in the strict sense. However, in light of the drastic epidemiological consequences of introduced fleas infected with plague, this example is included in the review. It is generally believed that the plague epidemic in San Francisco in 1899 led to the permanent establishment of plague as an endemic disease of wild rodents in the western United States (103).

INVASIVE VECTOR GROUPS OF THE TWENTIETH CENTURY

Mosquitoes (Especially Container Occupants)

The extensive mosquito literature includes records of long-distance dispersal of adults, unassisted by humans, far from their larval habitats (e.g., 155, 200). On occasion, such dispersals have led to short-term colonizations that temporarily extended the range of a species, such as inland-inhabiting populations of the salt marsh mosquitoes, *Aedes taeniorhynchus* and *Aedes sollicitans* (94, 155).

Most recent successful invasions of mosquitoes have resulted from human transport of immature stages. Mosquitoes that occupy small water bodies, especially container habitats, in their larval and pupal stages are responsible for the most notable invasions and range expansions in the United States (Table 1). The highly publicized invasion of the Asian tiger mosquito *Aedes albopictus* (33) and the more recent establishment and spread of *Aedes japonicus* in the United States (149) are considered subsequently in a separate section of this review. Both of these species are believed to have hitchhiked to their ports of arrival in shipments of used tires (34, 149, 156), recognized since World War II for their potential in mosquito transport (154).

A major range expansion of the native mosquito *Aedes atropalpus* in the United States is also attributable to the recent adaptation of this species to water-holding automobile tires (12). Prior to 1972 this larval inhabitant of lotic and lentic rock holes was unknown in the states of Ohio, Indiana, and Illinois (222). However, collections from discarded tires in the late 1970s and 1980s extended the range of this species into these midwestern states (9, 158). Its more recent establishment in Nebraska (87) was probably also facilitated by tire transport. Now, *Ae. atropalpus* occurs in tires in parts of its original range, such as Kentucky, New York, and Connecticut, where it was formerly confined to rock holes (3, 31, 212). After reaching Europe in tire shipments, this species has also become established in Italy (163).

*Aedes bahamensis* was first discovered in the United States in 1986 from light and oviposition trap collections in southern Florida (146). It was probably transported from the Bahamas, where it is a common peridomestic mosquito in used tires, a preferred larval habitat in Florida (145). In the 15 years since its original detection, *Ae. bahamensis* has not spread outside Broward and Miami-Dade counties in Florida (G.F. O'Meara, unpublished results).
<table>
<thead>
<tr>
<th>Species</th>
<th>Donor</th>
<th>Recipient</th>
<th>Transport</th>
<th>Date</th>
<th>Key reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aedes albopictus</em></td>
<td>Japan</td>
<td>Texas</td>
<td>Tires</td>
<td>1985</td>
<td>77</td>
</tr>
<tr>
<td><em>Aedes bahamensis</em></td>
<td>Bahamas</td>
<td>South Florida</td>
<td>Tires</td>
<td>1986</td>
<td>145</td>
</tr>
<tr>
<td><em>Aedes togoi</em></td>
<td>Asia</td>
<td>Pacific NW</td>
<td>Ships</td>
<td>1940–1950</td>
<td>11</td>
</tr>
<tr>
<td><em>Culex biscaynensis</em></td>
<td>Caribbean (?)</td>
<td>South Florida</td>
<td>Bromeliads</td>
<td>?</td>
<td>142</td>
</tr>
<tr>
<td><em>Toxorhynchites brevipalpis</em></td>
<td>E. Africa</td>
<td>Hawaii</td>
<td>Biocontrol</td>
<td>1950s</td>
<td>194</td>
</tr>
<tr>
<td><em>Toxorhynchites amboinensis</em></td>
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<td>Hawaii</td>
<td>Biocontrol</td>
<td>1950s</td>
<td>194</td>
</tr>
<tr>
<td><em>Wyeomyia mitchelli</em></td>
<td>Caribbean or Florida</td>
<td>Hawaii</td>
<td>Bromeliads</td>
<td>1970s</td>
<td>183</td>
</tr>
</tbody>
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*It remains unclear whether this recently described species (223) was introduced in exotic bromeliads to south Florida or is, rather, an indigenous species that had previously escaped recognition despite intensive mosquito collecting in the state.*

The maritime rockpool mosquito *Aedes togoi* has a tropical to subarctic distribution in the Oriental region (192) and in the New World occurs along a 250–300 km stretch of the coastlines of British Columbia and Washington state (11). Records of halophilic *Ae. togoi* larvae in tire shipments (34), bilges (83), and an adult female on board a ship (17) in Japan suggest that the North American founders may have reached the Pacific Northwest via shipping from Asia sometime before the late 1960s when the first larvae were recovered from rock holes in Vancouver (11).

*Wyeomyia mitchelli*, whose larvae inhabit water-containing plant axils, was discovered in Hawaii in 1979 (183). The immature stages of this species probably reached the Hawaiian Islands in the axils of ornamental bromeliads transported from Florida or the West Indies, where this species is native (183). Transport in the axils of exotic bromeliads may also explain the presence in southernmost Florida of a newly described and narrowly distributed species, *Culex biscaynensis* (142, 223). Known only from suburban Miami-Dade County in the vicinity of Fairchild Tropical Gardens, it is presently unclear whether this species was introduced recently from elsewhere in the Caribbean or is indigenous to south Florida, where it was first detected only recently (Table 1).
Two species of nonbiting mosquitoes of the genus *Toxorhynchites* became established in Hawaii (194) following their releases in the early 1950s for the biological control of *Ae. albopictus* by their predatory larvae (Table 1). Although nonindigenous species of *Toxorhynchites* were also released elsewhere, such as in the city of New Orleans (52), for the control of container mosquito pests, they did not survive temperate winters in the continental United States.

**Other Vector Diptera**

**Simuliidae** Long-distance aerial dispersal is characteristic of certain species of black flies, known to travel 150–200 km without human assistance (58, 60). For tropical vectors of onchocerciasis, such as *Simulium damnosum* s.s., wind-aided dispersal associated with the passage of the Intertropical Convergence Zone propels black fly adults to areas where rain is likely to fall and rivers, the larval habitat, flow (60). On a practical level, this long-distance dispersal caused the World Bank's Onchocerciasis Control Program, plagued by reinvasions from nontreated areas, to reevaluate and extend the boundaries of its treatment areas in West Africa (207). The long flight range of black fly vectors of disease may also be epidemiologically significant because infections acquired early in the adult fly’s life may be transported over vast distances (60).

**Ceratopogonidae** Biting midges of this family transmit the nematode * Mansonella ozzardi* and Oropouche fever virus to humans, although they are more important as vectors of domestic animal diseases. Wind-aided dispersal of *Culicoides* vectors has been documented as a mechanism of transport of such animal viral diseases as bluetongue, African horse sickness, and Douglas fever (18, 131, 179). *Culicoides belkini*, a pest species indigenous to Tahiti, successfully invaded other Polynesian islands after transport on aircraft (150).

**Glossinidae** Tsetse flies, like Ceratopogonidae, are better known as disease vectors to domestic animals but remain locally important in Africa as transmitters of human sleeping sickness. As for black flies, some evidence for invasiveness comes from reinfestations of areas from which tsetse were eradicated. The West African island of Principe was freed of *Glossina palpalis* for approximately 40 years before the species was reintroduced by ship or plane from Fernando Po, about 200 km distant (6).

Human alterations of the landscape may promote range extensions of tsetse species, such as hedgerow plantings in the Nyanza District of Kenya that led to local expansions of the distribution of *G. palpalis* (134). The *morsitans* group of *Glossina* are known for spreading into countryside from which they were previously absent at rates up to 11.3 km per year (134).

**Kissing Bugs**

Schofield (176) has provided evidence for recent, host-associated range expansions of species among the triatomine vectors of Chagas disease. The best documentation
is for the human-aided spread of *Triatoma infestans*, the most important vector of *Trypanosoma cruzi* in South America. Domestication of this bug species is presumed to be pre-Columbian, whereafter dispersal followed pre-Inca tribal migrations from native Bolivia to southern Peru and northern Chile (176). Early in the 1900s, *T. infestans* accompanied migrant workers across Paraguay and Argentina to coffee farms in the vicinity of São Paulo, Brazil (176). Later, following the clearing of Brazilian coastal forests, this vector species colonized more southerly regions of the country (161) and, independently, northeastern Brazil (8). These changes in distribution of *T. infestans* in the past century have been associated with outbreaks of acute Chagas disease in Brazil (8). Once *T. infestans* had been passively transported into an area, probably among domestic effects, it may have actively dispersed among houses by flights up to 200 m (178).

*Triatoma rubrofasciata*, a non-vector relative of *T. infestans*, occurs in both the New World and southeast Asia. Schofield (176) postulates that Old World populations, which are confined mainly to port cities, were derived from New World transport during the seventeenth through twentieth centuries with ship rats, a principal host of *T. rubrofasciata*.

*Rhodnius prolixus*, the Chagas disease vector species made famous by insect physiologists (215), has a disjunct distribution with a gap between Central American and Venezuelan/Colombian populations (45). Early researchers hypothesized that nymphs and eggs of this species were transported phoretically from South to Central America in the plumage of storks, which may harbor *R. prolixus* in nests and routinely migrate between these regions (59). However, other investigators (177, 224) favor a hypothesis that Central American *R. prolixus* are derived from an accidental release in El Salvador of laboratory-reared insects originally collected in Venezuela (138). These escapees and their descendants are presumed to have disseminated to other Central American countries by passive transport among immigrants (177). A recent establishment of this species west of Rio de Janeiro, Brazil, is also suspected of having resulted from a laboratory escape (152).

**Fleas and Lice**

Various species of fleas besides *X. cheopis* transmit plague (102); some flea species, such as the dog *Ctenocephalides canis*, cat *Ctenocephalides felis*, and human flea *Pulex irritans*, are cosmopolitan in distribution. Although human migrations undoubtedly promoted the range expansions that led to the contemporary distributions of these species, the historical timing and direction of these range extensions are not known (e.g., 82, 101).

Phoretic transport of the human body louse on migrating troops was responsible for the spread of typhus, which erupted in epidemic form during wars from the Middle Ages through World War II, when delousing with DDT interrupted transmission (30). Although human lice may have been present in an uninfected region before the arrival of troops, the massive influx of abundant and infected *Pediculus humanus* was the immediate cause of typhus epidemics during wartime.
TRANSPORT OF VECTORS ON AIRCRAFT

Airplanes were recognized as a mechanism of transport of undesirable insects, especially mosquitoes, not long after the implementation of commercial, transcontinental flights (69, 196). Fumigation, or “disinsectization” of aircraft arriving from the tropics, as well as insect control at receiving airports, were recommended to prevent the establishment of undesirable pests and disease vectors that might hitchhike aboard flights (214, 216). The malaria epidemics in northeastern Brazil vectored by An. gambiae, possibly transported on aircraft from Africa (191), heightened concerns about the dangerous consequences of vector arrivals aboard international flights. Mosquitoes representing five genera were identified from inspections of aircraft arriving in northeastern Brazil from Africa in 1941–1942 (191). Whitfield (214) provided a 13-page “world list” of all insects identified from captures in commercial aircraft through the 1930s and cautioned that catastrophic epidemics of malaria or yellow fever were inevitable unless improved precautions were undertaken to minimize mosquito transport via international flights.

Given such dire warnings and the ever-increasing volume of air traffic, it is perhaps surprising that, in the sixty-plus years since An. gambiae was eradicated from Brazil, no further disease epidemics have been associated with the arrival of vectors via aircraft. However, both dengue and malaria have since been transmitted on Pacific islands by mosquito species that probably arrived on military airplanes, and subsequently became established, during and after World War II (188). Despite fears about the international transport of Ae. aegypti (41), this notorious disease vector has been detected relatively infrequently aboard aircraft (41, 84). Monitoring between 1948 and 1960 of international mosquito arrivals at six airports in the continental United States and Hawaii detected 20 species nonindigenous to the continental United States and 31 nonindigenous to Hawaii (50, 84). None of these arrivals via aircraft became established.

Mosquitoes can survive moderately high atmospheric pressures aboard aircraft (96) and can be transported alive between international destinations even in wheel bays (170). Properly conducted insecticide applications, either on the ground or in-flight, are demonstrably effective in reducing the risk of insect imports by aircraft (171, 172). However, assiduous “disinsection” (the more modern term for fumigation of aircraft) is rare (98) and, thus, is probably not responsible for the lack of establishment success of the majority of vectors arriving on airplanes.

Although nonindigenous mosquito species arriving on aircraft rarely become established, irregular cases of insect-borne diseases unknown to a host country implicate transmission by vectors arriving on international flights. The best known example is “airport malaria,” infection with malaria, especially Plasmodium falciparum, among persons who live near international airports but have not themselves visited malaria-endemic countries. In continental Europe, where endemic malaria was eradicated by the end of World War II (75), such cases occurred, especially in summer months, in the vicinity of international airports in Belgium, England, France, Italy, the Netherlands, Spain, and Switzerland (16, 36, 81, 164, 188). There
is even evidence for malaria transmission on board an international flight (213). It is generally believed that native European anophelines are refractory to transmitting *P. falciparum* (160), precluding their involvement in these cases of airport malaria, although this assumption has recently been questioned (112).

**MOSQUITO INVASIONS OF PACIFIC ISLANDS**

Elton (49) called attention to the susceptibility of remote islands to invasive species, noting that 420/1100 of the insects catalogued for Hawaii at the time of his book were nonindigenous. Although Simberloff (186) pointed out that “every sort of havoc wrought by non-indigenous species on islands can be found on the mainland as well,” the fates of invasive mosquitoes on selected islands in the Pacific are worthy of attention because of (a) depauperate endemic faunas on some islands; (b) high propagule (arrival) pressure by sea and air; and (c) active vigilance and good faunal records.

**Hawaii**

All five species of biting mosquitoes currently known from Hawaii are nonindigenous (89, 183). *Aedes albopictus* is believed to have arrived by boat from elsewhere in the Oriental region sometime in the 1890s (89). The cosmopolitan *Aedes vexans*, believed to have been transported, possibly aboard aircraft, from more westerly Pacific islands was first detected in 1962 (90). *Ae. aegypti* formerly occurred in Oahu but was eradicated in the 1950s (132).

The first mosquito species to have invaded Hawaii was *Culex quinquefasciatus*, believed to have arrived on a ship from Mexico as early as 1826 (20, 43). This mosquito species is the unique local vector of *Plasmodium relictum*, the causative agent of avian malaria that contributed to the endangerment and extinction of native species of Hawaiian birds (204). Fonseca et al. (54) examined microsatellite markers and mtDNA haplotypes of *Cx. quinquefasciatus* from 38 collection sites on the four main Hawaiian Islands. This first application of DNA markers to trace vector invasions demonstrated genetic isolation of this mosquito species among islands and bottlenecks among populations on the Big Island of Hawaii, as well as evidence for multiple introductions.

**Guam**

In one of the most comprehensive studies of an invasive fauna, Ward (208) described the biogeographic origins of all mosquito species known to occur on the island of Guam, located 5000 km to the west of Hawaii. Only 7 of Guam’s 24 species are endemic, the majority of the 17 nonindigenous species having become established after World War II. Only three introduced mosquito species, *Ae. aegypti*, *Cx. quinquefasciatus*, and *Ae. vexans*, were present on the island in the early 1900s, and *Ae. aegypti* was eradicated late in the 1940s after vectoring frequent outbreaks of dengue during World War II (208).
The remaining 14 nonindigenous mosquitoes include five species of *Anopheles*, four *Culex*, two *Aedes*, and one each from the genera *Armigeres*, *Mansonia*, and *Aedeomyia*. Most of these species occur in the Oriental region, which is the most probable source of their introductions. The absence of invasive mosquitoes from the New World is believed attributable to intensive disinsection of aircraft arriving via Hawaii (208).

Based on intensive post-war collection records, most invading mosquitoes reached Guam between 1960–1969 (five species) and 1970–1979 (seven species). These arrivals were facilitated by increases in international air traffic, including inter-island transports such as Air Nauru. Several of the introduced species, such as *Mansonia uniformis* and *Aedeomyia castica*, whose larvae are associated with floating aquatic macrophytes, might have arrived as larvae amidst plants transported by seaplane.

After the eradication of *Ae. aegypti*, episodes of diseases transmitted by invasive mosquitoes have been rare on Guam. Dengue was believed to have been transmitted by *Ae. albopictus* in 1975 (188), and a few autochthonous cases of malaria may have been vectored by *Anopheles indefinitus* (208), both of which reached Guam in the 1940s with U.S. or Japanese forces.

**Australia**

Out of 242 mosquito species recognized in Australia, only 4 have invaded from abroad (113, 128, 211). The now cosmopolitan *Ae. aegypti* and *Cx. quinquefasciatus* arrived first, with or shortly after the colonial First Fleet (113), and subsequently vectored dengue and filariasis, respectively, in Queensland (63). *Culex molestus*, a member of the *Cx. pipiens* Complex that includes *Cx. quinquefasciatus*, was introduced from the Palearctic Region into Victoria (New South Wales) after World War II (113).

*Culex gelidus*, the first successful invader in more than 50 years, was identified in 1999 from collections near the Brisbane (Queensland) airport (128). Although this small population of *Cx. gelidus* was exterminated, subsequent surveillance for this species showed it to be widely distributed in New Territories (211), and it is now also known in Western Territories (R.C. Russell, personal communication). Examinations of undetermined voucher specimens in Australian collections revealed that *Cx. gelidus* arrived, probably from Indonesia or Papua New Guinea, and became established as early as 1996 (211).

Given northern Australia’s close proximity to tropical countries with diverse mosquito faunas, and its favorable climate for invasive tropical organisms, the presence of only four invasive mosquito species is surprising. Australia was the first country to apply quarantine code to aircraft (173); disinsection of aircraft, airport “sanitation,” and inspection and fumigation of vessels arriving by sea may have prevented the establishment of a greater number of invasive mosquito species (173; R.C. Russell, personal communication). Despite frequent international arrivals from malarious areas, only a single case of airport malaria has been recorded in Australia (173).
TABLE 2 Total culicid fauna and incidence of biting, invasive mosquitoes in two mainland and four island areas

<table>
<thead>
<tr>
<th>Area</th>
<th>Total culicid spp.</th>
<th>% Total</th>
<th>Most recent detection</th>
<th>Key citations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continental United States</td>
<td>174</td>
<td>8</td>
<td>4.6</td>
<td>1998</td>
</tr>
<tr>
<td>Italy</td>
<td>54</td>
<td>2</td>
<td>3.7</td>
<td>1996</td>
</tr>
<tr>
<td>Hawaii</td>
<td>5</td>
<td>5</td>
<td>100.0</td>
<td>1979</td>
</tr>
<tr>
<td>Guam</td>
<td>24</td>
<td>17</td>
<td>70.8</td>
<td>1979</td>
</tr>
<tr>
<td>New Zealand</td>
<td>17</td>
<td>4</td>
<td>23.5</td>
<td>1998</td>
</tr>
<tr>
<td>Australia</td>
<td>242</td>
<td>4</td>
<td>0.8</td>
<td>1999</td>
</tr>
</tbody>
</table>

*Excludes nonbiting Toxorhynchites spp. Listed in Table 1.

New Zealand

Compared with neighboring Australia, New Zealand has a depauperate native mosquito fauna composed of only 13 species (10). However, four nonnative species, a number equal to Australia's invasive mosquito species, brings this nation's total mosquito fauna to 17 (Table 2). Three of these, Aedes australis, Aedes notoscriptus, and Aedes camptorhynchus, are imports from Australia (78, 150; G. Browne, personal communication). Although the first two of these are believed to have arrived via ships early in the twentieth century (210), the salt-marsh species Ae. camptorhynchus was first detected only in December of 1998 and is also believed to have been ship-borne (139). The only invasive species shared by New Zealand and Australia, Cx. quinquefasciatus, supposedly reached New Zealand prior to 1848 aboard sailing vessels (210).

Owing to its sparse native mosquito fauna, isolation, and absence of tropical climates, no mosquito-borne diseases are known to occur in New Zealand (210). However, during the course of increased surveillance in the 1990s, the potential arbovirus vectors Ae. albopictus and Ae. japonicus have been intercepted in tire shipments from the Oriental region (78, 99).

INVASIONS BY Aedes Albopictus

Arrivals and Establishments

Widespread invasions by the Asian tiger mosquito Ae. albopictus in the past two decades, facilitated by tire shipments, are regarded as the "third wave" of human-aided dispersal of mosquito vectors of human disease, following the previous cosmotropical spread of Ae. aegypti and the Cx. pipiens Complex (21). The native range of Ae. albopictus is centered in the Oriental region and India (76) but extends
west to the African island nations of Mauritius, the Seychelles, and Madagascar (116). In the hundred years preceding its most recent diaspora (33), *Ae. albopictus* had spread to Hawaii, Guam, and other Pacific islands (76, 89, 208).

Before its establishment in the vicinity of Houston, Texas in 1985 (193), *Ae. albopictus* had been detected previously in tire shipments at North American ports (47) and in a cemetery in Tennessee (157). Based on diapause responses of U.S. populations founded shortly after its arrival, Hawley et al. (77) deduced that North American *Ae. albopictus* originated from temperate Japan. *Ae. albopictus* that nearly simultaneously colonized southeastern Brazil (55) showed no diapause, suggesting a tropical origin for Brazilian founders (77).

In southern Europe, *Ae. albopictus* was discovered established in Albania in 1979 (1), in Italy in 1990 (174), and in France in 1999 (181). Its puzzling absence from mainland Africa (116) was remedied by the detection of *Ae. albopictus* in Nigeria in 1991 (175). Following its establishment and spread in both the United States and Brazil, the Asian tiger mosquito was recorded from Mexico (86), Argentina (168), Guatemala (141), and Caribbean islands such as Hispaniola (148), Cuba (19), and the Caymans (G.F. O’Meara, personal communication). Shipments of used tires have been implicated as the primary dispersal mechanism of this spread (156).

**Spread**

The eastward and northward expansion of *Ae. albopictus* in the United States has been carefully documented from state and county surveillance records (126). The northern limits of the species (Figure 2a) correspond approximately to the −5°C isotherm, as predicted by cold-hardiness studies (136). Despite interceptions at western ports (34), *Ae. albopictus* has not colonized the western United States, possibly because of climatic incompatibilities (209). The species, which entered Florida in 1986 from the temperate north, was established in all Florida’s 67 counties by 1994 (143, 144).

Improved surveillance has filled in gaps of a previously reported patchy distribution of *Ae. albopictus* in Italy (162), which now extends from Naples in the south to the northern borders of that country (Figure 2b) (R. Romi, personal communication). The current known distribution of *Ae. albopictus* in Brazil suggests northern, southern, and westward expansion from the site of original infestation in the southeast of that country (Figure 2c) (Fundação Nacional da Saúde, unpublished information), although multiple introductions cannot be ruled out. It is not known whether seemingly isolated foci, such as on the northeast coast or in Amazonian regions of Mato Grosso State (Fundação Nacional da Saúde, unpublished information), represent a disjunct distribution in that country or, rather, gaps in surveillance.

**Population Genetics**

Isozyme analyses conducted shortly after the eastward and northward dispersal of *Ae. albopictus* in the United States were interpreted as indicating rapid local
Figure 2  Suspected ports of arrival (arrows with years) and recent distributions of *Ae. albopictus* in (a) the United States (modified from 126), (b) Italy (modified from R. Romi, personal communication), and (c) Brazil (modified from Fundação Nacional da Saúde, unpublished data, 1999). For Brazil, States referenced in text are indicated by abbreviations: MT, Upper Mato Grosso; SP, São Paulo; RJ, Rio de Janeiro; SC, Santa Catarina. Geographic divisions for the United States are states, and for Italy, provinces.
differentiation (13). Similar patterns of isozyme variation were detected at the heart of its native range in the tropics, suggesting that local genetic differentiation is characteristic of this species (14). A comparable electrophoretic study of Italian *Ae. albopictus* confirmed significant variation in allele frequencies among subpopulations attributable to genetic drift (202). Isozyme patterns were also interpreted as indicating a common geographic origin of *Ae. albopictus* in Brazil and the United States (92), although this conclusion conflicts with distinctive mtDNA profiles in samples from the two countries (12a), a more comprehensive analysis of 27 isozyme loci (L.E. Munstermann, unpublished data), and different diapause responses (77; L.P. Lounibos, unpublished data). An examination of DNA sequences of the mitochondrial ND5 subunit of NADH dehydrogenase showed that Brazilian populations of *Ae. albopictus* harbored private haplotypes not present in samples from the United States (12a).

**Competitive Exclusion**

The decline in abundance and widespread disappearance of *Ae. aegypti* in association with the *Ae. albopictus* invasion in the southeastern United States has been well documented (33, 80, 120, 143). Once broadly distributed throughout the Southeast, *Ae. aegypti* is now restricted to urban habitats in southern Texas, Florida, and in New Orleans (145a). Mechanisms proposed to explain the rapid range reduction of the yellow fever mosquito include (a) sterility from interspecific matings with *Ae. albopictus* (133); (b) differential mortality caused by infection of *Ae. aegypti* with *Ascoregarina taiwanensis*, a parasite introduced into the United States with *Ae. albopictus* (33, 130); (c) hatching inhibition of *Ae. aegypti* eggs by larvae of *Ae. albopictus* (48); and (d) superiority of *Ae. albopictus* in larval resource competition (91).

Although earlier laboratory studies, which used protein-rich diets, seemed to show that *Ae. aegypti* was the superior larval competitor (15, 79), Barrera (7) demonstrated superior performance of *Ae. albopictus* when leaf litter, a natural substrate, was used. In a natural Florida woodland where competitive exclusion had recently occurred, Juliano (91) showed that *Ae. albopictus* outcompeted *Ae. aegypti* in resource-limited automobile tires. Although the larval competition hypothesis satisfactorily explains most instances of displacement in the southeastern United States, mechanisms for *Ae. aegypti*’s urban persistence in selected southern states remain unclear (145a).

Based on experiments in laboratory microcosms, Livdahl & Willey (104) predicted that *Ae. albopictus* would exclude the native North American treehole mosquito *Aedes triseriatus* from tire habitats, but not from treeholes. Analyses of pre- and postinvasion larval samples in Florida confirmed coexistence of the two species in treeholes, but with a temporal trend in mean crowding that favors *Ae. albopictus* (107). In Florida, *Ae. triseriatus* was rare in discarded urban or suburban tires even before the arrival of *Ae. albopictus* (107). In South Carolina
Ae. triseriatus abundances in oviposition traps decreased after the Ae. albopictus invasion in that state (120).

Evolution of Diapause

Egg diapause is induced in temperate Ae. albopictus by exposing female pupae and adults of the preceding generation to short daylengths (76). A high incidence of egg diapause was reported for six populations of Ae. albopictus shortly after their establishment in the United States (77). Although Craig (33) claimed that diapause was lost after Ae. albopictus adapted to subtropical Florida, populations from that state tested in 1999–2000 all expressed this trait when exposed to short daylengths (10L:14D) at 21°C, with the incidence of diapause decreasing in a north to south geographic cline, ranging from 99% near the Florida-Georgia border (30.5° latitude) to 65% south of Miami (25.5°N latitude) (L.P. Lounibos & R.L. Escher, unpublished data). Conversely in Brazil, where collections in 2000 from Rio de Janeiro and São Paulo states did not respond to diapause-inducing photoperiods, 5–10% of eggs of Ae. albopictus from the more southerly and temperate Santa Catarina state (26.9 and 27.7°S latitude) (Figure 2c) entered diapause in response to short daylengths received by their mothers (L.P. Lounibos, R.L. Escher & R. Lourenço-de-Oliveira, unpublished data). Thus, selection for diapause expression since the establishment of Ae. albopictus in the two hemispheres has acted in opposite directions to facilitate adaptive evolution from temperate to subtropical habitats in the United States and from tropical to temperate in Brazil.

Arboviruses

In its native range Ae. albopictus is known as a vector of dengue virus, which was isolated from Mexican collections of the species after an epidemic (85). After its invasion of the United States, there was concern for the diverse arboviral zoonoses in which Ae. albopictus might participate in its new American environments (121, 127). Wild-caught Ae. albopictus females were recovered infected with the highly pathogenic eastern equine encephalitis virus at a tire dump in south Florida located on the edge of a swamp (123). Several other nonpathogenic viruses have been isolated from Ae. albopictus collected at other North American localities (56, 74). Recently, LaCrosse encephalitis virus was isolated from field-collected eggs of Ae. albopictus in areas of North Carolina and Tennessee where human cases of this disease had recently occurred (61). Risks of arbovirus transmission by Ae. albopictus in Europe have been discussed by Mitchell (122).

The high annual incidence of dengue in Brazil, with more than 250,000 cases registered in 1997 (38a), renders it probable that Ae. albopictus will play some role in transmission, although the first reported isolate of dengue virus from Ae. albopictus in this country (180) is regarded as disputable. A looming concern is that Ae. albopictus can be a bridge vector for sylvan yellow fever, which remains common in Brazil (64, 114). Use of abundant epiphytic bromeliads as larval habitats could expose Ae. albopictus to the natural reservoirs of yellow fever infection
in arboreal primates (135). Marques et al. (114) discuss other arboviruses that might be vectored by *Ae. albopictus* in Brazil.

**AEDES JAPONICUS IN THE UNITED STATES**

In 1998 *Ae. japonicus*, a container-inhabiting mosquito species native to Korea and Japan (198), was detected in light trap collections in New York and New Jersey, which it likely reached in tire shipments (149). Its presumed arrival in tires is supported by detection of this species on several occasions in imported tires intercepted in New Zealand (78, 99). The species was detected independently in 1998 in human biting collections in Connecticut (129), where its immatures now inhabit a wide variety of artificial and natural container habitats (4). The species has also spread westward and inland in Maryland, Pennsylvania, and Ohio (53).

Fonseca et al. (53) compared RAPD profiles and mtDNA haplotypes of *Ae. japonicus* from various sites in Japan and throughout its current range in the United States. Samples from New York, Connecticut, and New Jersey were separable from Pennsylvania and Maryland collections by distinctive DNA profiles. Small sample sizes precluded determination of whether exclusive haplotypes in these two areas were attributable to independent introductions or to rapid genetic divergence caused by founder effects (53). All North American samples bore genetic similarities to some Japanese populations, although the origin of founders could not be determined precisely.

During intensive arbovirus surveillance in the past two years in the northeastern United States, a pool of wild-caught *Ae. japonicus* was detected infected with the recently established West Nile virus (27). The demonstrated ability of this species to be infected by and to transmit West Nile virus (201) indicates that this combination of new pathogen and new vector could become epidemiologically significant in eastern North America.

**THE TENS RULE OF WILLIAMSON AND MOSQUITO INVASIONS**

Williamson (217–219) derived a statistical generalization, applicable to a range of invasive plants and animals, that states that approximately 10% of nonindigenous arriving species become established, and of the establishments, about 10% become pests. Exceptions to the “Tens Rule” included crop plants, Hawaiian birds, insects released for biological control, and island mammals, all of which had higher establishment success than predicted by this generalization (221).

Surveys of mosquito fauna arriving in the continental United States by international aircraft (50, 84) and ship (34) provide estimates of the number of species arriving via these transport mechanisms. In international aircraft disinfected between 1948–1960, 18 nonindigenous mosquito species were intercepted at airports in the continental United States (84) and 4 more species in tires on container ships
from Japan (34). For Hawaii, the number of mosquito species detected on aircraft was 33 (50, 84). Nonindigenous mosquito species in the continental United States include not only the five twentieth-century introductions of container occupants (Table 1), but also *Ae. aegypti*, *Cx. pipiens*, and *Cx. quinquefasciatus*, the latter two members of the *Cx. pipiens* Complex believed to have arrived by ships from the Old World (166). [DNA microsatellite genotype similarities support a West African origin of North American *Cx. quinquefasciatus* (D. Fonseca, personal communication).] The percentages of biting mosquitoes that became established are much higher for the continental United States (8/22 = 36.4%), but within the 5–20% confidence limits for Hawaii (5/33 = 15.2%), based on predictions by the Tens Rule. Mosquito interceptions from international aircraft and ships arriving in Australia have detected 16 nonindigenous mosquito species (173, 211; R.C. Russell, personal communication), yielding a 25% (4/16) establishment success. According to these calculations, the Tens Rule generally underestimates establishment success of mosquito arrivals. However, given that the North American mosquito identifications from aircraft were done more than 40 years ago, when international travel was less frequent and only ships at a few American and Australian ports were inspected, the denominators of these calculations undoubtedly underestimate the actual number of nonindigenous species of arriving mosquitoes. *Culex quinquefasciatus* is the only one of many nonindigenous species detected on aircraft arriving in Hawaii that became established (although it reached Hawaii via ships). By contrast, two of the four species detected on ships by Craven et al. (34), *Ae. albopictus* and *Ae. togoi*, are now established in the United States.

The second Tens Rule transition, from established to pest status, where pest is defined as “with a negative economic effect” (219, 221), is more difficult to apply to invasive disease vectors. A more apt negative transition would be involvement in the transmission of pathogens to humans. Among the 40 established invaders counted for Table 2, only *Ae. aegypti* as a vector of dengue in northern Australia and *Ae. albopictus* as a probable vector of La Crosse encephalitis virus in the United States (61) are currently involved in human disease transmission. Thus, for the six localities listed in Table 2, 2/40 (5.0%) of the invasive species have become disease vectors in their new environs, which is within the confidence limits of the Tens Rule.

**DETERMINANTS OF INVASION SUCCESS**

Williamson (220) has pointed out that the best correlates of invasion success, propagule pressure and previous success, are not truly biological. Population characteristics, such as abundance, range, or intrinsic rate of increase, or individual traits, such as climate matching, niche availability, or taxonomic isolation, are often moderate or poor correlates of invasion success (220). Certainly, propagule pressure and previous success appear to have favored the invasions of the three
most successful mosquito dispersers, *Ae. aegypti*, the *Cx. pipiens* Complex, and *Ae. albopictus*, which have become nearly cosmotropical or cosmopolitan through successive waves of human-aided dispersal (21).

Regarding propagule pressure, it is noteworthy that most successful mosquito invaders have arrived by ship. Among the 40 instances of culicid invaders recorded in Table 2, only *Cx. gelidus* in Brisbane (128), *Ae. vexans* in Hawaii (90) and a few species of mosquitoes in Guam (208) appear to have arrived on aircraft. The comparatively poor invasion success of aircraft arrivals may be due to the strong relationship between release size and the probability of population establishment (67, 68). Mosquito arrivals on aircraft are typically adults consisting of only a few individuals of any given species (50, 84). However, ships, especially modern container vessels (156, 157), can carry a large number of propagules, especially of the immature stages, of mosquitoes. The transport of desiccation-resistant *Aedes* eggs, especially in tires, may account for the establishment of such container-frequenting species as *Ae. togoi* in the Pacific Northwest (11) and Malaysia (150), *Ae. bahamensis* in south Florida (145), and *Ae. atropalpus* in Italy (163), as well as *Ae. albopictus* worldwide and *Ae. japonicus* in the United States. If Guam is omitted, mosquitoes of the genus *Aedes* account for 65.2% (15/23) of the successful mosquito invaders tallied for Table 2.

The dominance of a few species among the successful mosquito invaders suggests that previous success may be a potentially good predictor of vector invasiveness. The three most widely distributed mosquito species, cited above, have achieved this status through human-aided “jump” dispersals (186) followed by regional spread. The recent intercontinental dispersal of two additional tire-inhabiting species, *Ae. japonicus* and *Ae. atropalpus* (149, 163), may represent another wave of “repeat” invaders.

Elton (49) postulated that simple biological communities are more vulnerable to invasions, but Levine & D’Antonio (100) reviewed both models and observational and experimental studies and found no clear relationship between community diversity and invasibility. Elton (49) also presumed that islands are more susceptible to invasions than mainland communities, but Simberloff (185, 186) suggested that this difference is more apparent than real. Indeed, inspection of mosquito invasions from the nonrandom selection of four islands and two continental nations would seem to indicate no obvious relationships among these factors (Table 2). For example, the smaller, less diverse island nation of New Zealand has as many species of mosquito invaders as its much larger and more biologically diverse neighbor Australia, and smaller Guam has many more invasive mosquito species than Hawaii. Although the reasons for this variability among islands are not known, nonbiological factors, such as the frequency of noninspected arrivals of air and sea transport, may be important determinants of invasion success on these islands.

For phytophagous insects that live on trees and shrubs, 75% of the 400 invasive species in North America are of European origin (117). Although this high rate may be attributable partly to early trade routes, Niemelä & Mattson (140) have suggested that European phytophagous insects may be better competitors than
their North American counterparts. However, among eight species of invasive mosquitoes in the continental United States only *Cx. pipiens* s.s. is probably of European origin (166), suggesting no competitive advantage for European culicids in North America. Three species of twentieth century mosquito invaders of the United States are of Oriental origin, which corresponds to the predominant direction of tire exports (156).

**INVASION BIOLOGY AND VECTOR CONTROL**

Studies of invasion processes have broad applicability to vector control beyond the interception of unwanted arrivals or suppression of recent infestations. For example, the release, establishment, and spread of a pathogen or parasite for the biological control of a vector (203) follows dynamics comparable to an unintended invasion (67, 68). Similarly, genetic engineering approaches to vector control by population replacement (73) require the release of genetically altered organisms that will behave like invading propagules in the native vector habitat. Reinvasions of vectors after eradication schemes, such as that of the Onchocerciasis Control Program in West Africa (207) or the partial eradication of *Ae. aegypti* from the Americas (190), obey the population dynamics of arrival, establishment, and spread common to new invaders.

The unanticipated competitive displacement of *Ae. aegypti* in the southeastern United States by invasive *Ae. albopictus* (80, 91, 143) corroborated a principle in vector control tested many years earlier in an unsuccessful field experiment. Based on its superior competitive ability in laboratory comparisons (e.g., 71, 108), Rosen et al. (165) released large numbers of *Ae. albopictus* on a coral atoll, but this nonindigenous species failed to displace the native filarial vector *Aedes polynesiensis* and within 1–4 years disappeared from the island. Just as laboratory experiments were misleading about the competitive outcome of recent *Ae. albopictus–Ae. aegypti* encounters in the southern United States (91), laboratory simulations failed to predict the results of the *Ae. albopictus–Ae. polynesiensis* interaction on the atoll. Perhaps lessons learned from unintended invasions will instruct future considerations of experimental competitive displacement for vector control.

**FUTURE DIRECTIONS AND NEEDS**

Identifying future invaders is critically important because eradication of an established invader, as accomplished over 60 years ago for *An. gambiae* in Brazil (191), is rarely possible (110). Ecological shifts that promote the exploitation of habitats associated with human activities have accompanied many previous successful vector invasions and may provide clues to future threats. However, invasion biology is far from being a predictive science (219, 220).
In the wake of the diaspora of *Ae. albopictus* (33) that is still underway, it is hard to imagine what might be next in the worldwide reshuffling and homogenization of vector faunal distributions promoted by human-aided transport. In addition to transport systems, global climate changes could alter the boundaries of vector limits and distributions (115) and influence the invasion potential of species and habitats (105).

Because the application of invasion biology to vectors is new, this review is largely an accounting of past and recent events, some with important epidemiological consequences. Improved surveillance, such as the close scrutiny of the spread of *Ae. albopictus* in the United States and Italy, has provided more accurate data than previously available on the arrival and establishment of some invaders. However, on a global scale, most vector invasions probably go unnoticed because of a lack of surveillance [the presence of *Ae. albopictus* in Nigeria was recognized only because of a visit by a CDC surveillance team following a yellow fever epidemic (175)], and comprehensive data on the components of invasions by vectors are available for only a few regions. Generalizations, explanations, and predictions are hampered by a lack of detection and/or follow-up of invading vectors in most areas of the world and the absence of a universal reporting system.

Sensitive molecular genetic markers have great potential for tracing the origins and frequencies of vector introductions but are only just beginning to be used (e.g., 12a, 53, 54). Ideally, they are best suited if deployed at the earliest stages of an invasion. In order to characterize invasions beyond descriptive stages, experimentation, especially field manipulations (e.g., 91), will be increasingly important to explain the biological outcomes, such as competitive displacement, of invasions. As more quantitative ecological data become available to explain invasion patterns, such as that of *Ae. albopictus* in the United States, Brazil, and Italy (Figure 2), generalizations about invasible communities and species may be realized (205). These generalizations could be potentially important for guiding future initiatives in vector control, such as by the release of transgenic mosquitoes, whose population dynamics may mimic invasive species.

The impact of invasive vectors on human ecosystems is measured most appropriately in health consequences and hence is quite different from the economics of nonvector invaders (147). When a recently established vector promptly becomes the primary transmitter in an epidemic, as for malaria in Brazil in the 1930s and in Peru in the 1990s, the health impacts are obvious. On the other hand, as noted by Elton (49) for the gypsy moth, the negative consequences of an invasion may not be felt for a long period after establishment. The insinuation of a new vector into a multicomponent zoonosis, such as for *Ae. albopictus* with La Crosse virus (61), is liable to occur more gradually after invasion and requires careful monitoring. In addition, viruses may evolve within new vectors, potentially changing their pathogenicity and transmissibility (28). Whereas the physiological and molecular events of new vector-pathogen combinations may be examined experimentally in the lab, possible epidemiological consequences warrant a modeling approach, as has been applied to some noninsect-borne infectious diseases (182).
ACKNOWLEDGMENTS

For personal communications and access to prepublications I am grateful to T. Andreadis, C. Apperson, G. Browne, D. Fonseca, K. Gage, K. Gottfried, L. Munstermann, R. Lourenço-de-Oliveira, G. O’Meara, R. Romi, and R. Russell. For comments on a draft of this manuscript I thank S. Juliano, C. Moore, G. O’Meara, and W. Tabachnick. Work on this review was supported, in part, by NIH grant AI-44793. This is University of Florida Agricultural Experiment Station Publication No. R-08084.

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