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Where Vectors Collide: The Importance of Mechanisms Shaping the Realized Niche for Modeling Ranges of Invasive *Aedes* Mosquitoes

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Abstract

The vector mosquitoes *Aedes aegypti* (L.), native to Africa, and *Aedes albopictus* (Skuse), native to Asia, are widespread invasives whose spatial distributions frequently overlap. Predictive models of their distributions are typically correlative rather than mechanistic, and based on only abiotic variables describing putative environmental requirements despite extensive evidence of competitive interactions leading to displacements. Here we review putative roles of competition contributing to distribution changes where the two species meet. The strongest evidence for competitive displacements comes from multiple examples of habitat segregation where the two species co-occur and massive reductions in the range and abundance of *A. aegypti* attributable to *A. albopictus* invasions in the southeastern U.S.A. and Bermuda (U.K). We summarize evidence to support the primacy of asymmetric reproductive interference, or satyrization, and larval resource competition, both favoring *A. albopictus*, as displacement mechanisms. Where evidence of satyrization or interspecific resource competition is weak, differences in local environments or alternative ecologies or behaviors of these *Aedes* spp. may explain local variation in the outcomes of invasions. Predictive distribution modeling for both these major disease vectors needs to incorporate species interactions between them as an important process that is likely to limit their realized niches and future distributions. Experimental tests of satyrization and resource competition are needed across the broad ranges of these species, as are models that incorporate both reproductive interference and resource competition to evaluate interaction strengths and mechanisms. These vectors exemplify how fundamental principles of community ecology may influence distributions of invasive species.

Keywords

Aedes aegypti; *Aedes albopictus*; resource competition; distribution modeling; reproductive interference; realized/fundamental niche

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Introduction

Theory in community ecology is central to understanding biological invasions, and the ecological niche of the organisms and the niche opportunities present in the invaded community are central to this theory (Shea & Chesson 2002). The concept of ecological niche has a long history in ecology and has been defined by different authors in varied ways (reviewed by Whitaker et al. 1973, Hutchinson 1978, Giller 1984, Chase & Leibold 2003, Cadotte 2006, Soberón 2007). The link between biological invasions and niche theory reflects the influence of Charles Elton on the field of ecology. Elton's (1958) monograph on invasions continues to foster both academic discussion and research about the processes involved in invasion biology (e.g., Richardson 2011), and his early conception of the niche (Elton 1927) continues to influence modern theory of the niche that is the basis for community ecology (Chase & Leibold 2003, Soberón 2007). One purpose of this synthesis is to highlight the importance of a mechanistic understanding of fundamental and realized niches for understanding invasions (Hutchinson 1957). The fundamental niche is the set of environmental conditions in which a species' population could persist in the absence of species interactions (Hutchinson 1957, Chase & Leibold 2003). In contrast, the realized niche is those environmental conditions in which a species' population persists despite the constraints imposed by interacting species including competitors (Hutchinson 1957) and predators (Chase & Leibold 2003). A second, related purpose of this synthesis is to emphasize the importance of species interactions and the impacts organisms have on one another for understanding both success and effects of invasive species. Throughout, we rely on newer, synthetic theory of the ecological niche that treats quantitatively both species environmental needs (niche in the sense of Grinnell), which largely consist of abiotic conditions that define suitable environments for that species and species impacts on mostly biotic elements of their environments (niche in the sense of Elton) (Soberón 2007). Those impacts are central to understanding species interactions and coexistence of interacting species in nature, and figure prominently in modern theory of the ecological niche (Chase & Leibold 2003), which combines elements of both Grinnellian and Eltonian niche concepts (Soberón 2007).

Environmental niche modeling or species distribution modeling (terms used synonymously) is commonly used to predict likely geographic distributions of actually or potentially introduced nonnative species (Elith & Leathwick 2009), including mosquitoes (e.g., Kraemer et al. 2015). The same statistical tools and approaches are also used to predict future geographic ranges under climate change scenarios (Elith & Leathwick 2009). This approach predicts potential geographic distributions based on statistical models with predictor variables (e.g., climate variables, vegetation, other macro-habitat features, land use, etc.) based on records from focal species' native range or current geographic distribution. Rarely does environmental niche modeling include any measure of interactions with predators, competitors, and mutualists among the predictors. Because current distribution data usually confound abiotic variables and occurrence of interacting species, and because the list of potentially interacting species is both long and likely incomplete, most authors have used abiotic predictors alone (Elith & Leathwick 2009, Wisz et al. 2013). This leads to an important and difficult question: Does environmental niche modeling describe the fundamental niche or the realized niche of the focal species? At one level it seems the distribution data must describe the realized niche, because they are data on where a species actually occurs (e.g., in its native range), presumably after it interacts with other species in the native range (Vázquez 2006, Wisz et al. 2013). At another level, the predictors used in the model (virtually all abiotic) are more consistent with the concept of the fundamental niche (and the Grinnellian niche), and species interactions and their effects on the focal species are totally absent from the statistical model. This absence of species interactions from environmental niche models is often cited as a problem limiting the utility of the approach (Davis et al. 1998, Kearney 2006, Elith & Leathwick 2009, Wisz et al. 2013). It may be argued that species interactions are implicitly included in environmental niche modeling, to the extent that those interactions have influenced current distributions in the native range and to the extent that the abiotic environmental predictors are predictive of the distribution of any interacting species. This argument focuses on the real difficulty with environmental niche models: They are correlative and lack mechanisms (Davis et al. 1998, Kearney 2006, Kearney & Porter 2009, Elith & Leathwick 2009, Pellisier et al. 2012). This is obviously true for effects of species interactions and is true for any predictive ability of abiotic variables. Like simpler multiple regression approaches, environmental niche models are designed to be predictive, and not to describe cause and effect.

The lack of mechanistic inclusion of species interactions likely means that predictive ability of the models for the ranges of invasive species entering novel communities is uncertain at best, and wrong at worst. Consider this thought experiment: Build a predictive model for the distribution of a focal species in its native range, using geographic occurrence data and abiotic predictors. Across that native range, there are competitors and predators that impact the distribution and abundance of the focal species, but the correlative model is built without including these interacting species as predictors. Now imagine using that model to predict the range of the focal species as an invader in a new area. Table 1's column for interacting species 'Present; not used as predictors' gives a sense of what might result. The model would only provide an accurate prediction of the invasive range when the same interacting species (or one that is functionally equivalent) is present (Table 1, Cell 3). If no such similar species is present in the nonnative range, then the invasive range is likely to be much greater than predicted (Table 1, Cell 1). When predators affect the native range, this situation describes enemy release, a common hypothesis for success and impact of invaders (Colautti et al. 2004). When competitors affect the native range, this situation describes the empty niche hypothesis, another common hypothesis for success and impact of an invader, which can be traced back to Elton (Elton 1958, Mitchell et al. 2006, MacDougall et al. 2009). If instead, a functionally different interacting species is present in the nonnative range, the predicted invasive range is likely to be wrong in unpredictable ways (Table 1, Cell 5). In short, the realized niche in one environment, affected by one set of interacting species, is unlikely to be the same in a different environment, with a different set of interacting species (Vázquez 2006). Consider next building a model based only on physiological measures of tolerances and performance of focal species (the mechanistic model of the fundamental niche described by Kearney & Porter 2009), purposely excluding any effects of species interactions (Table 1, interacting species 'Absent or excluded from model'). This model is only likely to yield accurate predictions of the invasive range in the event no interacting species are present (Table 1, Cell 2). If instead the nonnative range is home to interacting species, the model overestimates the invasive range (Table 1, Cells 4, 6) which is actually limited by the biotic resistance of the resident community (Elton 1958, Mitchell et al. 2006). Thus for both types of models, only two rather unlikely scenarios will lead to accurate predictions of the invasive range of our focal species, and the reason is a failure to account for mechanistic interactions that are important parts of the niche biology of focal species.

Thus, we argue, as have others (Davis et al. 1998, Shea & Chesson 2002, Kearney 2006, Elith & Leathwick 2009, Wisz et al. 2013), that including effects of interacting species is vital for understanding invasions. We illustrate the complexity of this problem with a case study of two well-known and important invasive species that often meet and interact. Current invasive ranges of the world's two most invasive mosquito species, *Aedes aegypti* and *Aedes albopictus*, overlap extensively, especially in tropical and mild temperate regions. *Aedes aegypti*, native to Africa, were dispersed intercontinentally on sailing vessels between the 15th–19th centuries (Tabachnick 1991, Lounibos 2002). Major diasporas of *A. albopictus*, native to Asia, occurred mostly in the 20th century, facilitated by transport on container ships (Reiter 1988, Lounibos 2002). Diapause in the egg stage of temperate *A. albopictus*, which has favored the spread of this species into colder seasonal environments, is an adaptation (Urbanski et al. 2012) that does not occur in *A. aegypti*.

For this case study, we first use distributional data that show regional changes in relative abundances of one or the other species. We then interpret these distribution patterns in the context of known competitive interactions and displacement, and the ecology, behavior, and genetics of the individual species. Finally, we suggest that interactions between them could be a model for other, broadly invasive species that meet and influence one another's distributions outside and within their native ranges. Thus, beyond the epidemiological consequences of the distributions of these important vectors, these species represent one of the best examples of how fundamental principles of community ecology, particularly considerations of ecological niche, are central to understanding invasions (Shea & Chesson 2002)

Owing to their competence and importance in transmitting arboviruses of significant health concerns, currently dengue, chikungunya, and Zika, to humans, understanding the factors that control the ranges and abundances of these species is critical for evaluating health risks. Most range maps and projections for these species are based solely on environmental niche modeling using abiotic predictors for these species expanded to global (e.g. Benedict et al. 2007, Medley 2010, Kraemer et al. 2015, Ding et al. 2018) or regional and local scales (e.g., Rochlin et al. 2013, Hahn et al. 2016, Monaghan et al. 2016). Despite this, documented or strongly suspected interspecific competitive displacement of one or the other of these species has occurred where their distributions overlap (e.g., Gilotra et al. 1967, Craig 1993, Kaplan et al. 2010). Recent use of a range map of *A. aegypti* predicted by the environmental model of Kraemer et al. (2015) overstates Zika risk in Florida (Grubaugh et al 2017) because of this model's failure to account for competitive displacements that have reduced the distribution of this species in the southeastern USA (Lounibos et al. 2016).

Geographical Patterns

In Sympatry on Tropical Islands

The importance of islands for examining biogeographical patterns has been recognized since Darwin (MacArthur & Wilson 1973). Here we take advantage of mosquito surveillance information from islands or archipelagos where the two species have been sympatric, in some instances for >100 years, and that have been sampled over time, usually because of disease transmission by these invasive *Aedes*. Although interspecific competition has been inferred based on distribution changes, it has not been conclusively demonstrated in any of the five following examples.

Hawaiian Islands—Both *A. aegypti* and *A. albopictus* have been present for over a century in Hawaii, which has no native mosquito species (Winchester & Kapan 2003). Dengue in Honolulu was vectored by *A. aegypti* during the first decade of the 20th century, but in the subsequent decade this species was displaced by *A. albopictus*, which is now present on all islands of this archipelago (Winchester & Kapan 2003). Insecticides applied for mosquito control are believed to have facilitated local reductions of *A. aegypti*, both during displacement early in the 20th century and during WWII, when this species disappeared from the island of Oahu and the city of Hilo. Before the *A. aegypti* eradication campaign began in the USA, this species was present on only four islands but by 2002 was found only on the Big Island, especially on its drier, western side (Winchester & Kapan 2003).

Madagascar—Two extensive surveys of mosquito faunas allow for a comparison of *A. albopictus* and *A. aegypti* over time in Madagascar (Fontenille & Rodhain 1989, Raharimala et al. 2012), a comparatively old island, at least part of which is derived geologically from the African continent. It is not currently clear whether *A. aegypti* is indigenous to Madagascar, but *A. albopictus* is believed to have been introduced before 1900 during human migrations from SE Asia (Raharimala et al. 2012). Surveillance for the two species in 2009 reported decreases in the range and abundances of *A. aegypti*, both at sites with and without *A. albopictus*, compared to similar surveys in the 1980s (Raharimala et al. 2012). *Aedes aegypti* were more likely to be found in drier forested areas, which suggests that the feral subspecies *formosus* (McClelland 1968) might be the morph represented on Madagascar. By contrast, *A. albopictus* on Madagascar are comparatively more anthropophilic and were incriminated as the main vector of chikungunya virus on the island during Southwest Indian Ocean (SWIO) outbreaks of this arbovirus in 2006–09 (Vazeille et al. 2007, Ratsitorahina et al. 2008).

Reunion—Decreases in *A. aegypti* abundance relative to *A. albopictus* have also been reported for Reunion Island, an overseas department of France of relatively recent (4.5mya) geological age, located east of Madagascar (Bagny et al. 2009a). On this island immatures of *A. aegypti* are recovered primarily from rock pools and bamboo stumps in isolated ravines, whereas *A. albopictus* is widespread in both natural and artificial container habitats in rural and urban areas (Bagny et al. 2009a) and is the more anthropophilic of the two species (Delatte et al. 2010). Although both insecticide use and interspecific competition have been postulated as explanations of reductions in *A. aegypti* on Reunion (Bagny et al. 2009a), habitat degradation may also contribute to its imputed decline.

Seychelles—*Aedes albopictus* is common throughout much of this nation of 116 islands about one thousand miles east of the coast of Kenya. Upon last reconnaissance, *A. aegypti* was restricted to the capital city of Victoria on Mahé Island (Lambrecht 1971), a reduction in range from the 1940s, when it was also recorded from the opposite side of this island (Mattingly & Brown 1955). *Aedes aegypti* on the Seychelles appear to be more domestic than counterparts on SWIO islands, so its restriction to the most urbanized portion of this country conforms to the behavior of the domestic subspecies, *A. aegypti aegypti*, elsewhere in its native and invasive ranges.

Mayotte—Mayotte, politically a protectorate of France, is geographically part of the Comoros archipelago, located off the coast of East Africa in the Mozambique Channel. The establishment of *A. albopictus* around 2001 was purportedly associated with declines in *A. aegypti*, which subsequent surveys showed to be more prevalent than *A. albopictus* in rural habitats. (Bagny et al. 2009b), a reversal of the more common displacements of these species on habitat gradients (see below). Morphologically and behaviorally, *A. aegypti* on Mayotte appear to correspond to the feral subspecies *formosus* (Mattingly 1967, Bagny et al. 2009b). A recently described mosquito species known only from Mayotte, *Aedes pia*, is closely related to *A. aegypti* (Le Goff et al. 2013), but is not believed to undermine the conclusions of Bagny et al. (2009b) because *A. pia* is relatively uncommon (Le Goff et al. 2013).

Well Documented Competitive Displacements

Continental USA—The eastward and northward expansion of *A. albopictus* from its original establishment in Houston, Texas has been documented from state and county surveillance records (Moore 1999). Nearly simultaneously, reductions in abundance and distribution of *A. aegypti* were reported from four states in the southeastern USA (Hobbs et al. 1991, Mekuria et al. 1995, Nasci et al. 1989, O'Meara et al. 1995). By 1993, the range of *A. aegypti* was reduced in the Southeast to southern Florida and redoubts in the centers of major southern port cities, such as Houston and New Orleans (Craig 1993, O'Meara et al. 1995). Recent surveillance in Florida indicates that the reduced range and abundance of *A. aegypti* recognized by 1993 persisted through 2014 (Lounibos et al. 2016), although subtle changes were detected, suggesting limited local recoveries of this species in relation to *A. albopictus* (Lounibos et al. 2016, Hopperstad & Reiskind 2016).

Bermuda—*Aedes aegypti* was eradicated from the subtropical island of Bermuda (U.K.) in the 1960s but rediscovered there in 1997 (Kaplan et al. 2010). Upon recognition of the establishment of *A. albopictus* in 2000, surveillance for both species by trapping and identifying eggs laid in containers showed a rapid decline in abundance of *A. aegypti* concomitant with the rise in numbers of *A. albopictus* (Kaplan et al. 2010). Based on Lotka-Volterra models of competition, Kaplan et al. (2010) concluded that interspecific competition among larvae, by itself, was inadequate to explain the rapid decline and disappearance of *A. aegypti* on Bermuda following invasion by *A. albopictus*. Kaplan et al.'s (2010) estimates of carrying capacities (K) and competition coefficients (α) suggested that the two species were nearly equal as larval competitors. They argued that exclusion of *A. aegypti* would only be expected when *A. albopictus* had approached its carrying capacity. In fact, disappearance occurred at densities well below that density. Kaplan et al. (2010) suggested some additional impact of *A. albopictus* on *A. aegypti* must also have contributed to the latter's disappearance from the island.

Tropical Cities Where *A. albopictus* Has Been Displaced by *A. aegypti*

Phylogeographic and historical evidence supports that the invasion of *A. aegypti* into Asia did not occur until the 19th century, considerably later than the western expansion of this species into the Americas (Smith 1956, Tabachnick 1991). During its spread into cities of SE Asia, *A. aegypti* encountered native *A. albopictus*, which it displaced in Bangkok (Stanton 1920), Kuala Lumpur (Rudnick 1965), and Calcutta (Kolkata) (Gilotra et al. 1967); anecdotal information also supports urban displacements of *A. albopictus* in Manila and southern Taiwan (Gilotra et al. 1967). Distributions of these species in Calcutta in the 1960s (Gilotra et al. 1967) show patterns of habitat segregation similar to those described in the Americas decades later (e.g. Braks et al. 2003, Rey et al. 2006), where *A. aegypti* predominates in the absence of vegetation and *A. albopictus* in the presence of trees and shrubs (Table 2).

A more recent example of urban displacement occurred in the Colombian port of Leticia on the Amazon River, where invasive *A. albopictus* had been recognized in 1998 as established (Velez 1998). After *A. aegypti* re-invaded Leticia in 2009, it displaced *A. albopictus* to the periphery, outside of the borders of the concrete streets of this carefully planned riverine city (Carvajál 2013).

Species Distributions on Rural-Urban Gradients

Niche Compressions in Sympatry—Two separate studies have used aerial imagery to quantify patterns of habitat use by the two species in zones of sympatry in southern Florida. Sampling of these habitats with oviposition traps in three, non-contiguous counties confirmed that *A. aegypti* abundances were positively correlated to habitats associated with urbanization, such as buildings and pavement, while *A. albopictus* predominated in rural settings with vegetation (Rey et al. 2006). Similar patterns were confirmed from larval collections of the two species at tire shops and cemeteries elsewhere in southern Florida (Lounibos et al. 2016). These patterns are consistent with other reports of habitat segregation on urban-rural gradients in Rio de Janeiro (Braks et al. 2003), Gabon (Paupy et al. 2010), northern Thailand (Tsuda et al. 2006), Indonesia (Ishak et al. 1997), and Vietnam (Higa et al. 2010) (Table 2). However, a different pattern was observed on the French island of Mayotte, part of the Comoros archipelago, where larval collections of the two species in 2007 showed *A. albopictus* predominating in urban and suburban zones, especially in the dry season, and *A. aegypti* in rural habitats (Bagny et al. 2009b) (Table 2). A somewhat different pattern was observed by Leisnham & Juliano (2009), who found that within urban south Florida, *A. aegypti* attained greater relative abundance in urban residential neighborhoods, compared to cemeteries and industrial areas, where *A. albopictus* predominated. Locations of examples of habitat segregation and displacements between these species are shown in Figure 1.

Niche Expansions in Allopatry—In Guangzhou, China, *A. albopictus* are more productive in urban, than in suburban or rural, habitats, and have shorter larval developmental times, higher adult emergence rates, and longer lifespans in the urban settings (Li et al. 2014). Thus, in the absence of *A. aegypti*, the fundamental niche of *A. albopictus* has expanded to, and is facilitated by, urban habitats (Li et al. 2014). In southern USA, prior to the arrival of *A. albopictus*, the fundamental niche of *A. aegypti* included rural habitats (Morlan & Tinker 1965), which, after the invasion of *A. albopictus*, are uncommonly occupied by this species (Braks et al. 2003, Rey et al. 2006).

AIAI and Invasions by Container *Aedes*

Juliano and Lounibos (2016) described three behavioral traits of domestic *A. aegypti* in Africa that support the hypothesis that this form of the species is pre-adapted for invasion success, as predicted by the Anthropogenically Induced Adaptation to Invade (AIAI) hypothesis of Hufbauer et al. (2012). The three adult female behaviors noted were: (1) house entry (endophily); (2) the preference for oviposition in human-made domestic containers; (3) preference for blood-feeding from humans (Juliano & Lounibos 2016). Although tendencies toward domestication in *A. albopictus* were not discussed, Juliano and Lounibos (2016) noted the behavior of this species to occupy disturbed, forest-urban ecotonal habitats in both its native and invasive ranges, a pattern also present in the feral subspecies *A. aegypti formosus* in East Africa (Lounibos 1981). This suggests that as edge species, the feral forms of both species may have been pre-adapted to domestication, and thus to human transport and invasion success in human dominated landscapes, supporting AIAI (Hufbauer et al. 2012). World-wide colonization and invasions by *A. albopictus* depended on acceptance by this species of tires as oviposition sites (Hawley et al. 1987), another behavioral trait facilitating use of human-dominated habitats and contributing to invasion success in a manner consistent with AIAI.

Climate and Transition Zones of Co-occurrence

Climate influences the distributions of *A. aegypti* and *A. albopictus* differently. *Aedes albopictus* can enter a protective state of egg diapause to endure harsher winter conditions of temperate zones (Urbanski et al. 2012). In southern China, the Tropic of Cancer represents the approximate latitudinal line, north of which *A. aegypti* is rare or absent on the mainland (Wu et al. 2010) and on Taiwan (Yang et al. 2014). In both Macao and Hong Kong, as well as southern mainland China, *A. albopictus* replaces *A. aegypti* as the primary dengue vector (Almeida et al. 2005, Li et al. 2014). *Aedes aegypti* eggs and adults are, in contrast, more tolerant of desiccation and higher temperatures than are *A. albopictus* (Sota & Mogi 1992, Juliano et al. 2002). Differential mortality in the egg stage of the two species is believed to contribute to their patchy distribution in cemeteries in southern Florida, where their co-existence is associated with warmer dry-season temperatures and lower humidities (Lounibos et al. 2010). The tolerance of dryness may contribute to occurrence of *A. aegypti* in the arid southwestern US (Reiter et al. 2003) and to a general pattern of *A. aegypti* association with drier conditions on islands like Madagascar and Hawaii (Fontenille & Rhodain 1989, Winchester & Kapan 2003), and the absence of invasive *A. albopictus* and dominance by *A. aegypti* in drier Northern Cameroon (Simard et al. 2005). Abundance of *A.*

aegypti is strongly associated with seasonal dry periods in Florida (Juliano et al. 2002). In south Florida where the two species sometimes co-occur there is a consistent pattern of greater relative abundance of *A. aegypti* at the start of the wet season, suggesting relatively greater survivorship through the dry season, along with greater increase in relative abundance of *A. albopictus* as the wet season progresses (Juliano et al. 2002, Leisnham & Juliano 2009, Reiskind & Lounibos 2013). A similar seasonal pattern in areas of co-occurrence exists in Central African Republic (Kamgang et al. 2013) and in Thailand (Mogi et al. 1988). Camara et al. (2016) observed a similar pattern of greater success of *A. aegypti* in a field competition experiment in the dry spring (September – October) in Rio de Janeiro. Laboratory cage competition experiments demonstrated that experimental drying regimes imposed on populations were sufficient to eliminate the competitive advantage of *A. albopictus* over *A. aegypti* (Costanzo et al. 2005).

O’Neal & Juliano (2013) did field experiments testing specifically for effects of seasonal fluctuations in rainfall and differential mortality of eggs as a possible mechanism of coexistence in south Florida. They did not observe patterns of egg mortality consistent with this hypothesis (i.e., mortality of *A. albopictus* eggs was not greater in a dry-season experiment). They found, however, that interspecific competition was greatly reduced in the dry season, probably because of greater input of oak leaf detritus to containers, and greater input of oak flowers, which are a significantly more nutritious detrital resource for mosquito larvae (Lounibos et al. 1993). Thus, resource quantity and quality likely interact with seasonality, creating periods of reduced competitive interactions that may render coexistence more likely. See below for further review of the role of resource quality. Macroscopic climate variables such as temperature, precipitation, and seasonality thus encompass multiple, intercorrelated aspects of the environment – mortality due to desiccation and resource input, to name two - that influence these competitors in complex ways. This may mean that climate variables like rainfall or seasonality may be predictive of geographic ranges without a direct causal connection to population success. Whether climate variables in a new geographic area would be equally predictive of species’ success may depend on whether local species of trees respond to climate and seasonality in ways that are similar to those of the oak trees that dominate in Florida.

Mechanisms and Determinants of Co-existence and Exclusion

Although interspecific competition has been inferred or suggested to account for many observed changes in distribution and abundance where *A. aegypti* and *A. albopictus* co-occur, empirical tests of hypothesized mechanisms have been conducted only, to our knowledge, in the Western Hemisphere, where the two species co-exist as invasives. While many different mechanisms were proposed to account for competitive displacements observed in the USA (e.g., Craig 1993), over time only two have received sufficient empirical support to warrant inclusion for further consideration in this synthesis: reproductive (interference) competition and larval (resource) competition.

Asymmetric Mating Interference

A form of reproductive competition, often termed satyrization (Ribiero 1988), in which males of one species mate with a related species and produce inviable or less-fit hybrid offspring was proposed by Ribeiro (1988) as a biological control mechanism for insect pests or vectors. Nasci et al. (1989) provided some laboratory and field evidence that *A. albopictus* males copulating with *A. aegypti* females might account for competitive displacements of the latter species observed in Louisiana, USA, associated with the spread of *A. albopictus* in the late 1980s. However, the satyrization hypothesis received no support from early cage experiments that showed low rates of cross-insemination between these species (e.g., Harper & Paulson 1994).

The potential impact of satyrization generated renewed interest with the first report of interspecific matings in nature, in auto salvage yards in Florida, between *A. albopictus* and *A. aegypti*. This breakthrough was made possible by applying species-specific nucleotide probes to sperm dissected from spermathecae of wild-caught females (Tripet et al. 2011). Subsequent application of these methods to wild females captured at other sites of co-existence confirmed bidirectional interspecific matings at low (1–4%) frequencies on four continents (Bargielowski et al. 2015). Effects of cross-matings between these species are highly asymmetric, negatively affecting *A. aegypti* females much more than *A. albopictus* females, because male accessory gland products transferred during heterospecific matings permanently sterilize *A. aegypti* but not *A. albopictus* females (Tripet et al. 2011).

Testing multiple geographical populations of *A. aegypti* from the USA for susceptibility to cross-mating by *A. albopictus*, Bargielowski et al. (2013) reported that allopatric populations of *A. aegypti* were significantly more vulnerable than sympatric populations, and female origin, but not male origin, was a significant predictor in regression models that accounted for insemination success. The opposite cross, between *A. albopictus* females and *A. aegypti* males, occurred less frequently in the standardized cage environment and was influenced in the opposite direction by the allopatric-sympatric differences (Bargielowski et al. 2013). These authors concluded that reproductive character displacement had evolved in sympatric *A. aegypti* to mitigate the severe consequences of loss of reproduction in populations of this species in the presence of *A. albopictus* (Bargielowski et al. 2013). Character displacement attributable to reproductive competition was also demonstrated in male *A. aegypti*, allopatric populations of which were shown to be less effective than sympatric counterparts in mating conspecifics in the presence of *A. albopictus* females (Bargielowski et al. 2015b). Interestingly, the presence of conspecifics increased cross-matings in some cage exposures (Bargielowski et al. 2015b). Rapid selection for satyrization resistance was detectable in cage populations of allopatric *A. aegypti* females exposed to male *A. albopictus*, leading to reductions in cross-mating frequencies within 1–3 generations after exposure (Bargielowski & Lounibos 2014). Females derived from selected lines were significantly slower to mate with conspecific males, exposing a cost for the evolution of satyrization-resistance (Bargielowski & Lounibos 2014).

Aedes albopictus males from different geographical origins are not equally capable of satyrizing *A. aegypti* females. Males of *A. albopictus* derived from colonies of this species from three large cities in Brazil were relatively ineffective in inseminating *A. aegypti* from

Brazil or the USA in a standard cage environment (Honório et al. 2017). As *A. albopictus* that invaded Brazil are of tropical origin, in contrast to the temperate-derived *A. albopictus* in the USA (Hawley et al. 1987, Birungi & Munstermann 2002), the capacity to satyrize may be under genetic control and account for some of the geographic differences in displacement outcomes between the two countries (Honório et al. 2017).

Resource competition among larvae

Most investigations of competition among larvae of these species are done as density manipulations (response surface, replacement series, or addition series). It is relatively uncommon for resource type or availability to be manipulated along with species densities. Even rarer are experiments that attempt to test models of resource competition (Tilman 1982; Grover 1998, Chase & Leibold 2003). Murrell & Juliano (2012) designed experiments to estimate the minimum amount of a standardized detritus source, a mix of leaf detritus and dead insects similar to what is seen in many field studies (e.g., Yee et al. 2007, Murrell et al. 2011), that would be necessary for stable populations of each species (R_{index}). Their goal was an approximation of the R* values for resources that are at the heart of resource competition models (Tilman 1982). They found that *A. albopictus* had significantly lower R_{index} than either *A. aegypti* or *Culex pipiens*, indicating it should exclude either of the other two species. Pairwise competition experiments using that resource environment were consistent with the prediction of exclusion of *A. aegypti* (Murrell & Juliano 2012). Relevant to the comparison of competitive abilities of *A. albopictus* and *A. aegypti*, R_{index} for *A. albopictus* was not only significantly less than that of *A. aegypti*, but was also less than half the value of *A. aegypti*, suggesting that *A. albopictus* can persist as a population at detritus resource levels much lower than can *A. aegypti* and would thus be predicted to exclude *A. aegypti* in competition for the resource mix used in this experiment (Murrell & Juliano 2012). This remains the only experiment explicitly testing models of resource competition for any mosquitoes.

To evaluate the role of interspecific competition in changing field distributions, determining that natural densities of larvae are sufficient to produce significant interspecific competition is an important step toward establishing that interspecific competition is important under natural conditions. Field experiments on larvae at multiple sites in Florida showed that interspecific competition from *A. albopictus* had significant impacts on *A. aegypti* across a range of natural densities of larvae in cemeteries (Juliano et al. 2004). Similar experiments in suburban Brazil also showed that at natural densities, competitive effects of *A. albopictus* on *A. aegypti* were readily detectable in multiple seasons (Braks et al. 2004; Camara et al. 2016). Published accounts of field experiments on interspecific competition are rather rare (but see Kaplan et al. 2010). There have been several field experiments done at natural densities of larvae that show that intraspecific competition among larvae is also common. Two field experiments at natural densities of larvae of *A. aegypti* in residential areas in southern Mexico showed significant effects of intraspecific competition, and of delayed density dependence (i.e., effects of previous cohorts of larvae exploiting detritus resources in containers) acting on *A. aegypti* (Walsh et al. 2011, 2013). Similar studies done with *A. albopictus* in suburban residential areas of North Carolina demonstrated significant effects of delayed density dependence at natural densities of larvae (Walsh et al. 2012). Collectively these field studies indicate that both inter- and intra-specific competition among larvae of these *Aedes* are likely to occur relatively frequently in nature.

Field and laboratory experiments on competition among larval *A. aegypti* and *A. albopictus* have often found that *A. albopictus* is the superior competitor in many tested environments (reviewed by Juliano 2009, 2010). Meta-analysis of competition experiments (Juliano 2010) indicated significant heterogeneity of the outcome and degree of competitive asymmetry between these species that depended on the nature of the resources for larvae. When the resource base for larvae consisted of plant detritus of various kinds, *A. albopictus* had a clear competitive advantage, but when the resource base incorporated more rapidly decomposing substrates (e.g., dead insects) or resources that could be directly consumed (e.g., liver powder), the two species had approximately equal competitive effects and responses (Juliano 2010). Laboratory competition experiments show that some leaf types can also greatly reduce the competitive advantage of *A. albopictus* (Reiskind et al. 2012). Many of these laboratory results are consistent with field distributions in Florida, where *A. aegypti* populations persist and are robust in areas where nitrogen content of detritus is high, but are largely absent in areas where litter nitrogen content is lower (Murrell et al. 2011). Thus, it seems likely that one source of variation in the outcome of population encounters between *A. aegypti* and *A. albopictus* is environmental variation in the quality and composition (carbon, nitrogen, etc.) of the detrital resources encountered by larvae.

There is also evidence for interpopulation variation in competitive effects and responses of larvae of both species. Leisnham et al. (2009) tested nine North American populations of *A. albopictus* in competition with a standard population of *A. aegypti*. Although they found significant variation among *A. albopictus* populations in competitive effects on *A. aegypti* and in competitive responses to *A. aegypti*, this variation did not correlate with sites of coexistence or exclusion of *A. aegypti* following invasion by *A. albopictus*, or allopatry to *A. aegypti*. Thus, although variation among *A. albopictus* populations could contribute to local outcomes of competition when larvae meet, such variation does not seem to account for the broad pattern of coexistence or exclusion of *A. aegypti* in southern North America. Leisnham et al. (2010) similarly tested eight North American populations of *A. aegypti* in larval competition with a standard population of *A. albopictus*. They found that *A. aegypti* from allopatry to *A. albopictus* performed better in competition than did populations from sympatry, primarily because allopatric *A. aegypti* larvae had a greater competitive effect on *A. albopictus*. This result suggests that failure of *A. albopictus* to encroach further on the North American range of *A. aegypti* may in part be a result of superior competitive ability of larvae in some local populations of *A. aegypti*. If it is assumed that this difference in competitive ability between *A. aegypti* sympatric or allopatric to *A. albopictus* is a product of natural selection, it remains unknown what may have selected for that divergence. Improved performance in interspecific competition would seem more likely to be a product of selection in areas of sympatry, where encounters occur more frequently, but Leisnham et al. (2010) found, instead, better performance in interspecific competition in areas of allopatry to *A. albopictus*. The potential for evolution of competitive ability following contact of these species remains an important question for future research. No similar comparisons of intraspecfic variation in competitive abilities of these species has been conducted for other parts of their global invasive range.

Models of competition and mating interference

Although larval resource competition was formerly cited as the most common mechanism to account for competitive displacements among arthropod species (Reitz & Trimble 2002), there is a growing appreciation that reproductive interference may be an important cause of some displacements (Gröning & Hockrich 2008, Gao & Reitz 2017). It is fitting that several models analyze the joint effects of interspecific larval competition and reproductive interference on displacement and co-existence. Kishi & Nakazawa (2013) modeled how density dependent interactions affect population growth through both competition and reproductive interference and showed they may act synergistically to promote competitive exclusion. Their models do not explicitly include resource competition nor the stage structure inherent in the *A. aegypti – A. albopictus* system, wherein resource competition would occur among larvae, and affect survival, growth, and development and ultimately the production of adults, and reproductive interference among adults would affect fecundity and ultimately production of new larvae. Both Kishi & Nakazawa (2013) and the earlier models by Ribiero (1988) assume that interspecific competition (presumed among larvae) has a lesser impact than does intraspecific competition, rendering coexistence of competitors possible in the absence of reproductive interference. Owing to the potential for stronger, more direct, and more rapid impacts from reproductive interference, either co-existence or exclusion can prevail if advantages in the two competitive processes are in opposition (Kishi & Nakazawa 2013). Thus, the combination of interspecific competition among larvae and reproductive interference among adults could result in stable coexistence if there is a tradeoff in advantage, or competitive exclusion if one species has the advantage in both. These results are consistent with Ribeiro’s (1988) model, which like Kishi & Nakazawa’s (2013) is based on Lotka-Volterra dynamics, suggested that low levels of satyrization, enhanced by resource competition, could be used for control of pests and vectors. No one has yet modeled pure resource competition among larvae (i.e., the experimental system investigated by Murrell & Juliano 2012, described above) with one species having a strong advantage, and ability to exclude the other, in resource competition, and the added effect of reproductive interference. A stage-structured model seems likely to be necessary for this scenario.

Future Research Opportunities and Challenges

Testing Displacement Mechanisms

Despite the extensive sympatric ranges of these invasive *Aedes* species, experimental tests of putative displacement mechanisms have to date been conducted only for populations from the USA and Brazil (e.g., Juliano 1998, Braks et al. 2004, Camara et al. 2016, Honorio et al. 2017), leaving vast swaths of Asia and Africa unaccounted for to parameterize models that include interaction mechanisms. The opportunity to link the strength of a putative mechanism through experiments to the patterns of local displacement could extend models and increase understanding of competitive displacements in this system.

Population Genetics

The feral subspecies *A. aegypti formosus* is expected to behave differently than the domestic subspecies in encounters with *A. albopictus*, but populations of this species from

Madagascar, Reunion and Mayotte have not been tested for genetic distinctiveness from *A. aegypti aegypti* that may account for different patterns of habitat segregation observed on these SWIO islands.

Interpopulation variation in larval competitive performance of *A. aegypti* and *A. albopictus* populations from the USA (Leisnham et al. 2009, Leisnham & Juliano 2010) has been quantified, but there has been no systematic investigation of evolution of competitive performance (of either species) when they meet. This contrasts markedly with investigations of evolution of resistance to reproductive interference, which has been shown in the lab (Bargielowski & Lounibos 2014) and detected in nature (Bargielowski et al. 2013, Lounibos et al. 2016).

Interpopulation variation in reproductive interference is also suggested by the failure of Brazilian populations of *A. albopictus* to satyrize in contrast to N. American populations (Honorio et al 2017). More information on the genetic bases of both larval resource competitive ability and adult satyrization would be valuable. Genetic profiles of satyrization-resistant *A. aegypti* have displayed consistent regions of the genome that appear to be targets of natural selection (Buford Reiskind et al. submitted), leading to the possibility of identifying the genetic basis for this example of reproductive character displacement. Evolution of satyrization resistance has been detected in natural populations (Bargielowski et al. 2013, Lounibos et al 2016) and selected lines of *A. aegypti* (Bargielowski & Lounibos 2014). Evolution of satyrization resistance or of resource competitive ability (or of both) may stabilize range boundaries of parapatric populations of *A. albopictus* and *A. aegypti*.

Recent analyses of mtDNA haplotype diversity have identified admixtures of unrelated genomes that have occurred as a consequence of unpredictable dispersion by invasive *A. albopictus* (Manni et al. 2017). Successive waves of colonization, allowing for genomic reassortment between founder populations, may also apply to worldwide dispersion of *A. aegypti* (e.g., Brown et al. 2014). Such genetic reassortment processes may not only change the invasive characteristics of both species but alter gene X environment interactions, which argues in support of population genetic approaches for understanding the outcomes of interspecific competition between these species.

Climate Change

The majority of models that predict abundance and distributional changes in *A. albopictus* and *A. aegypti* with climate change are based upon fundamental niches of the vector species, and do not incorporate interspecific interactions (e.g., Kearney et al. 2009, Rochlin et al. 2013, Proestos et al. 2015). For localities where these species might encounter one another, consideration of possible displacement effects and mechanisms would improve predicted future distributions under climate change. Although some climate change scenarios for these species only model effects of temperature changes (e.g., Thomas et al. 2011), precipitation patterns are known to affect *A. albopictus* population dynamics in cages (Alto & Juliano 2001) and the outcome of interactions of this species with *A. aegypti* (Costanzo et al. 2005). More, broadly, climate change may facilitate invasion by other mosquitoes, such as *Aedes flavopictus*, which has recently been observed displacing *A. japonicus* and *A. albopictus* with temperature increases in their native ranges near Nagasaki, Japan (Chaves 2016).

Conclusions

Worldwide, outcomes of interspecific encounters between *A. albopictus* and *A. aegypti* are extremely diverse, ranging from wide-scale competitive displacements to local habitat segregation to no evident effects. It is doubtful that the potential invasive geographic ranges of either species can be predicted accurately without using the multifaceted and context-dependent competitive interactions between these important vectors as predictors. Outcomes of interactions of these species appear to depend on which of the local genotypes of the two species interact, as well as on the local environments in which they interact.

We suggest that incorporating the effects of interspecific interactions in global distribution models of the two species (Benedict et al. 2007, Medley 2010, Kraemer et al. 2015, Ding et al. 2018) is likely to be both important for accurate prediction, and to be challenging, a point that was also made by Eisen and Moore (2013). We also suggest that incorporating species interactions into predictive models of invasive range will be **generally important for most invasive species**. Several authors working in other systems have found ways to add species interactions to environmental niche models (e.g., Leathwick & Austin 2001, Anderson et al. 2002) and these may provide a guide for researchers pursuing environmental niche models of these *Aedes*. Wisz et al. (2013) suggest multiple mathematical/statistical approaches that could be used to account for effects of species interactions in predictive environmental niche models. We think *A. albopictus* and *A. aegypti* could be an important and productive test case for some of these proposed approaches. First, the mechanisms by which they interact are well documented, limiting uncertainty about whether the interactions should be included in models. Second, as occupants of small water holding vessels in human-dominated habitats, the set of other species that might impact their distributions is more limited than those for organisms from more species-rich communities, which keeps this problem relatively simple (Wisz et al. 2013). Third, as important vectors of human disease, they are well studied and their distributions are the focus of considerable public health surveillance. Their roles as vectors also enhance the importance of developing predictive models of their invasive distributions.

Though we have illustrated the importance of the realized niche using interspecific competition as the interaction that is critical for distribution modeling and prediction for these two species, we expect a similar case could be made for predation among other invasive species, but that is beyond the scope of this synthesis. Development of local distribution maps, which are probably most relevant for epidemiological interpretations (e.g., Rochlin et al. 2013, Hahn et al. 2016), should be done with incorporation of the documented processes contributing to competitive displacements to improve spatial resolution. Where sterile insect techniques or other genetic approaches (e.g., Lees et al. 2015) are contemplated for control of one of these species, the potential for population replacement by the other competing vector species should be considered (e.g., Bonsall et al. 2010). Niche compressions following the establishment of either invasive species in habitats formerly occupied by the other are the most common evidence for interspecific competition between *A. aegypti* and *A. albopictus*. Although mechanisms whereby the two species achieve relative superiority in their realized niches are not completely understood, especially for *A. aegypti* in urban environments, the typical advantage of *A. albopictus* in larval competition and fluctuations in competitive advantages attributable to variations in resources and weather seem to account for the predominance of *A. albopictus* in vegetated habitats and the patchy co-existence of the two species in sympatry.

However, resource competition alone cannot account for the rapid and expansive displacements of *A. aegypti* observed in Bermuda (Kaplan et al. 2010) or the southeastern USA (Nasci et al. 1989, Bargielowski & Lounibos 2016). We consider asymmetric reproductive interference, or satyrization, to be the most probable additional contributing cause of these conspicuous, swift, and, at least for Florida (Lounibos et al. 2016), durable outcomes. The rarity of such massive displacements suggests that either they occur only under exceptional circumstances, such as at the margins of the range of *A. aegypti*, or that only some populations of *A. albopictus* are capable of satyrization (Honório et al, 2017). Although interspecific mating between these species, as estimated from heterospecific sperm detected in the spermathecae of wild-caught females, is relatively rare (1–4%), this interaction seems to be ecologically important. All sympatric field populations sampled on four continents had co-existed long enough to have evolved resistance to cross-mating (Bargielowski et al. 2013B, 2015) and *A. aegypti* from allopatry to *A. albopictus* are more susceptible to interspecific insemination by *A. albopictus* (Bargielowski et al. 2013, Lounibos et al. 2016). The frequency of satyrization has likely been underestimated because interspecific transfer of male accessory gland substances without successful sperm transfer to the spermathecae can produce the detrimental effects causing satyrization (Carrasquilla & Lounibos 2015).

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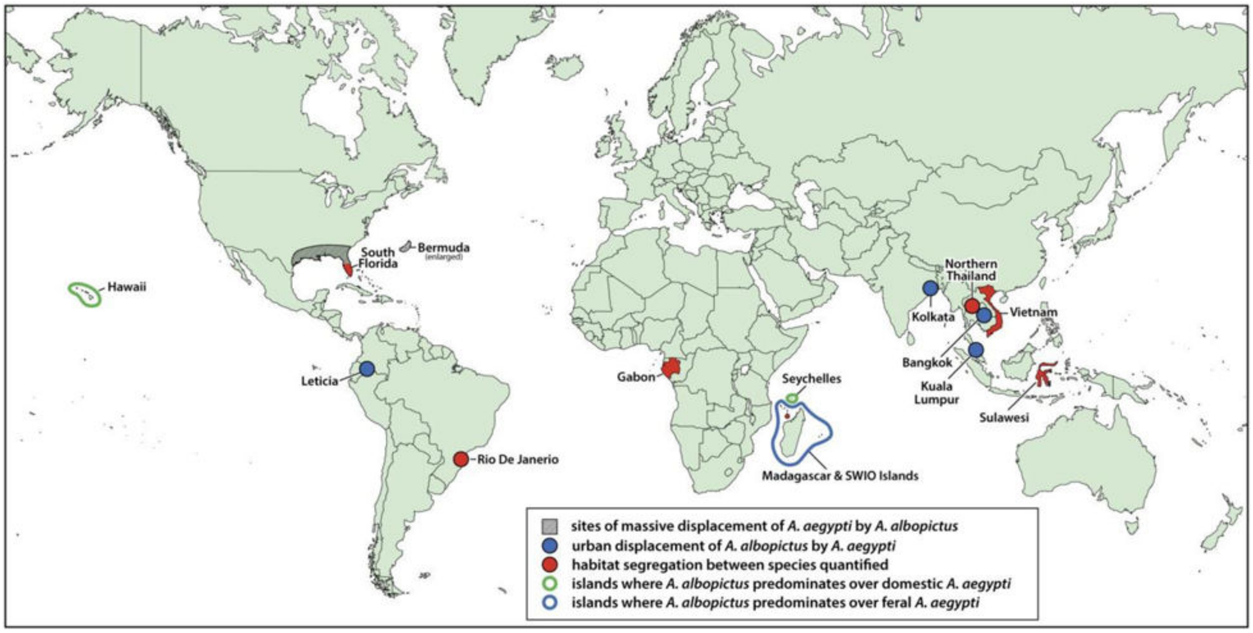

Figure 1.

Geographic locations of different outcomes (see inset for interpretations) where *A. aegypti* and *A. albopictus* have met.

Table 1

Effects of failure to include species interactions in models of species potential distributions in an introduced range.

	Model built based on native range [1]	
Potential introduced range	**Interacting species** [2]	
Interacting species	**Present; not used as predictors**	**Absent or excluded from model**
Absent	**Cell 1**. PREDICTED RANGE TOO NARROW [enemy release/empty niche]	**Cell 2.** ACCURATE PREDICTION
Same or functionally similar to those in native range	**Cell 3.** ACCURATE PREDICTION	**Cell 4.** PREDICTED RANGE TOO BROAD [biotic resistance]
Functionally dissimilar to those in native range	**Cell 5.** PREDICTED RANGE TOO BROAD OR TOO NARROW	**Cell 6.** PREDICTED RANGE TOO BROAD [biotic resistance]

[1] Environmental niche models are assumed to be predictive, correlative models based on conditions in the native range that are used to predict distributions in the introduced range.

[2] Interacting species (e.g., predators, parasites, competitors) are assumed to constrain the focal species to a realized niche that is narrower than its fundamental (pre-interactive) niche. A similarly structured table could be made assuming interacting species that render the realized niche broader than the fundamental niche (e.g., mutualists, ecosystem engineers); however, deviation of predicted from actual introduced ranges would likely be reversed.

Table 2

Examples of habitat segregation between *A. aegypti* and *A. albopictus* in rural-urban landscape gradients.

Location	Urban Species	Test for Negative Intersp. Correlation	References
South Florida	*A. aegypti*	yes	Braks et al. 2003; Rey et al. 2006; Lounibos et al. 2016
Rio de Janeiro	*A. aegypti*	yes	Braks et al. 2003
Gabon	*A. aegypti*	not done	Paupy et al. 2010
Mayotte	*A. albopictus*	not done	Bagny et al. 2009b
North Thailand	*A. aegypti*	yes	Tsuda et al 2006
Vietnam	*A. aegypti*	yes	Higa et al. 2010
Indonesia	*A. aegypti*	not done	Ishak et al. 1997