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REVIEWS AND SYNTHESES

Ecology of invasive mosquitoes: effects on resident species and on human health

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Abstract

Investigations of biological invasions focus on patterns and processes that are related to introduction, establishment, spread and impacts of introduced species. This review focuses on the ecological interactions operating during invasions by the most prominent group of insect vectors of disease, mosquitoes. First, we review characteristics of non-native mosquito species that have established viable populations, and those invasive species that have spread widely and had major impacts, testing whether biotic characteristics are associated with the transition from established non-native to invasive. Second, we review the roles of interspecific competition, apparent competition, predation, intraguild predation and climatic limitation as causes of impacts on residents or as barriers to invasion. We concentrate on the best-studied invasive mosquito, *Aedes albopictus*, evaluating the application of basic ecological theory to invasions by *Aedes albopictus*. We develop a model based on observations of *Aedes albopictus* for effects of resource competition and predation as barriers to invasion, evaluating which community and ecosystem characteristics favour invasion. Third, we evaluate the ways in which invasive mosquitoes have contributed to outbreaks of human and animal disease, considering specifically whether invasive mosquitoes create novel health threats, or modify disease transmission for existing pathogen–host systems.

Keywords

Aedes albopictus, apparent competition, Culicidae, disease ecology, disease vectors, interspecific competition, intraguild predation, invasion, local adaptation, predation.

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INTRODUCTION

Invasion biology focuses on patterns and processes related to introduction, establishment, spread and impacts of non-native species (Williamson 1996; Davis & Thompson 2000; Lounibos 2002). We will apply the term 'invasive' to introduced species that have increased and spread, creating the potential for impacts on native species and ecosystems, or on human activities (agriculture, conservation). We refer to species that have become established, but have neither spread widely nor had important impacts as 'non-native'. Invasive species produce impacts on other species and ecosystems primarily via their biotic interactions, including predation and parasitism, interspecific competition, or ecosystem engineering (Williamson 1996). Also among the potential biotic impacts of some invasive species are effects on human and animal health (Lounibos 2002). Invasive pathogens may affect health directly, and invasive vectors may alter the transmission cycles of native or non-native pathogens (McMichael & Bouma 2000). This review focuses on the ecological interactions that produce impacts associated with invasions by the most prominent group of insect vectors of disease, mosquitoes (Diptera, Culicidae). We are specifically interested in two kinds of impacts of invasive mosquitoes: effects – usually detrimental – on (i) resident species or ecosystems and (ii) human or vertebrate animal health. The first represents a class of effects that could apply to any invasive species, so that what we learn from investigations of impacts of mosquitoes may serve as a paradigm for investigations of any invasion. The second represents a class of impacts relevant primarily to vectors. For mosquitoes, different life cycle stages are likely to be central to the two kinds of impacts. The aquatic larval phase is most likely to interact with and to impact other species, whereas the terrestrial adult phase is the cause of threats to human health. In examining both kinds of effects, we wish to

identify the characteristics of the invasive species and the biological interactions that are associated with these impacts.

For mosquitoes, there is one well studied invasive species (Asian tiger mosquito, *Aedes albopictus* Skuse) for which multiple hypotheses concerning the ecological processes operating during its invasions have been tested in several locations. For other species there is very little information on the processes that operated during invasions. Although a broad review of the processes involved in invasions by mosquitoes would be desirable, relevant data are not available. In some cases (e.g. *Ochlerotatus japonicus*) the invasions are recent and research on ecological processes is ongoing. In other cases the invasions occurred sufficiently far in the past that the potential to investigate establishment and spread is long gone. We therefore begin with a simple review of the characteristics of the major invasive mosquitoes, evaluating which traits are associated with invasive potential. We then concentrate our review of processes primarily on *Aedes albopictus*, with a summary of what little is known or postulated about ecological processes involved in other invasions by mosquitoes. This portion of our review will enable us to test basic ecological theory as it applies to mosquitoes, and may thus improve our understanding of not only invasive mosquitoes, but of invasive species in general, and of the roles of biotic interactions that may apply to any invasive species.

We divide the ecological processes into: (i) species interactions that may influence invasions, either by affecting resident species, or by serving as barriers to invasions and (ii) effects of climate that may foster invasion success, act as barriers to invasion, alter the impacts of invasions, or act as agents of natural selection on invasive mosquitoes. Interspecific competition, predation and apparent competition via shared pathogens are the species interactions that have been best studied. We will review some models of these interactions and empirical data on the roles of these processes in invasions by *Aedes albopictus*. We also review data on known effects of climate on invasions by *Aedes albopictus*.

There are data on the health impacts of most invasions (Lounibos 2002), and we finish with a review of the disease ecology of invasive mosquitoes. We do this by posing questions about the origins of disease organisms (e.g. non-native, resident), and whether introduction of a new vector initiates or alters outbreaks of important diseases. We hope that this portion of our review will provide a paradigm for investigations necessary to understand which non-native species constitute the greatest hazard to human health.

CHARACTERISTICS OF INVASIVE MOSQUITOES

The list of successful invasive and non-native culicids (Table 1) is limited, hence we can only address simple questions about species characteristics, but they are questions deemed generally important by those working in the field of invasion biology (e.g. Sakai *et al.* 2001). First, we can ask what characteristics are associated with becoming an established non-native. Desiccation-resistant eggs, which enhance survival in inhospitable environments, occur in 14 of 31 invasive or non-native species (Table 1). Across the Culicidae, strongly desiccation-resistant eggs are confined to members of the genera *Aedes*, *Ochlerotatus*, *Psorophora*, *Haemagogus* and *Opifex* (Clements 1992), totalling some 1012 species, or about 29% of *c.* 3491 mosquito species (Walter Reed Biosystematics Unit 2005). Thus, desiccation-resistant eggs are strongly associated with becoming an introduced non-native species (Fisher's exact test, $P = 0.0024$), perhaps because they increase probability of successful transport. A second question we can ask is what characteristics are associated with making the transition from non-native to invasive (Sakai *et al.* 2001). Desiccation resistance (yes, no) and status (invasive, non-invasive) are not significantly associated (Fisher's exact test, $P = 0.693$), indicating that species with desiccation-resistant eggs are not more likely to become invasive. Development in small man-made containers, tree holes, bromeliads, or rock pools is also common among invasive and non-native mosquitoes (17 of 31 total species; Table 1), but again, larval habitat (container, non-container) and status (invasive, non-native) are not significantly associated (Fisher's exact test, $P = 0.132$). Occupying human-dominated habitats (i.e. urban, suburban, domestic) is significantly (Fisher's exact test, $P = 0.028$) more common among invasive (six of nine) than among non-native (three of 14) mosquitoes (Table 1). Association of invasion with human disturbance in some form (e.g. Moyle & Light 1996; Richardson *et al.* 2000) has been observed in other groups. There are at least two broad hypotheses explaining this association: human commensals may have traits (e.g. a high maximum rate of population increase) that make them more likely to become invasive; or expanding human population and urbanization may create new, relatively under exploited, macrohabitat suitable for human commensal specialists. Autogeny and diapause are not significantly associated with invasive status, but data are absent for many species (Table 1). Mode of introduction (natural dispersal vs. human transport) is uncertain for many of these mosquitoes, but hitchhiking on ships is probably common (Lounibos 2002).

ECOLOGICAL PROCESSES

In the context of invasions, effects of competition and predation can be important because they can be impacts of invasive species on native species, and because these processes may act as barriers to invasion. Both competition and predation can, in principle, affect whether invasive

Table 1 Established invasive and non-native mosquitoes and important natural history traits

Species (origin)	Invaded/colonized region	Macrohabitat preference	Larval habitats	Desiccation-resistant eggs	Autogeny*	Diapause	References
Invasive species							
Aedes aegypti (Africa)	Cosmotropical	Urban, domestic†	Man-made containers	Yes	Rarely	None	Christophers (1960)
Aedes albopictus (temperate and tropical Asia)	Americas, Europe, Africa	Urban, suburban	Phytotelmata‡, man-made containers	Yes	Rarely	Egg§	Hawley (1988)
Ochlerotatus atropalpus (E. N. America)	W. N. America, Europe	Riparian	Rock pools, man-made containers	Yes	Yes	Egg	Lounibos (2002)
Ochlerotatus japonicus (temperate Asia)	North America	Rural, sylvan	Rock pools, man-made containers	Yes	No	Egg	Lounibos (2002)
Ochlerotatus notoscriptus (Australia)	New Zealand	Urban, suburban, rural	Tree holes, rock pools	Yes	No	Egg, larva	Weinstein *et al.* (1997)
Culex pipiens (Old World)	North America	Urban, domestic, suburban	Man-made containers, subterranean, small groundwater pools	No	Yes	Adult	Vinogradova (2000)
Culex quinquefasciatus (Africa)	Americas, Asia, New Zealand, southern Europe	Urban, domestic, suburban	Man-made containers, small groundwater pools	No	Some	None	Vinogradova (2000)
Anopheles darlingi (neotropics, especially eastern Amazonia)	Peru	Rural	River margins and lagoons	No	No	None	Lounibos (2002)
Anopheles gambiae complex¶ (Africa)	Brazil, Mauritius	Domestic	Groundwater pools	No	No	None	Ross (1911); Soper & Wilson (1943)
Non-native, non-invasive species							
Aedes neopandani (Saipan and Tinian)	Guam		Phytotelmata	Yes			Ward (1984)
Aedes rotanus (Rota)	Guam		Phytotelmata	Yes			Ward (1984)
Aedes saipanensis (Saipan)	Guam		Phytotelmata	Yes			Ward (1984)
Aedes vexans (Cosmopolitan)	Guam		Ground pools	Yes		Egg§	Ward (1984)
Ochlerotatus australis (Australia)	New Zealand	Rocky marine shore	Rock pools	Yes	Yes	Larva	Weinstein *et al.* (1997)
Ochlerotatus camptorhynchus (Australia)	New Zealand	Suburban, rural	Salt marsh, brackish swamps	Yes			Weinstein *et al.* (1997)
Ochlerotatus vigilax (New Caledonia)	Fiji	Coastal	Salt marsh	Yes	Yes		Joyce (1961)
Ochlerotatus bahamensis (Bahamas)	Southern North America	Urban, suburban, rural	Tree holes, man-made containers	Yes	Yes	No	O'Meara *et al.* (1989)
Ochlerotatus togoi (temperate Asia)	North America	Rocky marine shoreline	Rock pools	Yes	Yes	Larva§	Sota (1994)

Aedeomyia catasticta (Oriental Region)	Guam	Rural?	Ponds with macrophytes	No		No	Ward (1984)
Mansonia uniformis (Old World tropics)	Guam	Swamps	Ponds with macrophytes	No		No	Ward (1984)
Culex fuscanus (Oriental Region)	Guam	Rural?	Ponds, streams, ditches	No		No	Ward (1984)
Culex fuscocephala (tropical Asia)	Guam	Rural	Rice fields and ponds with vegetation	No		No	Ward (1984)
Culex tritaeniorhynchus (Old World)	Guam	Variable, sometimes domestic	Groundwater pools, rice fields	No		Adult§	Ward (1984)
Culex sitiens (Old World tropics)	Guam	Coastal	Brackish pools, holes	No		No	Ward (1984)
Anopheles indefinitus (Oriental Region)	Guam	Coastal	Marshes, ground pools	No		No	Ward (1984)
Anopheles barbirostris (Vietnam)	Guam	Rural	River margins, pools, rice paddies, swamps	No		No	Ward (1984)
Anopheles litoralis (Philippines, Borneo)	Guam	Coastal?	Artificial containers	No		No	Ward (1984)
Anopheles subpictus (Oriental Region)	Guam		Fresh and saltwater ground pools	No		No	Ward (1984)
Anopheles vagus (Oriental Region)	Guam		Pools, ditches, containers	No		No	Ward (1984)
Armigeres subalbatus (Oriental Region)	Guam		Containers with foul water	No		No	Ward (1984)
Wyeomyia mitchellii (Caribbean & Florida)	Hawaii		Bromeliads	No	No	No	Shroyer (1981)

Blank cells indicate lack of information. Question marks associated with macrohabitat preferences indicate that other habitats may also be used but information is limited. See text for details.

*Egg production without a blood meal.

†Does not apply to *Aedes aegypti formosus*, the sylvan morph found only in East Africa.

‡Phytotelmata are parts of terrestrial plants that hold water and are occupied by a community of inquiline animals; includes tree holes, bromeliads, pitcher plants and bamboo.

§Diapause not present in tropical populations.

¶Only includes the anthropophilic species of the complex, *Anopheles gambiae s.s.* and *Anopheles arabiensis*.

mosquitoes alter the potential for disease transmission. An invasive mosquito that replaces a resident species via competition or apparent competition may alter disease transmission if it is either a more or less efficient disease vector. If invasion results in reduced disease transmission via vector replacement, then introduction of a novel mosquito species could be used as biological control of resident vectors via competitive displacement (e.g. Rozeboom 1971; Rosen *et al.* 1976). This is similar to logic behind attempts to use transgenic, disease-refractory mosquitoes to control disease (O'Brochta 2003). In both cases the goal is to replace a population of disease-competent mosquitoes with a population of disease-refractory mosquitoes (Takken & Boëte 2003). In the former case this replacement occurs via interspecific competitive exclusion. In the case of use of transgenic mosquitoes replacement may occur by intraspecific competition among genotypes or intrasexual competition (i.e. transgenic male mating competitiveness). It is also possible for invasive mosquitoes to alter disease transmission without impacting native vectors, if the invader takes on a novel role in the life cycle of a pathogen. For example, an invasive species that is an effective bridge vector (i.e. capable of transmitting the pathogen outside its enzootic cycle among non-human hosts) may alter disease transmission and may create new human health problems. Likewise, invasive vectors can transport novel pathogens that can spread rapidly in susceptible host populations (see below).

Interspecific competition

In this review, 'interspecific competition' encompasses any mechanism that produces negative effects on population growth of the focal species, excluding any mechanisms that involve predation or parasitism on the focal species. Thus, we include resource competition (negative effects via depletion of shared resources; Grover 1997), chemical or physical interference (negative effects via toxins, waste products, or aggression; Sunahara & Mogi 2002), and mating interference (negative effects via interspecific mating depressing reproductive output; Ribiero & Spielman 1986), but exclude intraguild predation and apparent competition (negative effects via a shared predator or parasite; Holt & Lawton 1994), which we consider forms of predation (see below).

Superiority in interspecific competition is often listed as a characteristic of non-native species that enhances the likelihood of becoming invasive (Williamson 1996; Sakai *et al.* 2001). But superiority in competition is only necessary for invasion and spread if the invader encounters similar species and if resources are limiting, or if interference competition dominates in the invaded community. Some invasive species may expand into new areas by filling an 'empty niche'; i.e. occupying previously unoccupied (or unsaturated) habitat or exploiting a previously unused resource (Williamson 1996). Thus, the first line of evidence that superiority in competition is important in an invasion is often that the invasion results in declines or elimination of ecologically similar species (Juliano 1998). Conversely, some non-native species may not spread beyond a limited area because they are not effective competitors, with competition from residents presumably limiting their spread. In either case, interspecific competition plays a role in determining the outcome of an introduction. Among mosquitoes, both declines of residents (see below) and failure of non-native species to spread (Rosen *et al.* 1976; O'Meara *et al.* 1989, 1995b) have been observed. Further, historical and natural history data on *Aedes aegypti* (L.) (whose domestic form larvae preferentially occupy man-made containers, Christophers 1960) may be interpreted as indicating that at least some invasions by mosquitoes have proceeded without much evidence for impacts of competition, suggesting that some invasive mosquitoes may have invaded 'empty niches'. Unfortunately, there have been very few experimental investigations of competitive interactions involving invasive or other non-native mosquitoes, and we therefore have a reasonable understanding of the roles of interspecific competition only for the recent invasions of North and South America by *Aedes albopictus*.

Aedes albopictus

Resource competition

Introductions of *A. albopictus* to North and South America (Forattini 1986; Hawley 1988; O'Meara *et al.* 1995a,b; Moore 1999), Europe (Romi *et al.* 1999) and Africa (Fontenille & Toto 2001) in the past two decades are well documented (Lounibos 2002 gives extensive references for this invasion). Concomitant with the spread of *A. albopictus* in southern North America, there has been a decline, sometimes to local extinction, of the previously resident invader *A. aegypti* (O'Meara *et al.* 1995a; Juliano *et al.* 2004, and references therein) that is consistent with interspecific competition. *Aedes aegypti* persists in southern and urban areas of the Florida peninsula (O'Meara *et al.* 1995b; Juliano *et al.* 2002, 2004), and in other urban areas of the southern USA (e.g. Houston, Savannah, New Orleans), and in these areas it coexists locally with *A. albopictus* (Juliano *et al.* 2004; G. F. O'Meara, personal communication; D. M. Wesson personal communication). Coexistence despite interspecific larval competition is one of the major unanswered questions concerning the invasion of North America by *A. albopictus*. *Aedes aegypti* remains dominant in Miami (O'Meara *et al.* 1995a,b) and in the Florida Keys, where *A. albopictus* is absent on most islands (G. F. O'Meara, personal communication), possibly due to dry conditions (Juliano *et al.* 2002) or intensive control efforts.

Laboratory experiments in microcosms with plant detritus as a substrate showed that North American *A. albopictus* are superior in competition with *A. aegypti* (Barrera 1996; Daugherty *et al.* 2000). Field experiments in tires showed a similar competitive advantage for *A. albopictus* (Juliano 1998). Field experiments in cemetery vases demonstrated that interspecific competition among larvae can cause significant reductions in survival of *A. aegypti* at the typical densities encountered in these habitats (Juliano *et al.* 2004), providing evidence that interspecific competition is important in nature. Laboratory experiments on competition between larvae of these species have used different detritus resources (e.g. liver powder, yeast, dead insects) and have tended to yield approximate competitive equality, or even an advantage for *A. aegypti* (Barrera 1996; Daugherty *et al.* 2000, and references therein). Temperatures between 24 and 30 °C had no significant effect on competition among larvae (Lounibos *et al.* 2002). Field and laboratory data suggest that habitat drying and resultant mortality of eggs differentially affects *A. albopictus* (Juliano *et al.* 2002), and dryer environments can reverse competitive advantage, favouring *A. aegypti* (K. S. Costanzo, B. Kesavaraju and S. A. Juliano, 2005, personal communication). It is obvious from studies of *A. albopictus* and *A. aegypti* that the effects of competition can vary with the environment in which the interaction occurs (condition-specific competition, Taniguchi & Nakano 2000). A more subtle point is that if the abiotic environment has effects on life cycle stages that do not compete (e.g. eggs), impacting one species more than another, those effects may alter the population level consequences of competition in another life cycle stage (e.g. larvae).

In Brazil, *A. albopictus* was also introduced in the mid-1980s, and it has spread widely throughout that country (Santos 2003). There is some evidence for local reductions of *A. aegypti* following invasion (Braks *et al.* 2004), and there are significant negative correlations of abundances of the two species across habitats in southern Brazil (Braks *et al.* 2003). Despite coexistence of these species in southern Brazil, there is strong evidence from field experiments that *A. albopictus* from Brazil are also superior to *A. aegypti* in competition among larvae in man-made containers, just as in North America (Braks *et al.* 2004), providing one of the few cases in which large-scale geographic variation in the outcome of an invasion has been evaluated. Invasion of Europe by *A. albopictus* has been suggested to be associated with declines in abundance of *A. aegypti* (Simberloff & Gibbons 2004), but the decline of *A. aegypti* in Spain and southern Europe preceded invasions by *A. albopictus* and probably results from eradication efforts (Eritja *et al.* 2005).

Laboratory investigations of competition among larvae of *A. albopictus* and the native North American tree hole mosquito *Ochlerotata triseriatus* (Say) have consistently shown competitive superiority of *A. albopictus* (Livdahl & Willey 1991; Novak *et al.* 1993; Teng & Apperson 2000; Aliabadi & Juliano 2002). In contrast to the case for *A. aegypti*, there is little evidence for competitive exclusion of *O. triseriatus* by *A. albopictus* and declines of *O. triseriatus* abundance are not apparent (Lounibos *et al.* 2001). *Aedes albopictus* and *O. triseriatus* are more likely to interact in wooded habitats that are both preferred by *O. triseriatus* and harbour a more diverse community of container-dwelling insects, including prominent predatory species (Lounibos *et al.* 2001; see below). In more northern, temperate areas like the Midwest, there is also little evidence for displacement of *O. triseriatus* by *A. albopictus* (Lancaster 2004), and the more severe detrimental effect of low temperatures on *A. albopictus* (Teng & Apperson 2000) probably contributes to its more limited invasion success in these habitats.

Invasion of *A. albopictus* in North America and Europe may also have affected *Culex pipiens* L. *Aedes albopictus* is strongly superior to *C. pipiens* in interspecific larval competition, and co-occurrence of these two species in man-made containers is common in the field in both Europe (Carrieri *et al.* 2003) and North America (Costanzo *et al.* 2005). Because *C. pipiens* larvae inhabit a very wide range of aquatic habitats, many not used by *A. albopictus* (Vinogradova 2000), the impact of competition on distribution and abundance of *C. pipiens* has not been obvious. Interaction of *A. albopictus* with *C. quinquefasciatus* Say in southern North America and the tropics has not been investigated. The interaction of *C. pipiens* with *A. albopictus* in North America is interesting because of the importance of *C. pipiens* in transmission of West Nile virus (WNV) among birds and to humans. *Culex pipiens* serves as an enzootic vector (i.e. transmitting WNV among birds) and appears to favour birds as a blood source, although it does feed on humans (Fonseca *et al.* 2004). The tendency of *C. pipiens* to feed on birds suggests that a bridge vector, attacking both birds (the amplification host) and humans (a dead end host) could enhance transmission of this disease to humans (Eldridge *et al.* 2000). *Aedes albopictus* is potentially such a bridge vector, having wide host range and high competence to transmit WNV (Turell *et al.* 2001). This complex set of interactions, with two vectors competing as larvae, and the invading potential bridge vector superior in interspecific competition among larvae, provides an opportunity for modelling of the invaded disease system as a means of forecasting the health consequences of this invasion, and more generally, of invasions by vectors with host preferences that differ from those of a native competitor.

Competitors may be a barrier to invasion as well. In some portions of its range, larvae of *A. albopictus* occur commonly in water-holding plant axils (Chow 1949; Joyce 1961). Within Florida, this species is productive in bromeliad axils only in the north, where native *Wyeomyia* spp. mosquito

occupants of this habitat are absent (O'Meara *et al.* 1995b). Interspecific interactions, probably through asymmetric larval competition, are responsible for the poor survivorship of *A. albopictus* in bromeliads co-occupied by larvae of *Wyeomyia* (Lounibos *et al.* 2003b). This is a clear example of a resident species limiting the invasive success of a mosquito.

Chemical interference

Competition between *A. albopictus* and *A. aegypti* is widely assumed to occur via resource depletion, and manipulating resource levels can alter the impact of competition (Juliano 1998; Daugherty *et al.* 2000; Braks *et al.* 2004). However, both species may be affected by interference competition produced by water-borne substances, presumably excretory products (Sunahara & Mogi 2002; Bédhomme *et al.* 2005). The role of interference competition in invasions by *A. albopictus* merits further investigation.

Mating interference

Mating interference is another hypothesized mechanism of competition between *A. albopictus* and *A. aegypti* ('satyrization', Ribiero & Spielman 1986; Harper & Paulson 1994). In the laboratory, male *A. albopictus* are more aggressive in attempting to mate with *A. aegypti* females, whereas male *A. aegypti* are less aggressive in attempting to mate with *A. albopictus* females (Nasci *et al.* 1989). This asymmetry can cause detrimental population level effects on the less aggressive species (Ribiero & Spielman 1986). Experiments testing this hypothesis showed that such differences in interspecific mating aggressiveness are not present under more realistic conditions, even in laboratory cages (Harper & Paulson 1994), suggesting that this mechanism is unlikely to explain observed displacement of *A. aegypti* in North America.

Hatching delays

Hatching delays are yet another mechanism of interference competition hypothesized to contribute to impacts of invading *A. albopictus* on both *A. aegypti* and *O. triseriatus* (Edgerly *et al.* 1993). Young larvae of *A. albopictus*, *A. aegypti* and *O. triseriatus* hatch from eggs when they are flooded, and all these species respond, to varying degrees, to the presence of older larvae feeding in the water by delaying hatching. *Aedes albopictus* is both least sensitive to this effect in the egg stage, and more likely as a fourth instar larva to produce this effect than the other species (Edgerly *et al.* 1993). The importance of this asymmetrical effect in nature is difficult to estimate.

Other invasive mosquitoes

There are relatively few data on competitive effects in invasions and introductions of other mosquito species (Table 2). A role for competition is suggested in the replacement of *A. albopictus* by *A. aegypti* in urban Southeast Asia, but definitive tests have not been conducted. The presence or absence of native competitors may have influenced invasion success of *C. quinquefasciatus*, which may also have affected native North American *Culex* via competition. The role of competition in determining the invasive vs. non-native status of *O. japonicus* vs. *Ochlerotatus bahamensis* should be tested in field and laboratory experiments.

Predation and parasitism

When a non-native species escapes the predators and parasites that attack it in its native range, the likelihood of that species attaining high abundance and spreading can be enhanced. Similarly, the presence of predators or parasites that are capable of attacking non-native species may help to keep those species from becoming invasive, or indeed from succeeding in becoming established. These effects have been documented in several invasions, and form the basis of most biological control efforts directed at invasive species (Williamson 1996), including attempts to control invasive mosquitoes (Focks & Sackett 1985). These kinds of effects of predation or parasitism are straightforward, but there are other more subtle effects of predators and parasites, such as 'apparent competition', in which a shared enemy produces effects on prey that mimic effects of interspecific competition (Holt & Lawton 1994).

Aedes albopictus

Apparent competition

Apparent competition caused by shared parasites is an alternative hypothesis for the mechanism of displacement of North American *Aedes aegypti* by invading *Aedes albopictus*. *Aedes* mosquitoes typically harbor protozoan parasites in the genus *Ascogregarina*, and the species that parasitizes *Aedes albopictus* [*Ascogregarina taiwanensis* (Lien & Levine)] can infect *Aedes aegypti*, and can, under some circumstances, cause high mortality of *Aedes aegypti* (Munstermann & Wesson 1990; Blackmore *et al.* 1995). *Ascogregarina culicis* (Ross), which parasitizes *Aedes aegypti*, does not infect *Aedes albopictus*. Thus, these parasites have asymmetrical negative effects on their hosts that could cause declines of *Aedes aegypti* as observed in North America. However, *Aedes albopictus* has an advantage over *Aedes aegypti* even when there is virtually no parasitism of *Aedes aegypti* (Juliano 1998). Further, parasitism of *Aedes aegypti* by *Ascogregarina taiwanensis* is relatively rare in nature, and mortality of *Aedes aegypti* induced by *Ascogregarina taiwanensis* at typical intensities of parasitism is approximately equal to that of *Aedes albopictus* (Garcia *et al.* 1994). Thus, apparent competition

Table 2 Synopsis of invasive and non-native mosquitoes (excluding *Aedes albopictus*) for which ecological processes are postulated to produce effects on invasion success and impact

Species (references)	Location and date of introduction (status)	Possible ecological processes (references)
Aedes aegypti (Christophers 1960; Tabachnick 1991; Lounibos 2002)	Southern North America 16–17th centuries (invasive, but reduced in distribution as introduction of *Aedes albopictus*)	Interspecific competition: *Aedes aegypti* is superior in larval competition to *Ochlerotatus triseriatus* (Ho *et al.* 1989) and may have displaced *O. triseriatus* in man-made containers in domestic areas. Predation: *Aedes aegypti* is more vulnerable to predation by *Toxorhynchites rutilus* than is *O. triseriatus* (Grill & Juliano 1996), and abundance of *T. rutilus* in containers in wooded areas may have limited invasion success of *Aedes aegypti* in these habitats
Aedes aegypti (Christophers 1960; Tabachnick 1991; Lounibos 2002)	Southeast Asia 19–20th centuries (invasive)	Interspecific competition: Declines of *Aedes albopictus* in tropical urban areas may have been caused by invasion of *Aedes aegypti* (Chan *et al.* 1971; Sucharit *et al.* 1978)
Culex pipiens (Vinogradova 2000; Lounibos 2002)	North America (16–17th centuries; invasive)	Interspecific competition: Absence of competitors at the time of invasion may have facilitated colonization of urban containers. More recently, competition with invading *Aedes albopictus* may impact *C. pipiens* in these habitats (Carrieri *et al.* 2003; Costanzo *et al.* 2005)
Culex quinquefasciatus (Weinstein *et al.* 1997)	New Zealand, Hawaii, 19th century (invasive)	Absence of competitors and predators: This may have contributed to invasive success in container habitats (Weinstein *et al.* 1997)
Culex quinquefasciatus	Australia 19th century (invasive)	Interspecific competition, or apparent competition via a gut symbiotic fungus: Asymmetrical interactions with tadpoles may have limited invasive success in pond habitats (Mokany & Shine 2003a,b,c)
Culex quinquefasciatus (Vinogradova 2000)	North America 19th century (invasive)	Interspecific competition: Superiority in interspecific competition with native *Culex* may have contributed to declines of *C. tarsalis* in California (Smith *et al.* 1995)
Anopheles gambiae complex (Soper & Wilson 1943)	Brazil, 1930s (invasive, but eradicated in 1941)	Intraguild predation: Last instar larvae of this complex are facultatively predaceous on smaller *Anopheles* larvae (Koenraadt & Takken 2003; Koenraadt *et al.* 2004), and thus have the potential to impact native *Anopheles* via intraguild predation. Interspecific competition: Absence of competitors may have facilitated invasion of man-made habitats
Ochlerotatus bahamensis (O'Meara *et al.* 1989, 1995a)	South Florida (non-native)	Interspecific competition: This with previously introduced *Aedes albopictus* may limit invasion success of *Ochlerotatus bahamensis*
Ochlerotatus japonicus (Andreadis *et al.* 2001)	Eastern North America (invasive)	Interspecific competition: This with invasive *Ochlerotatus atropalpus* and native *O. triseriatus* may limit invasion success of *Ochlerotatus japonicus*

via *Ascogregarina taiwanensis* may contribute to the declines of *Aedes aegypti*, but does not seem to be necessary for the negative effect of invading *Aedes albopictus* on *Aedes aegypti*.

Intraguild predation

Intraguild predation may limit invasion of *A. albopictus* into habitats dominated by *O. triseriatus*, which has fourth instar larvae that are more likely to prey upon newly hatched larvae of conspecifics, *A. albopictus*, or *A. aegypti*, and first instar larvae that are less vulnerable to such intraguild predation (Edgerly *et al.* 1999). In temperate regions, *O. triseriatus* hatches earlier in the year than does *A. albopictus* (Teng & Apperson 2000), so that this asymmetry in intraguild predation could favour coexistence of *O. triseriatus* and *A. albopictus*, despite the latter's superiority in resource competition (Novak *et al.* 1993; Teng & Apperson 2000;

Aliabadi & Juliano 2002, S. A. Juliano, unpublished data). This hypothesis remains untested and speculative.

Parasitism

Parasitism by gregarines may affect the interaction of *Aedes albopictus* and *O. triseriatus*. The gregarine parasites of *O. triseriatus* and *Aedes albopictus* [*Ascogregarina barretti* (Vavra) and *Ascogregarina taiwanensis*, respectively] cannot successfully infect each other's hosts, so apparent competition is unlikely. When *Aedes albopictus* invades a new geographic area, parasitism by *Ascogregarina taiwanensis* is low in the new area for about 2 years following colonization (Munstermann & Wesson 1990; Blackmore *et al.* 1995; Fukuda *et al.* 1997; Aliabadi & Juliano 2002). Unparasitized *Aedes albopictus* larvae have slightly, but significantly, greater negative effect on survivorship of competing *O. triseriatus* larvae (i.e. parasitism reduces competitive ability), and also have more rapid development, than do parasitized *Aedes albopictus* (Aliabadi & Juliano 2002). Thus, escape from its parasite during the initial phases of colonization of a new site may make *Aedes albopictus* more competitive and yield increased population growth rate, both of which would improve its ability to become established at a site (Aliabadi & Juliano 2002). Because parasitism rates by *Ascogregarina taiwanensis* increase following colonization, these effects may not contribute to long-term impacts of *Aedes albopictus* on the invaded community.

Predation

Predation is a prominent feature of tree holes and tires in forested areas of the southern USA. The predators *Toxorhynchites rutilus* (Coquillet) and *Corethrella appendiculata* Grabham produce strong top-down effects on these communities, which are dominated by *O. triseriatus* after abundances of predators and other mosquito species are reduced by drought (Bradshaw & Holzapfel 1983, 1985; Lounibos 1983, 1985). The failure of *A. albopictus* to dominate in these habitats suggests a prominent role for predation by native species in limiting invasions (Lounibos *et al.* 2001). Laboratory tests show that *A. albopictus* is more vulnerable to predation by these species (Lounibos *et al.* 2001; Griswold & Lounibos 2005a). One mechanism contributing to this difference is behavioural responses to water-borne cues from predation. *Ochlerotatus triseriatus* shows reduced movement and foraging, which is associated with reduced risk of predation, in response to water-borne cues from *T. rutilus* predation, whereas *A. albopictus* does not show these behavioural changes (Kesavaraju & Juliano 2004).

Other invasive mosquitoes

As with competition, data on the role of predation in other mosquito invasions are rare (Table 2). One intriguing case is the potential role of intraguild predation by invasive members of the *Anopheles gambiae* complex (Table 2). Field study of this question is no longer possible, but laboratory comparisons of predaceous tendencies of *Anopheles gambiae* complex and Brazilian *Anopheles* could yield data on the role of intraguild predation in this invasion.

Modelling combined effects of predation and competition

This review has shown that *A. albopictus* is a superior competitor to *O. triseriatus* (Livdahl & Willey 1991; Novak *et al.* 1993; Teng & Apperson 2000; Aliabadi & Juliano 2002) and that *A. albopictus* is more vulnerable to predation by *T. rutilus* (Kesavaraju & Juliano 2004) and by *C. appendiculata* (Griswold & Lounibos 2005a), which can foster coexistence of *A. albopictus* and *O. triseriatus* by selective predation on the competitively dominant invasive species (Griswold & Lounibos 2005a,b). These results suggest that a trade-off between competitive ability and vulnerability to predation may affect invasion success of *A. albopictus* or the potential for coexistence of *A. albopictus* and *O. triseriatus*.

To understand the potential combined effects of interspecific competition and predation in the invasion of *A. albopictus*, models of keystone predation and resource competition (Leibold 1996) can be adapted to invasions of container systems (Fig. 1). Although we describe this model for invasion of tree hole systems by *A. albopictus*, this model could describe the invasions of other prey mosquitoes, assuming relevant predators are present. For tree hole systems, we identify the predator as *T. rutilus*, although it should be applicable to other predators (e.g. *C. appendiculata*). In this model, developed using STELLA® RESEARCH v. 5.1.1, a population of micro-organisms (M) grows on a substrate (C) that enters the system from outside (e.g. plant detritus, stem flow). Micro-organism resource consumption is modelled as a type 2 functional response (Juliano 2001) to substrate abundance (Fig. 1), with a maximal feeding rate (F_M) and a half-saturation constant (K_M). Micro-organisms are in turn a shared resource for two mosquito species, a resident (i.e. *O. triseriatus*) and an invader (i.e. *A. albopictus*) that compete for this resource. Consumption of the micro-organisms also follows a type 2 functional response with two parameters each for resident and invader: maximum consumption rate (F_R and F_I, respectively) and half saturation constant (K_R and K_I, respectively). Population growth of the mosquitoes is a function of feeding rate and conversion efficiency (c_R and c_I, respectively). In this model, interspecific competition occurs only via the shared micro-organism resource. Competitive superiority is determined by the values of half saturation constant (Ks) for the competitors, with the lower K (i.e. able to feed successfully at low food availability) resulting in greater competitive ability (see Grover 1997 for a thorough development of theory behind this statement).

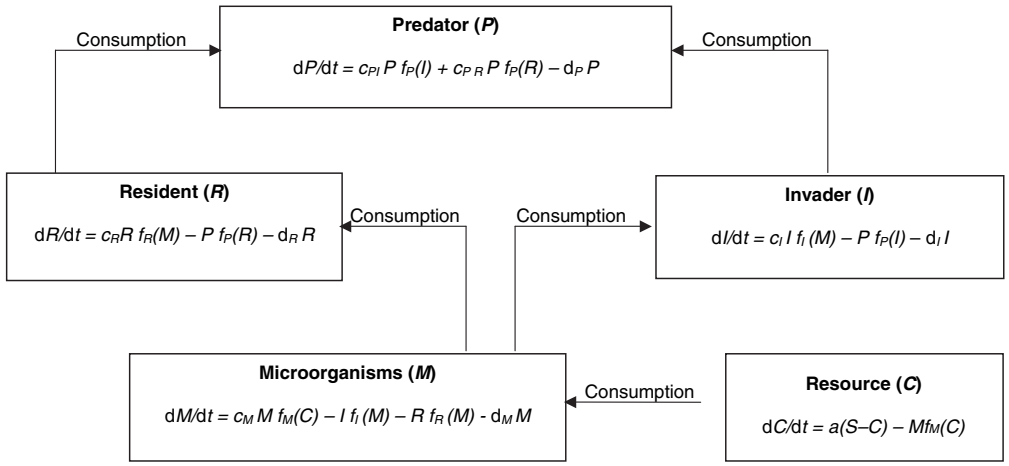

Figure 1 Model of predation after invasion by a superior competitor (I) into a community consisting of a resident prey (R), a predator (P), and micro-organisms (M). This model is an extension of that of Leibold (1996), adding a lower trophic level (M) that is a resource for the competitors, and incorporating type 2 functional responses for competing prey (R, I), P and M. Conversion efficiencies indicate the rate at which consumed food is converted into growth for micro-organisms (c_M), invader (c_I), resident (c_R), and predator feeding on invader (c_{PI}) and resident (c_{PR}). Feeding rates of micro-organisms feeding on the resource [$f_M(C)$], invader and resident feeding on micro-organisms [$f_I(M)$ and $f_R(M)$, respectively], and predator feeding on invader [$f_P(I)$] and resident [$f_P(R)$] are all hyperbolic functions of the general form: $f(X) = FX/(K + X)$, where $X =$ food abundance, $F =$ maximum feeding rate and $K =$ food abundance yielding one half maximum feeding rate. The two species functional responses for the predator feeding on resident and invader are $f(R) = F_{PR}R/(R + K_{PR} + I K_{PR}/K_{PI})$ and $f(I) = F_{PI}I/(I + K_{PI} + R K_{PI}/K_{PR})$, respectively. Lower Ks result in greater competitive ability for the consumer (i.e. ability to feed at low food availability) and greater vulnerability for the prey. Death rates (d_P, d_R, d_I, d_M) for each species are density-independent. Resources (C) for micro-organisms (e.g. plant detritus) become available at a rate logistically dependent on their abundance, with a maximum availability of S (supply).

These mosquitoes are in turn eaten by a predator (i.e. *T. rutilus*), with predator feeding a two-prey type 2 functional response with maximal feeding rate (F_{PR} and F_{PI}) and half saturation constant (K_{PR} and K_{PI}) for each prey species. In this context, values of K_P for the predator determine the relative vulnerabilities of the prey to predation, with lower K_P yielding greater prey vulnerability (i.e. the predator can find and eat prey even when they are scarce).

Simulations focused on the effects of vulnerability to predation (K_{PI}) and competitive ability (K_I) of the invader, and on overall productivity of the environment (as indicated by S, the maximum nutrient availability). We are specifically interested in the conditions under which a predator can serve as a barrier to invasion, and under which the presence of a predator can result in stable coexistence of the invader and the resident prey. We tested effects of relative vulnerability of the invading mosquito (K_{PI}) across a productivity (S) gradient, and when the invader has a large or a small competitive advantage over the resident (i.e. K_I much less than K_R vs. K_I slightly less than K_R, respectively). The invader was always the superior competitor. All other parameters were held constant, and parameters for the two prey mosquitoes (ds, cs, c_Ps, F_Ps, and Fs) were equal so that death rates, conversion efficiencies for food, nutritional value to the predator and maximal feeding rates are all the same for the resident and the invader.

In the first set of simulations, the invader has a strong competitive advantage (i.e. $K_I \ll K_R$) over the resident. In the absence of the predator, invasion always results in competitive exclusion of the resident. Further, the invader is always more vulnerable to predation ($K_{PI} \ll K_{PR}$). With the predator present, the outcome of the invasion depends on the invader's relative vulnerability to predation (horizontal axis, Fig. 2a). When the invader has relatively low vulnerability to predation (left in Fig. 2a), it always excludes the resident species, just as it would in the absence of predation. Further, when productivity of the system is low and the invader has low vulnerability to predation (lower left, Fig. 2a), the invader population goes through stable oscillations, and the predator population goes through expanding oscillations resulting in predator extinction following invasion, and extinction of the resident. When the invader is highly vulnerable to predation (right in Fig. 2a), the presence of a predator acts as a barrier to invasion by the superior competitor, particularly at high productivity (Fig. 2a, upper right). Between these extremes are values of predator K_{PR} and S that result in stable coexistence of the three species (Fig. 2a, shaded region). Under these conditions, the predator would foster coexistence of the invader and resident via a keystone predator effect. A greater range of conditions can permit coexistence (i.e. the width of the shaded area in Fig. 2a is greater) when productivity is lower

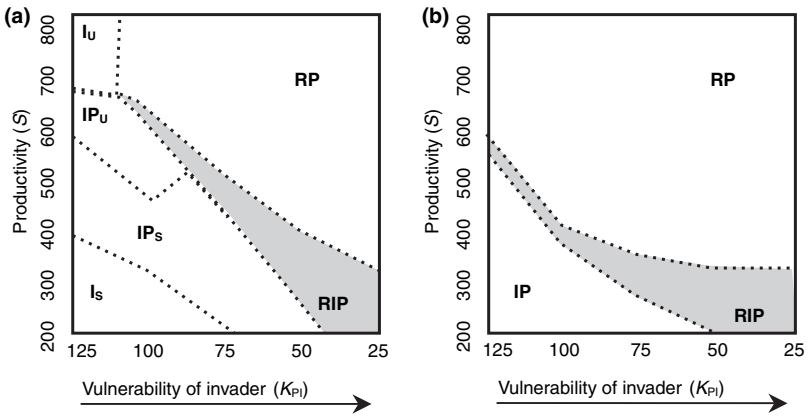

Figure 2 Simulations of invasion of a stable predator–prey system by a superior competitor, illustrating the sensitivity of the outcome to the invader's vulnerability to predation (increasing vulnerability with decreasing K_{PI}) and environmental productivity (S), the maximal resource availability for the micro-organism population. Simulations ran for 30 000 time steps with the invader invading at time 2000. Parameters are in arbitrary units so results only illustrate the qualitative trends expected in this system. Letters on the graph indicate species combinations attaining stable coexistence (I = invader, R = resident, P = predator, subscript S = stable oscillations, subscript U = unstable expanding oscillations; e.g., RP = resident + predator). Shaded regions indicate combinations of K_{PI} and S where the presence of the predator fosters coexistence of competing resident and invader via a keystone predator effect. (a) Competitive advantage of invader is large ($K_I = 100$, $K_R = 600$). (b) Competitive advantage of the invader is small ($K_I = 300$, $K_R = 600$).

and vulnerability to predation of the invader higher (lower right, Fig. 2a). This result may seem counterintuitive, but it emphasizes that coexistence of competitors is more likely when they are differentially affected and limited by their environment. In less productive environments, with high vulnerability to predation, the invading superior competitor would be relatively free from resource limitation and effects of competition, and almost exclusively limited by predation. Similarly, the resident poorer competitor would be limited almost totally by resource competition, and relatively unaffected by the predator, which disproportionately attacks (and benefits from) the invader.

The second set of simulations, in which the competitive advantage of the invader is less (Fig. 2b), also shows that predator-mediated coexistence is more likely when the invader is more vulnerable to predation and when the environment is less productive (Fig. 2b, lower right). When the competitive advantage of the invader is lower, the range of conditions under which the predator acts as a barrier to invasion encompasses a greater proportion of the range of simulated parameters (i.e. the region labelled RP is relatively larger in Fig. 2b than in Fig. 2a). When competitive advantage of the invader is smaller the outcomes of the invasion are less likely to include unstable (expanding) oscillations (Fig. 2b) at least in the range of S and K_{PI} used in these simulations. When the invader is highly effective at foraging for the microbial resource (i.e. Fig. 2a), there is a strong tendency for populations to oscillate, and this often destabilizes the invaded system, particularly as the invader's vulnerability to the predator decreases (towards the left, Fig. 2a). Under these conditions, as productivity increases, the amplitude of population oscillations for all members of the community increases with invasion, and stochastic extinctions occur, sometimes of all members of the community.

This model predicts that productivity of the environment should affect whether competitive exclusion of the resident (at low productivity), coexistence (at intermediate productivity), or failure of the invasion (at high productivity) should be the result of this invasion. Productivity for container systems would be directly related to the input rate of detritus and nutrients in stem flow. There is some evidence for greater productivity of tree holes compared with man-made containers in forested habitats (e.g. Livdahl & Willey 1991; Aspbury & Juliano 1998), suggesting that invasion success of *A. albopictus* and displacement of *O. triseriatus* should be more likely in man-made containers, which is consistent with observations in Florida (Lounibos *et al.* 2001). Empirical determination of the parameters of this model (mainly half saturation constants for predator and prey, and environmental productivity) would provide a means of making quantitative predictions about whether exclusion, coexistence, or failed invasion is expected in predator-dominated habitats. The model also predicts successful invasion should be less common in predator-dominated habitats, and this prediction should be tested using field observations and experiments.

Climatic limitations on invasions by *Aedes albopictus*

There is at least one case in which *A. albopictus* had a competitive advantage over a resident species in laboratory experiments, yet introduction of *A. albopictus* (which was

intentional) failed to result in an established population. On islands in the southern Pacific Ocean, *A. polynesiensis* Marks is the primary vector of *Wuchereria bancrofti*, which causes lymphatic filariasis in humans (Rozeboom 1971; Rosen *et al.* 1976). Cage experiments suggested that *A. albopictus*, which cannot transmit *W. bancrofti*, displaces *A. polynesiensis* in <1 year, probably via interspecific competition among larvae for food, and among adults via satyrization (Rozeboom 1971). Despite this laboratory outcome, and the demonstrated success of *A. albopictus* as an invader of other parts of the world, deliberate introduction of *A. albopictus* to an atoll in the Pacific with *A. polynesiensis* failed to establish populations of *A. albopictus* (Rosen *et al.* 1976). Because this investigation focused on the presumed impact of introduced *A. albopictus* on resident *A. polynesiensis*, there were no control introductions of *A. albopictus* without *A. polynesiensis*, hence it is unknown whether competition from the resident inhibited colonization by the introduced species. Alternative explanations for the failed introduction include the unsuitably dry, hot climate on this island (Rosen *et al.* 1976; see also Alto & Juliano 2001; Juliano *et al.* 2002; K. S. Costanzo, B. Kesavaraju and S. A. Juliano, 2005, personal communication), reliance on a single release period, and dispersal by *A. albopictus* adults off this isolated atoll and into the vast dispersal sink of the ocean (Rosen *et al.* 1976). This case illustrates how difficult it is to predict whether a non-native species will become invasive, even when there is some background information, and even when the process of introduction is controlled. Further, this field trial shows the limitations of laboratory studies like those of Rozeboom (1971) for predicting invasion outcomes.

Climate limits the ranges of most invasive species, and Nawrocki & Hawley (1987) accurately predicted the northern limits of the distribution of *A. albopictus* in North America based on the native range of the species in Japan, where North American colonists originated (Hawley *et al.* 1987). Cold-hardiness in temperate populations of *A. albopictus* results from egg diapause, which is absent in tropical populations of this species (Hawley *et al.* 1987, 1989). However, expression of diapause evolved relatively rapid during the spread of invasive populations (Lounibos *et al.* 2003a). Incidence of this trait decreased as temperate *A. albopictus* spread into warmer, southerly latitudes of the USA, and diapause appeared at low frequencies in tropical *A. albopictus* that spread southward from tropical to temperate regions of southern Brazil (Lounibos *et al.* 2003a). Diapause responses at similar (N vs. S) latitudes in Brazil and the USA have not converged, perhaps because of genetic constraints of different founder populations (tropical vs. temperate). Life history traits of size and age at pupation of North American *A. albopictus* may also have evolved rapidly, with data suggesting latitudinal differentiation at about 16 years post-introduction (P. Armbruster & J. E. Conn, in preparation). There is a non-significant trend towards increased size at pupation and decreased age at pupation for females from populations from more northern latitudes, suggesting counter gradient selection on growth and development rates of larvae (P. Armbruster & J. E. Conn, in preparation).

The interaction of abiotic and biotic factors in determining invasion success was suggested by field experiments demonstrating that the outcome of interspecific competition between *A. albopictus* and *A. aegypti* larvae was independent of whether the experiment was conducted at a site of coexistence or of exclusion of *A. aegypti* (Juliano *et al.* 2004). This result implies that differences in the aquatic environments at these types of sites do not account for the heterogeneous patterns of exclusion of *A. aegypti* or its coexistence with *A. albopictus* in south Florida cemeteries (Juliano *et al.* 2004). Cemetery-specific microclimates, which contribute to differential egg survivorship (Juliano *et al.* 2002; K. S. Costanzo, B. Kesavaraju and S. A. Juliano, 2005, personal communication; L. P. Lounibos, unpublished data) are believed to shift competitive advantage and to determine whether coexistence or exclusion is the outcome of invasion. Thus, climate impacts life cycle stages that are not involved in competition, and these impacts can determine invasion success, effects of invaders and community composition following invasion.

DISEASE OUTBREAKS ASSOCIATED WITH INVASIVE MOSQUITOES

Introduced mosquitoes may affect human health by (i) simultaneous introduction of a novel vector and novel pathogen, (ii) acquisition by an introduced vector of a native pathogen, or (iii) independent introductions of a novel vector and a novel pathogen. Simultaneous introduction of a novel vector and a novel pathogen may be sufficient to create a new public health threat, with potential to cause large outbreaks of disease, particularly because the host population will likely have limited herd immunity (=reduced probability of epidemic transmission of a disease, even among susceptible individuals, which arises because of the presence of a substantial proportion of immune individuals within a population). If an invasive vector takes on a role in an existing disease transmission cycle, it changes (presumably for the worse) the nature of an existing public health threat. In such cases, the risk to public health derives not from the novelty of the disease, but only from an increase in the transmission rate because of the efficiency of the invasive vector. If an invasive vector acquires, sometime after establishment, an association with an independently introduced pathogen, susceptible hosts are exposed to a novel pathogen with a new vector. This situation may be particularly prone to unpredictable disease dynamics. All three paths to mosquito-borne disease outbreaks have occurred (Table 3).

Table 3 Human and animal disease outbreaks associated with invasive mosquitoes

Disease	Location	Dates of epidemics	Reference	Invasive mosquito	Source of pathogen
Yellow fever	Americas	16–20th centuries	Tabachnick (1991)	*Aedes aegypti*	Introduced with the mosquito
Dengue	Americas	17–20th centuries	Gubler (1997)	*Aedes aegypti*	Introduced with the mosquito
Dengue	Asia	19–20th centuries	Gubler (1997)	*Aedes aegypti*	Native
Dengue	Hawaii	2001	Mortality and Morbidity Weekly Reports (MMWR) (2002)	*Aedes albopictus*	Introduced after the mosquito
West Nile encephalitis	North America	1999–present	Kramer & Bernard (2001)	*Culex pipiens**	Introduced after the mosquitoes
Avian malaria	Hawaii	20th century	Van Riper *et al.* (1986)	*Culex quinquefasciatus**	Introduced after the mosquito
Human malaria	Brazil	1930–1940	Soper & Wilson (1943)	*Anopheles gambiae* complex†	Native
Human malaria	Mauritius	1866–67	Ross (1911)	*Anopheles gambiae* complex	Introduced before the mosquito
Human malaria	Peru	1992–1999	Lounibos (2002)	*Anopheles darlingi*	Native

*Species of the *C. pipiens* complex.
†Only includes the anthropophilic species of the complex, *Anopheles gambiae s.s.* and *Anopheles arabiensis*.

Simultaneous introduction of vector and pathogen

Simultaneous introduction of vector and pathogen appears possible in only two disease outbreaks, and both involve historical introductions of *Aedes aegypti* and associated viruses. Yellow fever originated in Africa and appears to have been spread initially by the slave trade of the 16–17th centuries (Lounibos 2002). Outbreaks of yellow fever occurred in many North American cities, as far north as New York City, and it is virtually certain that these outbreaks occurred when both the vector and virus arrived via ship. *Aedes aegypti* is a tropical mosquito, lacking diapause (Christophers 1960), hence it is unlikely that this mosquito became permanently established in these northern cities. Introduction of dengue to South America may also have occurred with the introduction of *A. aegypti* in the 16–17th centuries, based on reports of 'Dengue like illnesses' in the 17th century (Gubler 1997). This implies a West African origin of introduced dengue. Because these simultaneous introductions were associated with ship transport of enslaved Africans, they may present a special case of simultaneous introduction of vector, pathogen and a substantial population of infected hosts. The limited data suggest this situation has not occurred with recent mosquito introductions.

Introduced vectors transmitting native pathogens

Introduced vectors transmitting native pathogens appear to have caused outbreaks in two very different disease systems. *Aedes aegypti* is the major vector of urban dengue in tropical Asia (Eldridge *et al.* 2000, Table 2), where dengue is likely native, with all four serotypes of this virus circulating in sylvan cycles in Southeast Asia (Eldridge *et al.* 2000). Thus, since its invasion of Asia in the late 19th century, *A. aegypti* became the primary vector of a resident pathogen. Thus, *A. aegypti* provides examples of both enhanced transmission of a resident disease (dengue in Asia) and transmission of a disease introduced with the vector (yellow fever and dengue in the Americas). A similar case involves invading *Anopheles gambiae* complex in Brazil and resident pathogens causing malaria (*Plasmodium falciparum*, *P. vivax*; Lounibos 2002). This case is unusual in that *Anopheles gambiae* had a long association with these *Plasmodium* species in its native range (Lounibos 2002), hence the pathogens were not 'new' to the vector. In Brazil, native *Anopheles* species had been responsible for transmitting malaria, but arrival of a new, more efficient vector resulted in epidemics of the disease.

Independent introductions of vectors and pathogens

Independent introductions of vectors and pathogens that have associations in their native ranges appear to be the most common cause of disease outbreaks (Table 2). For *A. albopictus* in Hawaii in 2001, it seems likely that dengue virus arrived in Hawaii (probably with infected humans; the viral strain was identical to isolates from Tahiti) sometime after the vector was established (Mortality and Morbidity Weekly Reports (MMWR) 2002). Thus, this case represents

a two-step relocation of a vector–pathogen system from Asia to Hawaii. Members of the *C. pipiens* complex are major vectors of WNV in Eurasia, and appear to have taken on this same role in North America where the pathogen was introduced long after the mosquito (Fonseca *et al.* 2004). Fonseca *et al.* (2004) proposed that hybridization of two Old World taxa (bird-biting *C. pipiens* and mammal-biting *C. molestus* – the latter which may be a race, subspecies, or separate species) in North America resulted in populations that readily take blood from both kinds of hosts, thus functioning as both enzootic and bridge vectors of WNV (Fonseca *et al.* 2004). The importance of vector hybrids in the North American WNV life cycle, which includes other vector species, remains speculative. *Culex quinquefasciatus* became established in the Hawaiian Islands in the early 19th century, well before the arrival of avian malaria (Van Riper *et al.* 1986). Outbreaks of this disease among native Hawaiian birds have had serious consequences for conservation of endemic avian species, particularly at low elevations (Van Riper *et al.* 1986). Malaria was almost certainly present among Indian railway workers who immigrated to Mauritius prior to the arrival of *Anopheles gambiae* (*s.l.*) by ship from the African mainland or Madagascar (Ross 1911).

WHAT WE LEARN FROM INVASIVE MOSQUITOES

The interactions of invasive species vary in space and time and depend on local conditions and their interacting species. Even for the best-studied invasive mosquito species, *A. albopictus*, there is no single answer to the question of which ecological processes predominate. Effects of interspecific competition are evident in interactions with *A. aegypti* and to a lesser extent *C. pipiens*, but in other invaded systems, the role of predation as a barrier to invasion seems to be paramount. Climatic limitation is evident, but so is evolution of locally adapted life history traits that overcome climatic limitation. Despite the absence of a single dominant pattern in the interactions of this invasive species, the extensive investigations of the ecology of *A. albopictus* as an invasive species provide us with a guide to the investigation of the mechanisms controlling impacts of and barriers to invasions, not just for other mosquitoes, but more generally for any animal species. For *A. albopictus*, multiple hypotheses accounting for observed effects on resident species and communities have been tested, and, equally important, similar hypotheses have been tested in the field in multiple locations, with multiple populations, and with reference to multiple interacting native species. These diverse investigations of *A. albopictus* have yielded a clear understanding of the mechanisms acting during invasion, and how they vary. The extent of ecological investigations of *A. albopictus* is further justified by its potential for impacts on human health (e.g. Hawley 1988).

Invasion by *Aedes albopictus* illustrates the importance of monitoring the process from its early phases until it has stabilized for a thorough understanding of the dynamics of effects of invaders. The dynamics of invader and resident populations and communities are likely to be obscured, at best, or obliterated by the passage of time, and in the case of mosquitoes this makes it now impossible to recover information on interactions that took place during historical invasions by *Anopheles gambiae* complex in Brazil or Mauritius, *Aedes aegypti* in the Americas and Asia, and members of the *C. pipiens* complex worldwide (Lounibos 2002). Monitoring alone is insufficient. Experimental tests of alternative hypotheses for mechanisms producing effects of invaders on native populations and communities, for barriers to successful invasion, and in the case of invasive mosquitoes, for effects on transmission of human disease, are necessary.

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