

# Interpopulation differences in competitive effect and response of the mosquito *Aedes aegypti* and resistance to invasion by a superior competitor

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**Abstract** Geographic variation in species interactions can have major effects on species distributions and can be important for the resistance of resident communities to invasive species. We tested the hypothesis that coexistence or replacement of a resident North American mosquito *Aedes aegypti* with the invasive *Aedes albopictus* is affected by interpopulation variation in the inherent competitive ability of *A. aegypti* and variation in the fecundity–size relationship. We postulated that such variation creates differential population-level outcomes of competition with *A. albopictus*. We compared competitive abilities of eight North American populations of *A. aegypti*, four populations sympatric to *A. albopictus*, and four populations allopatric to *A. albopictus*. Competition among larvae from each *A. aegypti* population and a single *A. albopictus* population was tested in laboratory microcosms in a response-surface design. We found origin of *A. aegypti* influences its competitive response to competition from *A. albopictus* and competitive effect on *A. albopictus*. *A. aegypti* from allopatric sites performed better in competition with

*A. albopictus* than did *A. aegypti* from sympatric sites because they had a stronger average effect on *A. albopictus*. This average was strongly influenced by the allopatric population from Miami. Competitive effect and response were uncorrelated among populations, indicating inconsistent ranking of *A. aegypti* in competitive effect and response. Although *A. albopictus* is generally a superior competitor to *A. aegypti*, a stronger competitive effect of particular *A. aegypti* populations on invading *A. albopictus* may contribute to competition-mediated biotic resistance to the invader. These results suggest that interpopulation variation in competitive ability of *A. aegypti* may contribute to failure of *A. albopictus* to invade parts of the southeastern United States and offer evidence of a contribution to biotic resistance by an inferior competitor. Geographic variation in competitive ability may be common and one general cause of variation in invasion success and impact.

**Keywords** Biotic resistance · Fecundity–size relationship · Invasive · Reproductive tactics

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## Introduction

Geographic variation in species interactions can be a major cause of geographic patterns in the diversity of genotypes and phenotypes (Travis 1996). Despite these important effects of geographic variation of species interactions, most empirical studies of species interactions have been restricted to documenting the presence of species interactions as important factors for local populations (Travis 1996; Sakai et al. 2001; Juliano 2009 for reviews). Most studies on the establishment and spread of exotic insects

have focused on the roles of vacant niches or release from natural predators as being important determinants of invasion success. Competition clearly also occurs between invaders and resident species (Duyck et al. 2006), and is considered an important mechanism of biotic resistance of residents to exotic invaders in plants (Levine et al. 2004). Competition-mediated resistance is not well studied in animals and the importance of interspecific competition in determining when and where invasions occur for all organisms is usually ascribed to variation in community properties (Levine 2000; Levine et al. 2004; Diez et al. 2008). When invaders interact strongly with particular resident species, intraspecific variation in population characteristics of the residents may also be important for biotic resistance. However, there is little known of how local differentiation of competitive ability of resident species, either in response to selection from different biotic environments (Sakai et al. 2001; Siemann and Rogers 2001) or because of heterogeneous founding genotypes (Levine et al. 2004; Abbott et al. 2007; Keller and Taylor 2008) affects their interactions with an invasive species.

Impacts of invasive species may vary across their introduced range from limited impacts and the persistence of residents to the competitive displacement of residents (Juliano et al. 2004; Abbott et al. 2007). Investigations of the causes of such variation provide an opportunity to understand how intraspecific variation in species interactions arises (Keller and Taylor 2008). Investigations into the impacts of invasives across their introduced range are also of potential practical importance because such variation may help to predict where resident species are most resistant to invasive impacts and thus provide a metric of vulnerability of a system to ecological, economic, and health impacts of invasion (Levine et al. 2004; Abbott et al. 2007). Ideal model systems for such investigations involve a widespread, well-studied resident that varies in its persistence after the invasion of invasive species, from resistance to invasion to coexistence with invasive species (Leisnham et al. 2009).

The yellow-fever mosquito, *Aedes aegypti*, originated in tropical Africa but has invaded numerous tropical and subtropical regions worldwide, including the Americas in the sixteenth century (Lounibos 2002). *A. aegypti* is the principal vector of yellow fever, chikungunya, and dengue viruses worldwide (Lounibos 2002). Since its invasion, *A. aegypti* has spread throughout much of North and South America to become one of the most common human-biting mosquitoes in its range (Lounibos 2002). In the mid-1980s the Asian tiger mosquito, *Aedes albopictus*, invaded the continental United States from Japan. The spread of *A. albopictus* has been associated with a decline, sometimes to local extinction, of *A. aegypti* (O'Meara et al. 1995). Most field (e.g., Juliano 1998; Braks et al. 2004) and

laboratory (e.g., Barrera 1996; Murrell and Juliano 2008; Leisnham et al. 2009) competition experiments have shown that *A. albopictus* are superior in competition for resources with *A. aegypti* when leaf detritus is the nutrient base. With the exception of some studies that have examined the effects of larval competition on adults (e.g., Hawley 1985; Alto et al. 2005, 2008; Costanzo et al. 2005a, b; Leisnham et al. 2009; Reiskind and Lounibos 2009), these experiments have typically only involved the effects of competition on the immature stages, ignoring effects that may be expressed in resulting adults. Despite an apparent competitive advantage for North American *A. albopictus*, *A. aegypti* remains dominant in some areas in the southern USA, particularly in urban and southern sites in the Florida peninsula (O'Meara et al. 1995) and New Orleans (Comiskey et al. 1999).

At least two sets of hypotheses could account for the observations that *A. albopictus* is typically superior in competition to *A. aegypti* yet *A. aegypti* coexists with *A. albopictus* at some sites. One set of hypotheses suggests that ecological context, including abiotic and biotic environments, differs among sites, with conditions at some sites favoring *A. aegypti* (Juliano et al. 2002, 2004, Costanzo et al. 2005a, b). For example, Juliano et al. (2002) found that, in Florida, occupancy of containers was greater for *A. aegypti* at warm sites with little winter rainfall compared to relatively cool sites with greater winter rain.

The second set of hypotheses is that local populations of these *Aedes* may differ in their competitive characteristics. First, local populations of the invasive *A. albopictus* differ in competitive interactions with *A. aegypti*. Leisnham et al. (2009), using laboratory microcosms and a response-surface design, tested this hypothesis by comparing larval competitive abilities of nine North American populations of *A. albopictus* falling into three site types: extinction of *A. aegypti* following *A. albopictus* invasion, coexistence following *A. albopictus* invasion, and *A. albopictus* allopatric to *A. aegypti*. Leisnham et al. (2009) found interpopulation differences in competitive ability of *A. albopictus* but no strong patterns among site types, and thus suggested that the first hypothesis of geographic variation in competitive ability of *A. albopictus* did not adequately explain its invasion success and local extinction of *A. aegypti*. The second hypothesis concerning geographic variation of competition in *Aedes* is that there is geographic variation in the competitive ability of *A. aegypti*. This hypothesis is yet to be tested and until it is the role of geographic variation in competition among *Aedes* enabling invasion by *A. albopictus* remains unclear.

In this study, we test the hypothesis that variation in the outcome of *A. albopictus* invasion (i.e., coexistence vs. replacement of *A. aegypti*) is affected by variation among local populations of *A. aegypti* in competitive interactions

with *A. albopictus*. We do this by comparing the competitive ability of eight North American populations of *A. aegypti* with known population histories of contact with *A. albopictus*. As in the study by Leisnham et al. (2009) on *Aedes* and other studies on species interactions (Black et al. 1989), we compare populations under a single set of environmental conditions, and thus correlate phenotypic differences with underlying genotypic variation. To quantify effects of heterospecific and conspecific competition, we employed a response surface design (Goldberg and Scheiner 2001), in which regression slopes of population performance versus heterospecific and conspecific densities quantify per capita competitive effect (the negative effects of a species on other species) and response (the ability of a species to withstand competition exerted by other species) to interspecific and intraspecific competition (Goldberg and Fleetwood 1987). Based on our hypothesis, we predict that *A. aegypti* from sites where *A. albopictus* has not established will have better competitive response, or stronger competitive effect, than will *A. aegypti* from sites where *A. albopictus* has established.

We estimate population performance by calculating an estimate of the finite rate of population increase ( $\lambda'$ ), which is a composite index based on individual fitness components: survivorship, female development time, and female wing length (Livdahl and Sugihara 1984; Juliano 1998). Traditional experimental methods that only consider individual fitness components yield limited inference of competitive effects. For example, strongly competing mosquito larvae often grow more slowly, and thus cohorts under strong competition may have the same or greater survivorship as larvae that do not compete, simply because larval development is delayed (e.g., Knight et al. 2004; Leisnham et al. 2009). Further, prior experiments using  $\lambda'$  have yielded different conclusions for  $\lambda'$  and survivorship of species, reaffirming the importance of including an analysis of population rate of increase in competition studies (Livdahl and Sugihara 1984; Juliano 1998; Leisnham et al. 2009).

## Materials and methods

### Collection and maintenance of mosquitoes

Approximately 500 *A. aegypti* larvae were collected from ten to 20 containers from each of eight geographic populations in the eastern United States, four populations each from sites allopatric to *A. albopictus* and sympatric to *A. albopictus* (Electronic Supplementary Material). With the exception of New Orleans, all other sites have been routinely sampled at least once every 2–3 years from the mid-1990s, and usually more often (G. F. O'Meara, unpublished data; P. Leisnham, unpublished data). At

allopatric sites (Fort Lauderdale, Key West, Miami, and St. Petersburg, FL, USA), *A. albopictus* was considered locally absent (unpublished data). At Fort Lauderdale, Miami, and St. Petersburg, though *A. albopictus* was absent in our samples, it has been present in low numbers at some stage in the past (G. F. O'Meara, unpublished data; P. Leisnham, unpublished data), and there may be occasional oviposition of *A. albopictus* from individuals of neighboring populations. At Key West, there is no evidence that *A. albopictus* has ever been present. At sympatric sites (Fort Myers, Florida, New Orleans, Louisiana, Palmetto, Florida, and West Palm Beach, FL, USA) *A. albopictus* has been established since the early 1990s, yet *A. aegypti* remains present (O'Meara et al. 1995; Comiskey et al. 1999). *A. albopictus* for this experiment were collected as larvae (~500 individuals) from a single population in Fort Denaud, FL, USA where *A. aegypti* went extinct after invasion by *A. albopictus* (O'Meara et al. 1995).

*A. albopictus* and *A. aegypti* used in the experiment were first generation progeny of field-collected individuals. Field-collected larvae were reared to adulthood at 26°C at 16:8 h (light:dark; L:D) photoperiod and then released into 0.6-m<sup>3</sup> cages. Adults were kept at 26°C and 75% relative humidity at 17:7 h (L:D) photoperiod with a graduated dawn-dusk period. Adults had continuous access to 20% sugar solution. Females were regularly blood fed from anesthetized guinea pigs and laid eggs on paper towels in water-filled cups.

### Experiment 1: competition

The experiment had a replicated, blocked design with within-block replication of all populations. For each block, eggs of both species were hatched synchronously in a solution of 0.44 g nutrient broth per 1 l deionized (DI) water. Within 24 h, larvae were rinsed and transferred into the experiment. The experiment consisted of the following initial combinations of larvae (*A. albopictus*: *A. aegypti*): 10:0, 20:0, 40:0, 10:10, 20:20, 10:30, 30:10, 0:10, 0:20, and 0:40 to create a response surface design (Goldberg and Scheiner 2001). Each combination was replicated 3 times for each of the eight *A. aegypti* populations. Inadequate numbers of eggs after hatching prevented us setting-up three experimental units containing *A. aegypti* and seven experimental units containing both species, but excess *A. albopictus* larvae allowed two additional units containing *A. albopictus*. In total, there were 161 experimental units with *A. albopictus*, 160 experimental units with *A. aegypti*, and 232 total experimental units. The experiment was executed in 400-ml cups containing 350 ml DI water and provisioned with 0.70 g of dried senescent live oak (*Quercus virginiana*) leaves. This amount of detritus mimics typical conditions in the field under which

competition for food occurs. Cups were set up 4 days prior to the addition of larvae to allow microbial communities to establish. On days 14, 28, 42 and 56 after the start of each replicate, 0.70 g of additional dried live oak was added to each cup to avoid complete resource depletion and to mimic the natural condition of continuous resource inputs to containers.

The experiment was housed in an environmental chamber at 28°C and 14:10 h (L:D) photoperiod. Treatments were randomly assigned cups and cup position was shuffled daily. Each day we collected pupae into individual vials and held them until adult emergence, when adults were killed by drying (24 h, 50°C). To represent the range of adult body sizes emerging from each cohort, the first, middle and last males and females from each cup were weighed and the females also had their wing lengths measured. Dry mass and wing length of adult females were highly correlated (*A. albopictus*:  $r^2 = 0.834$ ,  $n = 433$ ; *A. aegypti*:  $r^2 = 0.721$ ,  $n = 334$ ), and wing length was used as a measure of female size to estimate fecundity of *A. albopictus* and *A. aegypti* (see below).

Proportion survivorship to adulthood, mean development time (female and male), mean adult mass (female and male), and mean female wing length were recorded for each species' mosquito cohort in each cup. Survivorship, female development time, and female wing length were used to calculate  $\lambda'$ , a composite index of population performance based on  $r'$  (Livdahl and Sugihara 1984), which estimates the realized per capita rate of population change ( $dN/N dt = r$ , the exponential growth rate) for each replicate cohort (details in given by Leisnham et al. 2009). Our index is  $\lambda' = \exp(r')$  and thus estimates the finite rate of increase (Juliano 1998).

#### Experiment 2: fecundity–size relationships

We used a regression relating adult wing length ( $w$ ) to fecundity ( $f$ ) for *A. albopictus*:  $f(w_x) = -121.240 + 78.02w_x$  ( $r^2 = 0.714$ ,  $n = 91$ ,  $P < 0.001$ ; Lounibos et al. 2002). To test differences in the relationship between fecundity and body size in *A. aegypti*, *A. aegypti* larvae from each colony were reared to adulthood in the laboratory. As adults enclosed they were placed in 20-l nylon-screen cages and within 5–10 days were fed to repletion from an anaesthetized mouse, then isolated individually in 600-ml containers with a 40 ml cup of water lined with paper towel for oviposition. Eggs were counted and the mean dry mass determined for ten randomly chosen eggs from each female. Eggs were weighed in groups of five to ten, to 0.1  $\mu\text{g}$ . After oviposition, all females were killed, dissected, and numbers of mature eggs (stages 4 and 5; Detinova 1962) in their ovaries counted. Fecundity was calculated by adding laid and unlaid mature eggs. Wings

of all females were removed and measured. A total of 193 females (16–30 for each population) entered the experiment. Killing and dissecting females after the first gonotrophic cycle is consistent with most prior studies that have examined the fecundity of *A. albopictus* (e.g., Armbruster and Hutchinson 2002; Lounibos et al. 2002). Data on the parous rate of wild *A. albopictus* females suggest that the average female matures one batch of eggs (Hawley 1988).

#### Data analyses

##### Experiment 1: competition

For each species, linear models with effects of densities of *A. albopictus* and *A. aegypti* (continuous variables) and population (class variable) were tested with  $\lambda'$ , survivorship, development time (female and male), mass (female and male), and female wing length as dependent variables. An effect of competition was detected as a significant slope for a species' performance versus heterospecific or conspecific density. If population affects the outcome of competition, we expect an interaction between density and population. *A. aegypti* populations with stronger effects on *A. albopictus* will yield steeper slopes of *A. albopictus* population performance versus *A. aegypti* density. Populations with better competitive responses to *A. albopictus* will yield shallower slopes of *A. aegypti* population performance versus *A. albopictus* density. Competitive hierarchy among populations was tested by estimating Spearman rank correlation between slopes for effect and response. A strong negative correlation indicates that strong competitive effect and response are associated across populations.

Populations selected for this study were not a random sample of all possible populations of each site type. Therefore, in all analyses, population was treated as a fixed effect and statistical inferences extend only to the populations selected. This strategy follows that of previous studies on geographic variation of life history traits (e.g., Reznick et al. 2001; Leisnham et al. 2008, 2009). For all analyses, we tested for significant differences among populations using pairwise contrasts (Scheiner 2001), with sequential Bonferroni correction for all possible comparisons (33) within each analysis. We tested for a site type effect using the a priori contrast comparing mean values of coexistence versus allopatric sites. We arcsine-square root transformed proportion surviving, and log transformed  $\lambda' + 1$ , mass, and development time to meet assumptions of normality and homogeneity of variances. All analyses were done using SAS (SAS Institute 2003) using experiment-wise  $\alpha = 0.05$ .

## Experiment 2: fecundity–size relationships

Multivariate analysis of covariance (MANCOVA) was used to test for differences between populations in the relationships of wing length with fecundity and egg size, using  $F$  statistics derived from Pillai's trace (SAS Institute 2003). We interpret contributions of dependent variables to significant MANCOVA effects using standardized canonical coefficients (Scheiner 2001). Population was a class variable and wing length a continuous variable. Interaction of wing length with population was also included. Thirty-seven females either did not lay eggs before dying or their eggs were damaged, and thus their eggs were not weighed and they were excluded from the MANCOVA. Although we tested population differences in the relationship of wing length with fecundity and egg size using data from all populations, we conducted separate univariate linear regressions of fecundity on wing length for each population to predict fecundity from wing length for calculating  $\lambda'$  for each population.

Because there is no evidence that *A. albopictus* has ever been present at Key West, and thus there is the possibility that *A. aegypti* may not experience the same selection on *Aedes* competition as *A. aegypti* in the other allopatric populations, we undertook all statistical analyses after the removing Key West population. We found no difference in the outcomes of these tests with those that included Key West and thus do not report their results.

## Results

### Experiment 1: competition

#### *Estimated finite rate of increase*

The origin of *A. aegypti* influenced its competitive response to density of *A. albopictus* ( $F_{7,136} = 3.37$ ,  $P = 0.0024$ ) and competitive effect on *A. albopictus* ( $F_{7,136} = 4.70$ ,  $P < 0.0001$ ), with *A. aegypti* from allopatric sites having stronger effect on *A. albopictus* than *A. aegypti* from sympatric sites ( $P = 0.0002$ ; Table 1). Miami and New Orleans had an average of 14.2 and 13.1 times better competitive response than St. Petersburg, respectively ( $P < 0.0007$ ; Table 2). Miami had a 2.9–4.3 times stronger competitive effect than most other populations ( $P < 0.002$ ) except St. Petersburg (1.5 times,  $P = 0.0684$ ; Table 2). Competitive effect and response slopes were uncorrelated ( $r_s = 0.119$ ,  $P = 0.749$ ), indicating inconsistent ranking of populations of *A. aegypti* in competitive effect and response (Table 2). Particularly at high combined densities, *A. albopictus* usually had higher  $\lambda'$  than *A. aegypti* (Fig. 1).

### *Other univariate measures*

For survivorship (Table 1) and adult female mass and development time (Table 3) there were no significant interactions of population and either conspecific or heterospecific density, indicating that effects of density on these variables were consistent among populations. Heterospecific and conspecific densities negatively affected survivorship (Table 1), mass, and development time of *A. albopictus* and *A. aegypti* (Table 3). No *A. albopictus* females survived from two cups (Miami 10:30 and St. Petersburg 10:30) and no *A. aegypti* females survived from 18 cups; nine from cups with 30:10, four with 20:20, two each with 10:30 and 0:40, and one with 10:10.

### Experiment 2: fecundity–size relationships

There was no significant interaction of wing length with population, indicating that fecundity–size relationships were similar across all populations. Wing length positively affected fecundity in all populations and only weakly affected egg size (Table 4; Fig. 2). Multivariate pairwise contrasts showed no difference between sympatric and allopatric sites, and among individual populations. Separate linear regressions of fecundity on wing length for use in estimating  $\lambda'$  for each population yielded  $r^2$ -values from 0.336 to 0.763.

## Discussion

There are inherent interpopulation differences in competitive effect and response of *A. aegypti*, but these differences are only evident when examining the composite index of performance, and are not evident in individual components of population performance. Thus, as noted by Livdahl and Sugihara (1984), simple analysis of individual components of fitness or population rate of increase often provides a highly inadequate assessment of the biotic processes affecting population dynamics and fitness.

Consistent with our prediction, *A. aegypti* from sites where *A. albopictus* has not established (allopatric) were superior in competition with *A. albopictus* to *A. aegypti* from sites where *A. albopictus* has established (sympatric), having a stronger effect on the  $\lambda'$  of *A. albopictus*. Miami, in particular, had the strongest effect and best response of all populations, but effect and response slopes of all populations were uncorrelated, indicating inconsistent ranking of *A. aegypti* in competitive effect and response. This lack of correlation is a similar pattern to that observed for effect and response of *A. albopictus* (Leisnham et al. 2009). There was no difference in the average fecundity–size relationships between sympatric and allopatric sites indicating that a

**Table 1** Least squares linear models for the estimated finite rate of increase ( $\lambda'$ ;  $\log_{10}\lambda' + 1$ ) and arcsin survivorship of both species in response to the independent variables of *Aedes albopictus* density, *Aedes aegypti* density, and population

Source	$\lambda'$						Survivorship					
	<i>A. albopictus</i>			<i>A. aegypti</i>			<i>A. albopictus</i>			<i>A. aegypti</i>		
	df	F	P	df	F	P	df	F	P	df	F	P
<i>A. albopictus</i> density	1, 137	24.98	<b>&lt;0.0001</b>	1, 136	46.37	<b>&lt;0.001</b>	1, 137	431.89	<b>&lt;0.0001</b>	1, 136	7.87	<b>0.0058</b>
<i>A. aegypti</i> density	1, 137	60.92	<b>&lt;0.0001</b>	1, 136	6.85	<b>0.0098</b>	1, 137	26.83	<b>&lt;0.0001</b>	1, 136	347.41	<b>&lt;0.0001</b>
Population	7, 137	0.04	0.9999	7, 136	0.21	0.9822	7, 137	0.04	0.9999	7, 136	0.17	0.6766
<i>A. albopictus</i> × population	7, 137	0.18	0.9893	7, 136	3.37	<b>0.0024</b>	7, 137	0.13	0.9962	7, 136	0.11	0.9979
Sympatric versus allopatric	1, 137	0.27	0.6062	1, 136	0.97	0.3252	1, 137	0.00	0.9957	1, 136	0.17	0.6766
<i>A. aegypti</i> × population	7, 137	4.70	<b>&lt;0.0001</b>	7, 136	0.55	0.7939	7, 137	0.21	0.9819	7, 136	0.14	0.9952
Sympatric versus Allopatric	1, 137	9.23	<b>0.0029</b>	1, 137	0.08	0.7734	1, 137	0.01	0.9432	1, 136	0.07	0.9432

Significant effects and pairwise contrasts are indicated in *bold* and are reported in the main text

Only pairwise contrasts between average slopes of site types for interaction effects are shown for brevity

**Table 2** Regression slope estimates ( $\pm$ SE) for the competitive response of *A. aegypti* to *A. albopictus* and competitive effect of *A. aegypti* on *A. albopictus* of eight *A. aegypti* populations originating from sites where *A. aegypti* is either allopatric or sympatric to *A. albopictus*

Population	Site type	Regression slope estimate ( $\pm$ SE)
Competitive response		
Miami	Allopatric	-0.00074 $\pm$ 0.00205 a, b
New Orleans	Sympatric	-0.00080 $\pm$ 0.00203 a, b
Key West	Allopatric	-0.00276 $\pm$ 0.00198 b
Ft. Meyers	Sympatric	-0.00360 $\pm$ 0.00195 b
Palmetto	Sympatric	-0.00383 $\pm$ 0.00199 b
Ft. Lauderdale	Allopatric	-0.00791 $\pm$ 0.00198 b
West Palm Beach	Sympatric	-0.00812 $\pm$ 0.00199 b
St. Petersburg	Allopatric	-0.01049 $\pm$ 0.00285 b, c
Competitive effect		
Miami	Allopatric	-0.02509 $\pm$ 0.00344 a
St. Petersburg	Allopatric	-0.01685 $\pm$ 0.00285 a, b
Ft. Meyers	Sympatric	-0.00869 $\pm$ 0.00301 b
Palmetto	Sympatric	-0.00752 $\pm$ 0.00308 b
New Orleans	Sympatric	-0.00718 $\pm$ 0.00293 b
West Palm Beach	Sympatric	-0.00626 $\pm$ 0.00308 b
Ft. Lauderdale	Allopatric	-0.00616 $\pm$ 0.00286 b
Key West	Allopatric	-0.00580 $\pm$ 0.00285 b

Significant pairwise contrasts are indicated by *different letters* and are reported in the main text

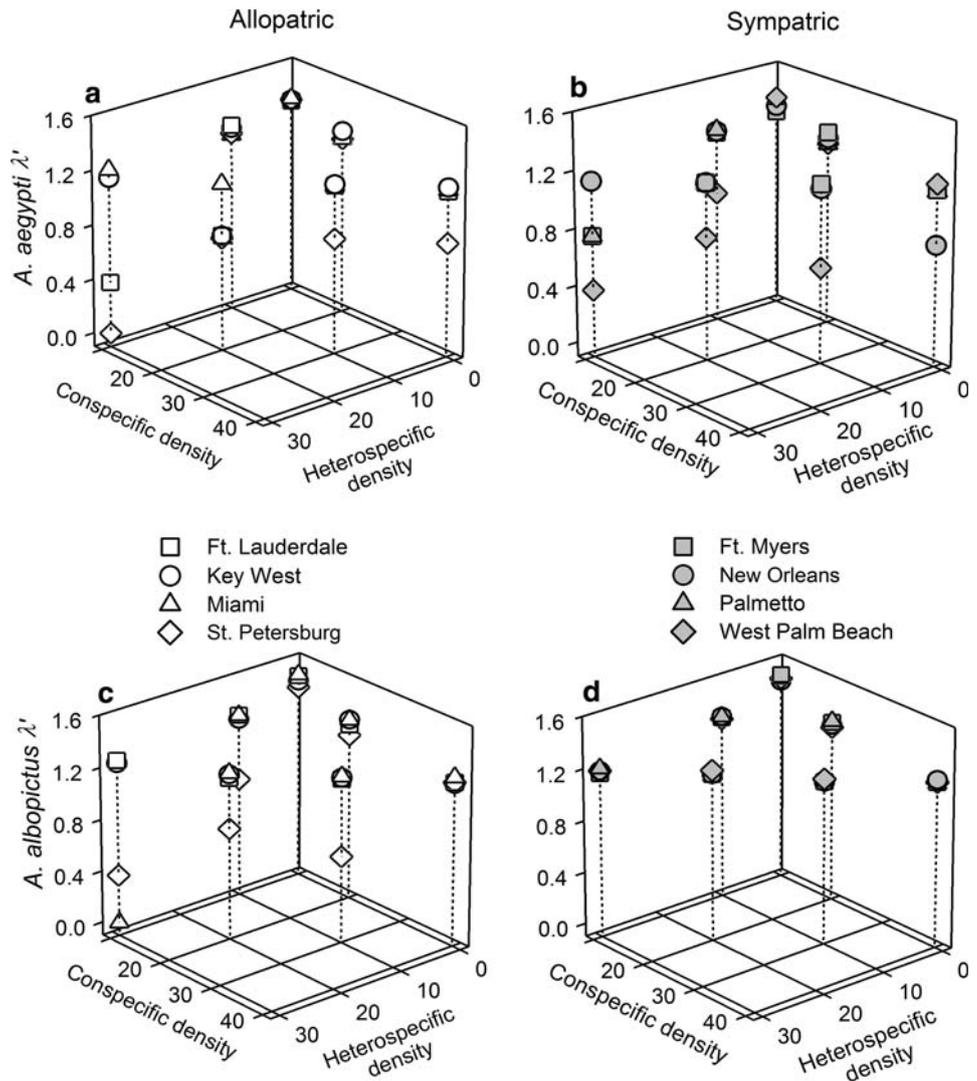
superior competitive effect of *A. aegypti* from sympatric sites is not strongly related to the fecundity–size relationship. This result is consistent with the observation that results of competition experiments with these species, analyzed using this composite index of performance, are not dependent on the fecundity–size relationship (Juliano 1998).

*A. albopictus* always yielded greater  $\lambda'$  than *A. aegypti* at high combined densities. This result is consistent with

previous field (Juliano 1998; Braks et al. 2004) and laboratory (Barrera 1996; Leisnham et al. 2009) experiments using natural leaf detritus as the nutrient base because it shows competitive superiority of *A. albopictus* over *A. aegypti*. Competition from all *A. aegypti* populations affected survivorship to adulthood, female size, and female development time of *A. albopictus* in the same way, arguing against strong population effects of competition on separate demographic variables. Prior studies have shown effects of competition on separate demographic variables of *Aedes* and *Culex* mosquitoes (e.g., Aspbury and Juliano 1998, Costanzo and Juliano 2005b), and our results again reaffirm the importance of estimating population rate of increase in competition studies (Livdahl and Sugihara 1984).

Our study is one of the first to show interpopulation divergence in competitive ability of a resident species associated with the pattern of invasion of an exotic species. Competition has been invoked as a major process conferring biotic resistance of resident communities to exotic invaders in plants (Levine et al. 2004) but is relatively unstudied among insects. Superior competition of *A. aegypti* from allopatric sites compared to sympatric sites may make an important contribution to reducing the performance of *A. albopictus* at allopatric sites, and thus may contribute to the lack of success of *A. albopictus* as an invader at these sites. This result suggests that inherent differences in competitive ability of *A. aegypti* may help prevent the establishment of *A. albopictus*. Comparing the competitive ability of *A. aegypti* from sites where *A. aegypti* have gone extinct to sites where *A. aegypti* coexists with *A. albopictus* would provide another (more direct) test of the role of biotic resistance in the invasion success of *A. albopictus*. Obviously, we cannot make such a comparison now. A previous study by Leisnham et al. (2009) showed no association of competitive ability of

**Fig. 1** Observed conspecific and heterospecific effects of larval densities on backtransformed estimated finite rate of increase ( $\lambda'$ ) of **a, b** *Aedes aegypti* and **c, d** *Aedes albopictus*. Panels are grouped by species (rows) and origin of *A. aegypti* populations that are either allopatric or sympatric to *A. albopictus* (columns)



**Table 3** Least squares linear model for  $\log_{10}$  mean mass and  $\log_{10}$  mean development time of females for both species in response to the independent variables of *A. albopictus* density, *A. aegypti* density, and population

Source	Mass						Development time					
	<i>A. albopictus</i>			<i>A. aegypti</i>			<i>A. albopictus</i>			<i>A. aegypti</i>		
	df	F	P	df	F	P	df	F	P	df	F	P
<i>A. albopictus</i> density	1, 135	12.17	<b>0.0007</b>	1, 118	14.84	<b>0.0002</b>	1, 135	<b>459.22</b>	<b>&lt;0.0001</b>	1, 118	14.84	<b>0.0002</b>
<i>A. aegypti</i> density	1, 135	9.25	<b>0.0028</b>	1, 118	14.88	<b>0.0002</b>	1, 135	<b>268.62</b>	<b>&lt;0.0001</b>	1, 118	14.88	<b>0.0002</b>
Population	7, 135	0.26	0.9692	7, 118	1.60	0.1409	7, 135	0.30	0.9507	7, 118	1.60	0.1409
<i>A. albopictus</i> × population	7, 135	0.25	0.9726	7, 118	0.70	0.6761	7, 135	1.20	0.3088	7, 118	0.70	0.6761
<i>A. aegypti</i> × population	7, 135	0.34	0.9324	7, 118	1.47	0.1852	7, 135	0.94	0.4815	7, 118	1.47	0.1852

Significant effects are indicated in *bold* and are reported in the main text

*A. albopictus* with the pattern of coexistence and displacement with *A. aegypti*. The results of our study in combination with those of Leisham et al. (2009) suggest that interpopulation variation among resident *A. aegypti*

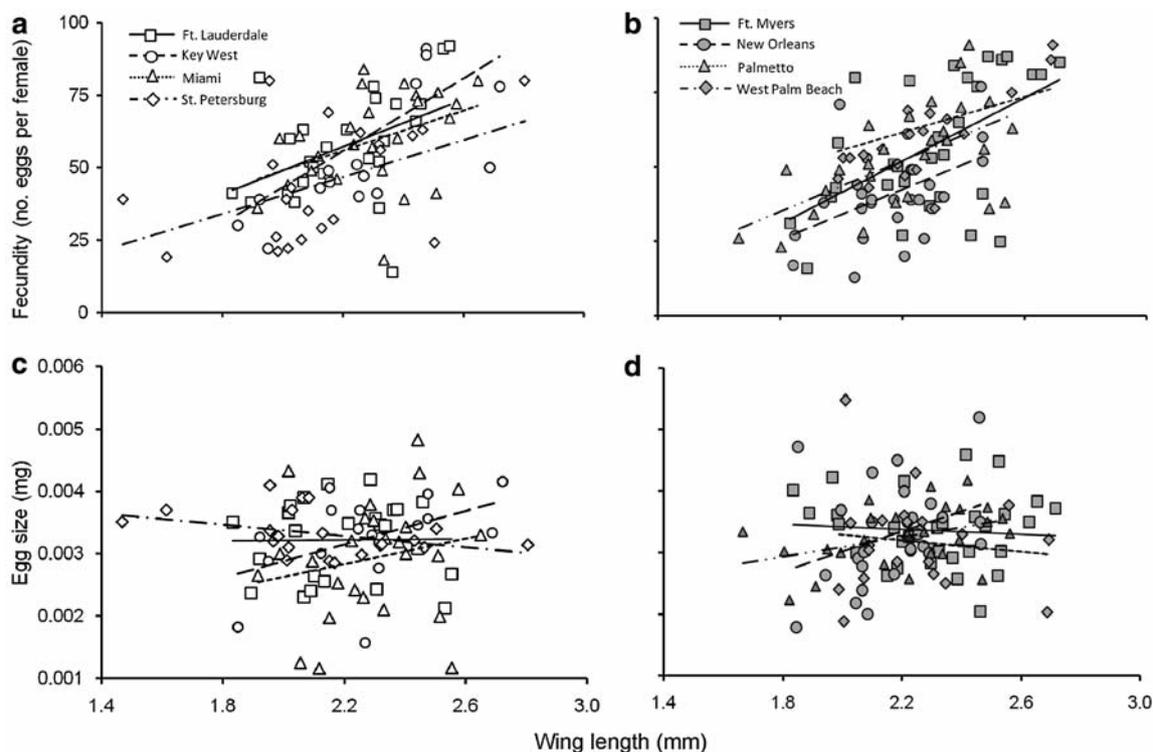
may make an important contribution to competition-mediated biotic resistance of *A. albopictus*.

At Miami, Fort Lauderdale, and St. Petersburg, *A. albopictus* has been present in low numbers at some stage in

**Table 4** Least squares multivariate analysis of covariance (MANCOVA) on fecundity and mean egg size of *A. aegypti* in response to the independent variables of population and wing length

Source of variation	MANCOVA			Standardized canonical coefficients	
	Pillai's trace ( <i>F</i> )	<i>df</i>	<i>P</i>	Fecundity	Egg size
Population	0.93	14, 354	0.5270	0.99	1.00
Wing length	<b>22.31</b>	<b>2, 176</b>	<b>&lt;0.0001</b>	<b>1.11</b>	<b>0.20</b>
Population × wing length	0.90	14, 354	0.5615	0.13	0.99

Significant effects and pairwise comparisons are indicated in *bold*. Only first variates are shown; all second variates are nonsignificant. See text for the results of pairwise contrasts between populations.

**Fig. 2** Relationships of wing length with **a, b** fecundity and **c, d** egg size in *A. aegypti* from populations that are either allopatric or sympatric to *A. albopictus*

the past (G. F. O'Meara, unpublished data; P. Leisnham, unpublished data) but has never become permanently established or spread, even at the same specific location within a city site (i.e., same cemetery). Our results that *A. aegypti* from Miami had the strongest effect and best response of all populations is consistent with the idea that characteristics of Miami *A. aegypti* may act as a barrier for *A. albopictus* invasion. However, *A. aegypti* from Fort Lauderdale or St. Petersburg did not show competitive ability superior to all other populations, thus suggesting that other abiotic and biotic factors, including temperature, rainfall, and detritus resources, specific to site types, are likely also important in limiting invasion success of *A. albopictus* (Juliano et al. 2002).

Coexistence of *A. aegypti* with *A. albopictus* may be also affected by the phenotypic responses of both species to environmental conditions, which differ among sites, with conditions at some sites favoring *A. aegypti* (Juliano et al. 2002, 2004; Costanzo et al. 2005a, b). Even if *A. aegypti* is consistently inferior in competition to *A. albopictus* under our lab conditions, when coupled with abiotic factors, *A. aegypti* populations with inherently better competitive ability may create barriers to *A. albopictus* invasion when *A. aegypti* populations with poorer competitive ability may not.

Interpopulation divergence in competitive effect and response of *A. aegypti* is consistent with the findings of Leisnham et al. (2009) who documented interpopulation

divergence in competitive effect and response of *A. albopictus*. Competitive effect is usually thought to be associated with ability to harvest and to deplete scarce resources (Tilman 1982). Competition between *A. albopictus* and *A. aegypti* is widely assumed to occur via resource depletion, and manipulating resources levels can alter the impact of competition (e.g., Braks et al. 2004; Juliano 1998). However, both species may be affected by interference competition produced by water-borne substances (Dye 1984; Broadie and Bradshaw 1991). Competition between invertebrates can involve multiple mechanisms (e.g., Byers 2000). Interpopulation differences in the specific mechanisms of competition between *A. albopictus* and *A. aegypti* could explain geographic divergence both in effect and response of *Aedes* in North America and competitive effect of *A. aegypti* on the superior competitor *A. albopictus*.

More generally, our results suggest that geographic variation among native or resident species in competitive characteristics is an under-appreciated aspect of variation in invasion success and impact. Whether such variation among populations arises due to strong selection for competitive ability (e.g., due to a history of inter- or intra-specific competition) or due to founder effects or other random processes resulting in interpopulation variation, it has the potential to be an important contributor to variation in invasion success and impact in many systems involving geographically widespread invaders (Travis 1996; Keller and Taylor 2008). Invasibility of native communities has been linked to community-level factors like diversity (e.g., Levine 2000) or taxonomic similarity of native species (e.g., Diez et al. 2008). Our results indicate that intraspecific variation of particular competitors that interact strongly with invaders can be another factor contributing to biotic resistance.

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