

Roles of spatial partitioning, competition, and predation in the North American invasion of an exotic mosquito

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Received: 2 July 2013 / Accepted: 13 February 2014
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Abstract Invasion success and species coexistence are often mediated by species interactions across patchily distributed habitats and resources. The invasive mosquito *Aedes japonicus japonicus* has established in the North American range of the competitively superior resident congener, *Aedes albopictus*, and the predatory native mosquito *Toxorhynchites rutilus*. We tested predictions for two hypotheses of invasion success and species coexistence: keystone predation and spatial partitioning. We tested competition between *A. japonicus japonicus* and *A. albopictus* with or without *T. rutilus* in laboratory microcosms, and measured abundances of *A. japonicus japonicus*, *A. albopictus*, other resident competing mosquito species, and the presence of *T. rutilus* among tree holes and tires in metropolitan Washington, DC. In laboratory microcosms, *A. albopictus* was competitively dominant over *A. japonicus japonicus*, which is consistent with the few prior studies of competition between these two *Aedes* species. *T. rutilus* predation severely lowered performances of both *Aedes* species but more severely lowered *A. japonicus japonicus* performance than *A. albopictus* performance when all three species co-occurred, thus yielding no evidence for keystone predation. Consistent with the spatial partitioning hypothesis, *A. japonicus japonicus* was negatively correlated and

independently aggregated with *A. albopictus* and all combined resident mosquito competitors and was not associated with *T. rutilus* among field containers. These results suggest that predation from *T. rutilus* and competition from *A. albopictus* are barriers to the spread of *A. japonicus japonicus*, but that *A. japonicus japonicus* may escape these interspecific effects by utilizing spatially partitioned container habitats.

Keywords Aggregation · Invasive · Keystone predation · Patchy habitat · Patchy resources

Introduction

Biological invasions are affected by interactions among traits of the invader, the resident community, and the environment (Shea and Chesson 2002). Ecological theory indicates that resident enemies can have strong effects on invaders and their spread via multiple possible mechanisms (Lodge 1993). In the simplest cases, resident enemies can limit invasion success directly through interference and resource competition, predation, and/or parasitism (Simberloff and Boecklen 1991). In more complex cases, interactions among resident enemies can affect invasion success via indirect effects, such as when an interaction between two species is indirectly mediated by a third species (Wootton 2002). For example, keystone predation, wherein a predator maintains greater community diversity by preying disproportionately on competitively dominant prey, can relieve competition on a competitively inferior invader and facilitate its spread (Blaustein and Chase 2007).

Species interactions can be affected by the distribution of habitats (Shea and Chesson 2002). Patchily distributed habitats can influence invasion success by altering the

Communicated by Steven Kohler.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-2909-7) contains supplementary material, which is available to authorized users.

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distributions of species and mediating interspecific interactions. When competitively asymmetric species co-occur, ecological theory predicts exclusion of the competitively inferior species (Hardin 1960). Predators can also negatively impact the growth of prey populations and in some cases cause extinction (Lodge 1993). However, when interacting species are distributed among patchy habitats, they may not co-occur in all patches, reducing their impact and fostering regional species coexistence (Shorrocks et al. 1979).

Container-dwelling mosquitoes provide an excellent model to investigate the effects of resident enemies on invasions. Natural (e.g., plant axils, tree holes) and artificial (e.g., birdbaths, buckets, discarded tires) water-holding containers are commonly utilized by the developmental stages (eggs, larvae, and pupae) of many native and invasive mosquitoes (Juliano and Lounibos 2005). Containers are patchily distributed, ephemeral, and typically resource limiting (Carpenter 1983; Leonard and Juliano 1995). Containers can also be colonized by predatory dipteran larvae that can strongly suppress prey mosquito populations (Lounibos et al. 1993; Grill and Juliano 1996). Thus, many mosquito communities are likely regulated by a variable mosaic of bottom-up resource competition and top-down predation (Lounibos et al. 1997; Juliano 2009).

In the eastern United States, the invasive *Aedes japonicus japonicus* (Theobald) co-occurs with the resident congener *Aedes albopictus* (Skuse) and the predatory native mosquito *Toxorhynchites rutilus septentrionalis* (Coquillett) in natural and artificial containers (Yee 2008; Farajollahi et al. 2009). *A. japonicus japonicus* invaded North America in the late 1990s via used tires from Japan (Peyton et al. 1999), and is a competent laboratory vector of La Crosse virus (Sardelis et al. 2002a), eastern equine encephalitis virus (Sardelis et al. 2002b), St. Louis encephalitis virus (Sardelis et al. 2003), and West Nile virus (Sardelis and Turell 2001). *A. albopictus* is native to Asia but is now a resident invader of the eastern United States (Hawley et al. 1987). Since its introduction in the mid-1980s, *A. albopictus* has rapidly become the most dominant container species in many urban areas in the eastern United States (Juliano and Lounibos 2005). The dominance of *A. albopictus* is likely due to its superior competitive ability as larvae (Juliano 2009; Juliano and Lounibos 2005), although some studies propose satyrization as adults to be a second mechanism for their dominance (Tripet et al. 2011; Bargielowski et al. 2013). At least one study has demonstrated that *A. albopictus* is competitively superior to *A. japonicus japonicus* (Armistead et al. 2008b). However, inconsistent with the simplest predictions of competitive exclusion theory, *A. japonicus japonicus* has continued to spread throughout the eastern United States into the ranges of both *A. albopictus* and *T. rutilus*, and coexist with both resident species (Fonseca et al. 2010).

A number of hypotheses could explain the invasion of *A. japonicus japonicus* among patchy container habitats in the ranges of *A. albopictus* and *T. rutilus*. In this study, we used a controlled laboratory experiment and field container surveys to test two alternative (but not mutually exclusive) hypotheses. One hypothesis is that keystone predation by *T. rutilus* is facilitating the invasion of *A. japonicus japonicus* into containers where it co-occurs with competitively superior *A. albopictus*. A second hypothesis is spatial segregation, in which *A. japonicus japonicus* invasion success is due to its independent aggregation from *A. albopictus* and *T. rutilus*. Some of the conditions necessary for the coexistence mechanisms postulated by these hypotheses are present in this system.

Keystone predation by *T. rutilus* may relieve the effect of competition on *A. japonicus japonicus* if co-occurring *A. albopictus* is preferentially preyed upon. Past studies have shown that *T. rutilus* predation can alter the outcome of competition among prey species (Griswold and Lounibos 2005, 2006), but the effect of *T. rutilus* predation on competition between *A. albopictus* and *A. japonicus japonicus* has not yet been examined. The highly active foraging behavior of *A. albopictus* larvae allows it to be competitively superior to many other mosquito species, but it increases the number of times *A. albopictus* encounters predators, including *T. rutilus* (Kesavaraju et al. 2011), thus providing an ecological mechanism that may promote keystone predation. *A. japonicus japonicus* exhibits predator avoidance behavior in the presence of chemical cues released by *T. rutilus* predation, which is likely to decrease predator-induced mortality while incurring indirect costs, such as reduced foraging time (Kesavaraju et al. 2011).

Spatial segregation among enemies can reduce the effect of interspecific interactions. The aggregation model of coexistence postulates that species coexistence is facilitated if intraspecific aggregation is greater than interspecific aggregation (Ives 1988a, b; Sevenster 1996). If *A. japonicus japonicus* is aggregated independently among individual containers, its overlap with *A. albopictus* is reduced, lessening the effect of interspecific competition. Coexistence of *A. japonicus japonicus* and *A. albopictus* via independent aggregation is most likely to occur if each species is attracted to different environmental cues, either at the landscape scale (e.g., urban vs. forest) or container level (e.g., physiochemical characteristics) (Ives 1988a; Hartley and Shorrocks 2002). This can be considered a form of spatial resource partitioning (Chesson 2000). However, some (Hartley and Shorrocks 2002) have argued that if random aggregation is sufficiently strong, competitors could be more limited by intraspecific than interspecific competition, resulting in coexistence (Chesson 2000; Hartley and Shorrocks 2002). Similarly, spatial segregation of predators and prey among habitats can reduce predation impacts

(Mogi and Sembel 1996; Nachman 2006). If *A. japonicus japonicus* is aggregated independently of *T. rutilus* among individual containers, negative impacts of predation are likely to be reduced.

In this paper, we test whether predation and competition among *A. japonicus japonicus*, *A. albopictus*, and *T. rutilus*, and the spatial distribution of these species in the field, are consistent with these two hypotheses. A laboratory experiment directly tested the roles of competition and *T. rutilus* predation on the population performances of *A. albopictus* and *A. japonicus japonicus*. Mosquito co-occurrence was measured among tree hole and tire habitats to investigate relative roles of these interspecific interactions in the field. Each hypothesis has distinct, testable predictions about the distribution and abundance of these mosquitoes in the field and relative impacts of competition and *T. rutilus* predation:

1. Keystone predation predicts that in the field, *A. japonicus japonicus* abundance will be negatively correlated with *A. albopictus* abundance, and *A. albopictus* abundance will be more strongly negatively associated with *T. rutilus* presence than *A. japonicus japonicus* abundance. In laboratory microcosms, population performance and survival of *A. japonicus japonicus* will be higher in the presence of both *A. albopictus* and *T. rutilus* compared to in the presence of *A. albopictus* only.
2. The spatial segregation hypothesis predicts that abundances of *A. japonicus japonicus* and *A. albopictus* will be aggregated intraspecifically, that intraspecific aggregation will be stronger than interspecific aggregation for both *Aedes* species, and that *A. japonicus japonicus* will be associated with the absence *T. rutilus*.

Materials and methods

Laboratory experiment

Aedes japonicus japonicus (F₁₋₃ generation; Center for Vector Biology, Rutgers University, NJ) and *Aedes albopictus* (F₁ generation; University of Maryland, College Park, MD) eggs were synchronously hatched in a solution of 0.3 g Brewer's yeast per 1 L of distilled water. Within 24 h, larvae were rinsed and transferred to the experiment. One of five competition densities of *A. japonicus japonicus*:*A. albopictus* (150:0, 300:0, 150:150, 0:300, 0:150) were added to six container microcosms (800-mL cups containing 720 mL distilled water and provisioned with 3 g of senescent *Quercus alba* litter). These competition densities represented three competition conditions for each species: low intraspecific competition (150:0 or 0:150), high intraspecific competition (300:0 or

0:300), and interspecific competition (150:150), with high intraspecific competition and interspecific competition having the same density of total larvae. One first-instar *Toxorhynchites rutilus* was added to three containers of each competition density 3 days after the addition of the prey species, while three containers of each competition density acted as controls without *T. rutilus*. The predator was added after a 3-day delay to mimic the likely timeline of *T. rutilus* oviposition and hatching in a recently flooded tree hole. This design yielded 18 experimental units with *A. japonicus japonicus*, 18 experimental units with *A. albopictus*, and 30 total experimental units. Cups were established 4 days prior to the addition of larvae and inoculated with 200 μ L of pond water to allow microbial communities to colonize and establish (Smith et al. 2013). One gram of additional leaf litter from the same collection date and location was added on day 7 of the experiment and every 14 days thereafter, mimicking the periodic addition of litter in natural systems. These per capita resource amounts (0.01–0.02 g per larva) are similar to those of past studies testing competition between *Aedes* mosquitoes (e.g., Griswold and Lounibos 2005; Armistead et al. 2008a).

The experiment was housed in an environmental chamber at 26 °C with a light:dark 14:10-h photoperiod to approximate summer conditions. Treatments were randomly assigned cups, and cup position was shuffled daily. Pupae were removed from containers daily and placed into individual vials until adult emergence. Adults were sexed, identified, and dried (>24 h, 50 °C), and females' wings were measured. For each cup, proportion survivorship, median female development time, and mean female wing length were calculated for *A. japonicus japonicus* and *A. albopictus*. These fitness parameters were used to estimate the finite rate of population increase (λ') (Juliano 1998; details in Online Resource 1).

Field study

Mosquitoes were sampled from containers within five tree hole sites and six tire sites in the metropolitan Washington DC area, where *A. albopictus* has been a resident since the late 1980s (Moore et al. 1988). Sampling occurred from late July to early September 2011, which represents the peak period of mosquito activity in the area (Kilpatrick et al. 2006). Tree hole sites were located in forested areas at least 50 m from the forest edge. Used tires were sampled in urban areas. Surveys occurred 3–4 days after rainfall events of at least 6 mm, and consisted of destructively sampling all containers (from six to 18 per site) at each site. Each individual container and each site was only sampled once, to yield a total of 100 containers. Entire contents of each container (water,

detritus, and all biota) were collected. Detritus was dried at 35 °C for >48 h and weighed as a measure of resource quantity. All larvae and pupae were identified to species level and counted. Container water was measured for volume and pH, and a 75-mL subsample was acidified at pH 2.0 and refrigerated for later analysis of total N (TN) and total P (TP) using Hach test kits (TNT826 and TNT844, respectively) and a Hach 3800 spectrophotometer (Hach, CO).

Mosquito aggregation was assessed by calculating the index of intraspecific aggregation (J), which is the proportionate increase in the average number of conspecifics found in a patch relative to the number expected of a random distribution; an index of interspecific aggregation (C), which is proportionate increase in the average number of heterospecifics found in a patch relative to the number expected of a random distribution; and an index of relative aggregation (T), which is the relative strength of intraspecific vs. interspecific aggregation (Ives 1991; Sevenster 1996; see details in Online Resource 2). Patches are allowed to differ in size and quality (Sevenster 1996). In addition to collecting *A. albopictus*, *A. japonicus japonicus*, and *T. rutilus* (see Results), we also collected *Culex pipiens* (L.) and *Aedes triseriatus* (Say) from 27 % (27/100) and 67 % (67/100) of all containers, respectively. Numerous studies have shown that *C. pipiens* and *A. triseriatus* are generally poor resource competitors (Juliano 2009), and that their competitive effects on *A. japonicus japonicus* are weak (Hardstone and Andreadis 2012). Therefore, we expect *A. albopictus* to be the greatest competitive barrier to *A. japonicus japonicus* invasion in containers, and it is the focus of this study. However, competition from weak competitors, particularly multiple weak competitors, may not be trivial as a contributor to barriers to invasion (MacArthur 1972; Moen 1989); thus we also compare the spatial distribution of *A. japonicus japonicus* invasion with the entire community of competing resident mosquitoes. Aggregation of multiple (more than two) species can be analyzed either by calculating C and T for all pairwise species comparisons (Ives 1991) or by combining the abundances of all competitors and treating them as one theoretical super-organism (Shorrocks and Rosewell 1986; Abós et al. 2006). We utilize the latter method when including *C. pipiens* and *A. triseriatus* in aggregation analyses. Aggregation of the larval competing stages could result from either aggregation of female oviposition visits or deposition of eggs aggregated in clutches (Hartley and Shorrocks 2002). Following prior studies, this paper does not attempt to separate aggregation of oviposition visits from aggregation due to multi-egg clutches, but accounts only for aggregation of competing stages (see Hartley and Shorrocks 2002; Leisnham and Juliano 2009).

Statistical analyses

Laboratory experiment

We used two-way ANOVAs to test effects of competition and predation on survival and λ' using SAS Proc Mixed (SAS Institute 2003). Differences among competition conditions and between predation treatments were determined using pairwise tests with Bonferroni correction for all possible comparisons within each analysis. Survival was $\log_{10}(y + 1)$ transformed to account for assumptions of normality and homogeneity of variances. For λ' , a cone-shaped plot of the residuals indicated a systematic pattern of variation, with increasing variation with treatment means. Plots of treatment means (Fig. 1c, d) subjectively indicate a competition \times predation interaction effect on λ' of each species, but these were not statistically significant ($P > 0.05$) due to increased variation caused by systematic heterogeneity ($P < 0.0001$). Therefore, we used the two-way ANOVA to compare simple effects (Steel and Torrie 1980) of predation and competition factors on λ' .

Field survey

Wilcoxon signed rank tests were used to test for independent aggregation of *A. japonicus japonicus* vs. *A. albopictus* and *A. japonicus japonicus* vs. the entire competing community, among individual container habitats with the null hypotheses that $J = 0$, $C = 0$, and $T = 1$. To test relationships among mosquito abundances, sites, and physiochemical container characteristics, we performed three multivariate ANOVAs (MANOVAs) using SAS Proc GLM (SAS Institute 2003). The first MANOVA analyzed *A. japonicus japonicus* and *A. albopictus* abundances as dependent variables and site as an independent variable. Containers that had no mosquitoes were removed from the analysis since they give no information of relative densities of each species between habitat types, thus yielding 94 total containers in the analysis. The second MANOVA analyzed detritus (g dry weight), TN (mg L^{-1}), and TP (mg L^{-1}) as dependent variables and site as an independent variable. TN tests were not done on one container, so that container was excluded from the analysis. Because volume strongly covaried with detritus amount ($r = 0.79$, $P < 0.0001$) and is likely to vary by site we re-ran this MANOVA with volume (mL) as an independent variable instead of detritus. The third MANOVA analyzed *A. japonicus japonicus* and *A. albopictus* abundances as dependent variables and detritus amount, TN, and TP as independent variables. Because volume may also influence oviposition of container mosquitoes, we re-ran this MANOVA with volume as an independent variable instead of detritus. Consistent with our aggregation analyses above, we also re-ran MANOVAs on mosquito abundances after including *C. pipiens* and

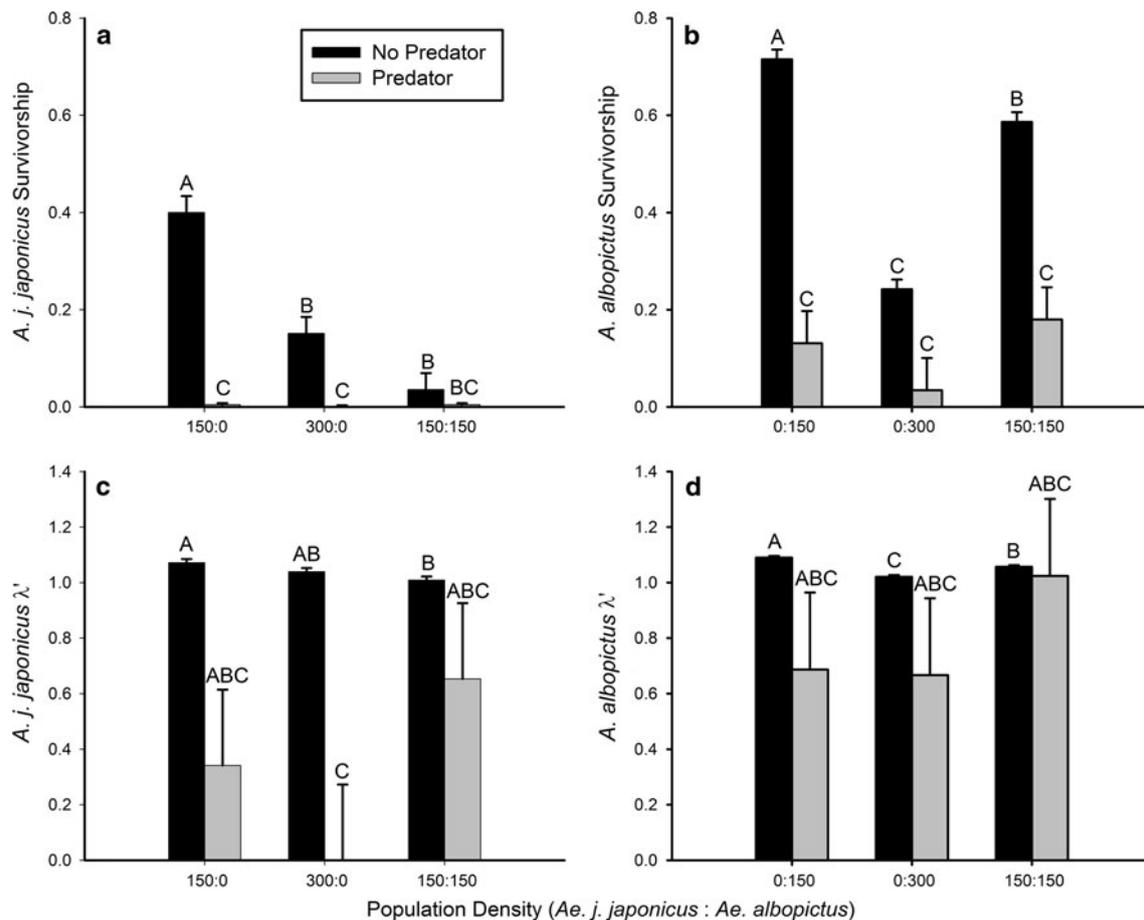


Fig. 1 Effects of competition densities and presence or absence of *Toxorhynchites rutilus* on survival (a, b) and finite rate of population increase (c, d) of *Aedes japonicus japonicus* and *Aedes albopictus*

($n = 3$). Data were statistically tested using ANOVA. Least squares mean values are \pm SE. Significant pairwise comparisons are indicated by different letters above bars

A. triseriatus as dependent variables, along with *A. japonicus japonicus* and *A. albopictus*, to consider the entire community of competitors. For all MANOVAs, F -statistics were derived from Pillai's trace (SAS Institute 2003). Standardized canonical coefficients (SCCs) (Scheiner 2001) were used to analyze correlations among dependent variables and determine the relative contributions of dependent variables to significant effects. *Aedes japonicus japonicus* and *A. albopictus* abundances were $\log_{10}(y + 1)$ transformed to account for assumptions of normality and homogeneity of variances. We used logistic regression tests to explore associations of *T. rutilus* presence with site and physiochemical container characteristics using Proc Logistic (SAS Institute 2003). In two tests *T. rutilus* presence was the dependent variable. In the first test, site was the independent variable. In the second test, detritus, TN, TP, *A. japonicus japonicus* abundance, and *A. albopictus* abundance were independent variables. Significant differences among sites and mean differences between tire sites and tree hole sites in MANOVAs and logistic regressions were determined using pairwise

contrasts with sequential Bonferroni correction for all possible comparisons within each analysis (Scheiner 2001). Sites in this study were not randomly selected, so we treated site as a fixed effect and all statistical inferences are restricted to the sites chosen. This strategy is consistent with past studies (e.g., Reznick et al. 2001; Leisham et al. 2009; Leisham and Juliano 2010) and follows a strict interpretation of random effects in linear models (Sokal and Rohlf 1995).

For all analyses, two-way interactions were included in initial models but were removed from final models if all were non-significant. Experiment-wise $\alpha = 0.05$; marginal significance was defined at $\alpha = 0.05$ –0.10.

Results

Laboratory experiment

Survival and λ' of both *A. japonicus japonicus* and *A. albopictus* only varied among competition conditions

without *T. rutilus* predation (Fig. 1), and a clear competition \times predation interaction for *A. japonicus japonicus* ($F_{2, 12} = 30.03$, $P < 0.0001$) and *A. albopictus* ($F_{2, 12} = 6.81$, $P = 0.0106$) survival was detected. Without *T. rutilus*, *A. japonicus japonicus* had the lowest survival and λ' under interspecific competition, indicating that *A. albopictus* has a greater negative impact than conspecifics on *A. japonicus japonicus* performance (Fig. 1a, c). In contrast, *A. albopictus* had the lowest survival and λ' under high intraspecific competition, indicating that conspecifics have a greater negative impact than *A. japonicus japonicus* on *A. albopictus* performance (Fig. 1b, d). With *T. rutilus*, *A. albopictus* had higher λ' and survival than *A. japonicus japonicus* under all competition conditions, indicating that it is less affected by predation, although variation around treatment means was high (Fig. 1). *T. rutilus* predation negatively affected *A. japonicus japonicus* survival under high and low intraspecific competition (Fig. 1a), and negatively affected *A. japonicus japonicus* λ' under high intraspecific competition (Fig. 1c), but did not affect *A. japonicus japonicus* survival or λ' under interspecific competition (Fig. 1a, c). *A. albopictus* survival was negatively affected by predation under low intraspecific competition and under interspecific competition, but not under high intraspecific competition (Fig. 1b), and did not affect *A. albopictus* λ' under any competition conditions (Fig. 1d).

Field survey

A. albopictus, *A. japonicus japonicus*, and *T. rutilus* were collected from 65.0 % (65/100), 28 % (28/100), and 15 % (15/100) of all containers, and constituted 28.2 % (3,178/11,270), 3.7 % (419/11,270), and 0.3 % (36/11,270) of total larvae, respectively. All three species were collected from both tree hole and tire habitats and 91.7 % (10,337/11,270) of all organisms were early instar larvae.

A. japonicus japonicus ($J_j = 2.89$, $P = 0.0020$) and *A. albopictus* ($J_a = 1.51$, $P = 0.0039$) abundances were aggregated among all containers, and the index of aggregation showed independent aggregation ($T_{ja} = 0.60$, $P = 0.0020$), indicating that aggregation is strong enough to be both necessary and sufficient for coexistence. The index of aggregation was marginally different from unity among tires ($T_{ja} = 0.77$, $P = 0.0625$) and tree holes ($T_{ja} = 0.46$, $P = 0.0625$). Interspecific aggregation (C_{ja}) was never different from zero (C_{ja} values = 0.25–0.76), indicating that interspecific aggregation is weak. Pooled abundances of all resident competitors (*A. albopictus* + *C. pipiens* + *A. triseriatus*) were aggregated among all containers ($J_c = 1.23$, $P = 0.0032$), and the index of aggregation showed independent aggregation of the entire resident community with respect to *A. japonicus japonicus* among all habitats ($T_{jc} = 0.79$, $P = 0.0008$), among tires only ($T_{jc} = 0.64$,

$P = 0.0670$), and among tree holes only ($T_{jc} = 0.69$, $P = 0.0715$).

There was an effect of site on *A. japonicus japonicus* and *A. albopictus* abundances ($F_{20, 126} = 7.07$, $P < 0.0001$). SCCs indicated that *A. japonicus japonicus* (SCC = -1.15) and *A. albopictus* (SCC = 1.44) both contributed strongly to this result but were negatively correlated among sites. Mean abundances among tire sites and tree hole sites were different ($F_{2, 62} = 21.88$, $P < 0.0001$), signifying that *A. japonicus japonicus* and *A. albopictus* abundances vary by site type (Fig. 2). Abundances of both *A. japonicus japonicus* and *A. albopictus* were higher in tire sites than in tree hole sites (Fig. 2). SCCs indicate that the site type mean abundances of *A. japonicus japonicus* (SCC = -0.20) were negatively correlated with the site type mean abundance of *A. albopictus* (SCC = 1.44), and *A. albopictus* abundance explained most of the difference between tires and tree holes. When *C. pipiens* and *A. triseriatus* were added as dependent variables to the model, the effect of site ($F_{40, 332} = 6.20$, $P < 0.001$) and the relationship between *A. albopictus* (SCC = -1.31) and *A. japonicus japonicus* (SCC = 1.03) did not change, and SCCs indicated that *C. pipiens* (SCC = 0.58) and *A. triseriatus* (SCC = 0.37) contributed weakly to the result.

There was an effect of site on physiochemical container characteristics ($F_{30, 246} = 2.49$, $P < 0.0001$). SCCs showed that detritus (SCC = 1.18) contributed most strongly to this effect, while TN (SCC = -0.23) and TP (SCC = 0.38) had weak contributions. In models that replaced detritus with container volume, there was a similar effect of site on physiochemical container characteristics ($F_{30, 246} = 3.95$, $P < 0.0001$) and volume contributed most strongly to the effect (SCC = 1.75) while TN (SCC = -0.20) and TP (SCC = 0.32) had weak contributions. Mean physiochemical characteristics varied between tires and tree holes ($F_{3, 80} = 6.64$, $P = 0.0005$). Tires had more detritus and greater volume, but lower concentrations of TN and TP, than tree holes (Online Resource 3; Fig. 1).

Detritus was significantly related to *A. japonicus japonicus* and *A. albopictus* abundances (Table 1). Both species were positively related to increasing detritus but *A. japonicus japonicus* contributed more strongly to this relationship than *A. albopictus* (Table 1). TN was marginally significantly related to *A. japonicus japonicus* and *A. albopictus* abundances (Table 1). *A. albopictus* contributed more strongly to the effect of TN than *A. japonicus japonicus*, and was negatively correlated with *A. japonicus japonicus* across TN concentrations (Table 1). TP did not affect abundances of mosquitoes. Container volume had a similarly strong and positive effect on *A. japonicus japonicus* and *A. albopictus* abundances when replacing detritus in models ($F_{2, 88} = 67.77$, $P < 0.0001$; *A. japonicus japonicus*

Fig. 2 Bivariate plot of species abundances among tire (filled symbols; $n = 48$) and tree hole (open symbols; $n = 46$) sites. Data were statistically tested using multivariate ANOVA. Abundances are $\log_{10}(y + 1)$ -transformed least squares mean \pm SE

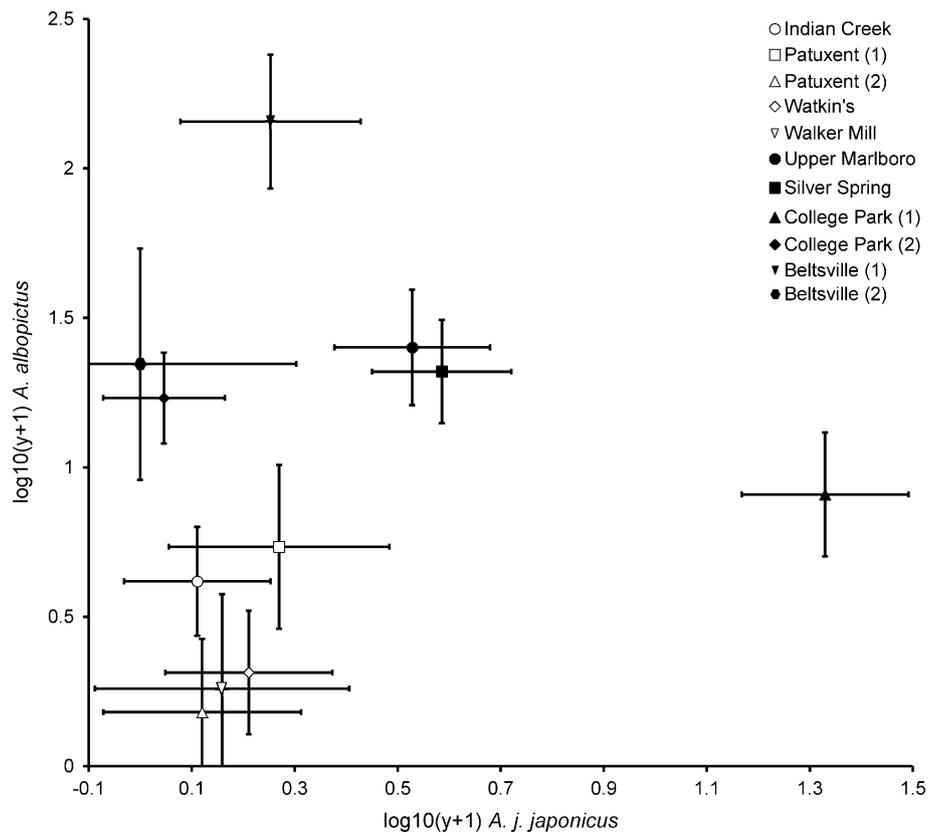


Table 1 Multivariate ANOVA of the effects of physiochemical container characteristics on $\log_{10}(y + 1)$ -transformed abundances of *Aedes japonicus japonicus* and *Aedes albopictus* ($n = 94$)

Source of variation	Multivariate statistics			Standardized canonical coefficients	
	Pillai's trace (<i>F</i>)	<i>df</i>	<i>P</i>	<i>A. japonicus japonicus</i>	<i>A. albopictus</i>
Detritus	75.82	2, 88	<0.0001	1.50	0.29
Total N	2.57	2, 88	0.0822	-0.58	1.12
Total P	1.92	2, 88	0.1528	0.73	0.96

Significant ($P < 0.05$) and marginally significant ($P = 0.05-0.10$) effects are indicated in *italic*

SCC = 1.33; *A. albopictus* SCC = 0.47); however, TN was no longer significant ($P > 0.10$). When *C. pipiens* and *A. triseriatus* were added to the model, the effects of detritus ($F_{4, 86} = 37.62, P < 0.0001$) and volume ($F_{4, 86} = 54.68, P < 0.0001$) were unchanged, but TN was non-significant ($P > 0.10$).

Presence of *T. rutilus* did not vary by site ($\chi^2_{10} = 9.31, P = 0.501$) or between tire sites and tree hole sites ($\chi^2_1 = 0.001, P = 0.9920$), but did vary with abundances of both *A. japonicus japonicus* and *A. albopictus* (Table 2). When *C. pipiens* and *A. triseriatus* were added as independent variables to the model, presence of *T. rutilus* varied by abundance of *A. japonicus japonicus* ($\chi^2_1 = 4.48, P = 0.0342$), but not by abundance of *A. albopictus*, TN, TP, detritus, or volume.

Discussion

A. japonicus japonicus has invaded into the North American range of the resident competitor *A. albopictus* and the native predator *T. rutilus*, and continues to coexist with these species and spread despite evidence from at least one study that it is an inferior resource competitor (Armistead et al. 2008a). Consistent with Armistead et al. (2008a), results of the laboratory experiment in our study indicate that *A. albopictus* is competitively superior to *A. japonicus japonicus*. We also found *A. japonicus japonicus* was more severely negatively impacted by *T. rutilus* predation than *A. albopictus*. These results indicate that there may be ecological barriers to *A. japonicus japonicus* invasion by resident mosquito enemies. However, spatial patterns of *A.*

Table 2 Logistic regression of the effects of *A. japonicus japonicus* abundance, *A. albopictus* abundance, and physiochemical container characteristics on the presence or absence of *T. rutilus* ($n = 94$)

Source of variation	χ^2	df	P
<i>A. japonicus japonicus</i> abundance	4.49	1	0.0340
<i>A. albopictus</i> abundance	3.81	1	0.0506
Detritus	1.72	1	0.1885
Total N	0.02	1	0.8854
Total P	1.45	1	0.2284

Significant ($P < 0.05$) and marginally significant ($P = 0.05$ – 0.10) effects are indicated in *italic*

japonicus japonicus and the resident enemies among field containers were consistent with predictions of the spatial segregation hypothesis, providing evidence that *A. japonicus japonicus* may sufficiently utilize refuge from negative species interactions to successfully invade into North America.

In this study, intraspecific aggregation was stronger than interspecific aggregation for both *A. japonicus japonicus* and *A. albopictus* among all containers and among tire sites and tree hole sites separately, fulfilling necessary and sufficient conditions for coexistence among competing species due to aggregation (Sevenster and VanAlphen 1996). Moreover, intraspecific aggregation was also stronger than interspecific aggregation for *A. japonicus japonicus* vs. the entire resident community of mosquito competitors, which also included *C. pipiens* and *A. triseriatus*. Interspecific aggregation (C_{ja}) of *A. japonicus japonicus* vs. *A. albopictus* and of *A. japonicus japonicus* vs. the entire resident community was weak or non-existent. The results of this study are consistent with prior surveys (Leisnham and Juliano 2009; Fader and Juliano 2013) and experiments (Fader and Juliano 2013) of mosquito competition, as well as studies of other patchily distributed freshwater invertebrates (e.g., Williams et al. 1993; Murphy et al. 1998; Schmera 2004; Abós et al. 2006).

Spatial separation due to independent aggregation is most likely to arise due to attraction of competitors to different environmental conditions that have some spatial independence (Ives 1988a; Chesson 2000; Hartley and Shorrocks 2002). In this study, *A. japonicus japonicus* and *A. albopictus* abundances were both higher in tires than in tree holes, providing no evidence for spatial segregation on the landscape scale between these two site types. Both species were also similarly positively related to detritus amount and volume. There is strong selection on *Aedes* females to oviposit in habitats that favor survival of their offspring (Yoshioka et al. 2012). Larger volume and detritus amounts are container parameters that likely indicate greater habitat permanence (Sota et al. 1994) and food resources (Yee and Juliano 2006), respectively, and likely

provide strong oviposition cues to *A. japonicus japonicus* and other mosquitoes. Interestingly, *A. japonicus japonicus* and *A. albopictus* showed different responses to TN. Past studies have indicated that TN is strongly positively related with mosquito abundances (Carpenter 1983; Walker et al. 1991; Kaufman et al. 2002), perhaps because TN stimulates growth of microorganisms and facilitates the microbial decomposition of leaf detritus (e.g., Kaufman and Walker 2006; Yee and Juliano 2006). Our results show that *A. albopictus* is positively associated with TN, while *A. japonicus japonicus* is negatively associated with TN. The negative relationship of *A. japonicus japonicus* with TN is particularly interesting and may be an indirect result of strong oviposition avoidance behavior against containers with *A. albopictus*. Further studies need to be done to ascertain the specific ecological and evolutionary mechanisms behind this relationship.

There were distinct differences of the aggregation index T_{ja} among tires compared to among tree holes, indicating that site type may affect intraspecific and interspecific aggregation. Despite having a lower index of aggregation T_{ja} , both intraspecific and interspecific aggregation were lower in tree holes than in tires, indicating that abundances of both species among tree holes are more randomly distributed than in tires. Differences in aggregation between site types are likely due to physiochemical and biological characteristics of the containers or characteristics of the surrounding environment, and this is another aspect of the spatial ecology of container mosquitoes that merits further study. Aggregation of the larval competing stages could result from either aggregation of female oviposition visits or deposition of eggs aggregated in clutches (Hartley and Shorrocks 2002), and this study does not attempt to separate aggregation of oviposition visits from aggregation due to multi-egg clutches. Future research involving an oviposition preference study of *A. albopictus* and *A. japonicus japonicus* could directly test clutch aggregation due to female choice.

The presence of *T. rutilus* was associated with abundances of both prey species. The association of *T. rutilus* with *Aedes* prey may be because ovipositing *T. rutilus* are attracted to containers that have higher numbers of prey (Trimble 1979; Macias-Duarte et al. 2009), or that have environmental cues that are similarly attractive to prey and predator (e.g., Sunahara et al. 2002). Regardless of the ecological mechanism that may underpin this association, the number of containers that we sampled that had *T. rutilus* was much lower compared to the number that contained prey species. This finding is consistent with past studies (Lounibos et al. 1997), and likely limits their impacts on prey fitness and survival.

In this study, we measured spatial patterns of larval mosquitoes which is consistent with many prior studies that

have measured aggregation using competing stages (e.g., Abós et al. 2006; Fader and Juliano 2013). There is the possibility that spatial segregation among species is affected by prior competition and predation rather than only oviposition selection by parental female adults. However, we sampled previously dry containers 3–4 days after rainfall and likely only 1–2 days after egg hatching and larval emergence. The vast majority of collected larvae (91.7 %) was first or second instar. Thus, it was unlikely that the patterns of the species in this study were substantially affected by competition and predation before being sampled.

This study provided no evidence for keystone predation, but revealed the relative effects of predation and competition on the invasion of *A. japonicus japonicus*. *T. rutilus* predation had strong negative effects on λ' and survival of both *A. japonicus japonicus* and *A. albopictus*, but especially on the new invader. This result is inconsistent with a prior study that showed that *A. japonicus japonicus* was more effective at utilizing behavioral responses to escape predation than *A. albopictus* (Kesavaraju et al. 2011). Effects of competition were only apparent in treatments without a predator because so few individuals survived in the presence of *T. rutilus*. Without *T. rutilus*, competition decreased λ' and survival of both *Aedes* species, but there were clear differences in the relative roles of interspecific vs. intraspecific competition. Interspecific competition had the strongest effect on *A. japonicus japonicus* while intraspecific competition had the strongest effect on *A. albopictus*. Our results are consistent with findings from the only other study testing competition between North American *A. japonicus japonicus* and *A. albopictus* (Armistead et al. 2008a), which also found *A. albopictus* to be a clearly superior resource competitor than *A. japonicus japonicus*. Interestingly, *A. japonicus japonicus* had lower λ' and survival than *A. albopictus* in high-resource intraspecific (150:0) containers, indicating poorer population performance even without the effects of interspecific competition and predation. This finding may be because *A. albopictus* was better suited to the laboratory conditions used in the experiment. Although we chose abiotic and biotic conditions common in the field, both *Aedes* species utilize larval habitats that may vary considerably in a range of factors that affect population dynamics, including temperature, resource amounts and type, habitat permanence, and environmental toxins. The performance of mosquito species and the outcome of species interactions can vary across habitat gradients (e.g., Juliano 2009). Therefore, while this study is one of the first to provide a rigorous evaluation of competition and predation on the invasion of *A. japonicus japonicus*, further studies under different conditions that are commonly seen in the field are needed.

The inclusion of *C. pipiens* and *A. triseriatus* abundances in MANOVA models and aggregation analyses generally gave similar conclusions as those with only *A. japonicus japonicus* and *A. albopictus*. These findings indicate that *C. pipiens* and *A. triseriatus* larvae probably do not directly influence the abundance (and invasion) of *A. japonicus japonicus*, which is consistent with the conclusions of Hardstone and Andreadis (2012). However, there are likely many other ecological factors that may influence *A. japonicus japonicus* abundances and observed coexistence with *A. albopictus*. For example, past studies have shown that *A. japonicus japonicus* may be able to emerge earlier in the season than *A. albopictus*, and this phenological difference may allow *A. japonicus japonicus* to utilize a temporal refuge from the competitive effects of *A. albopictus* (Armistead et al. 2012). Competitors can escape local extinction via a number of mechanisms, including differential resource use (e.g., Tilman 1982), condition-specific competition (Chesson 2000), or trade-offs between competitive ability and environmental tolerances (Dunson and Travis 1991), and many of these mechanisms have been invoked to explain the invasion of *A. japonicus japonicus* into North America (see Juliano and Lounibos 2005). Addressing the roles of these and other mechanisms in governing the invasion of *A. japonicus japonicus* will be important in further understanding the ecological and medical impacts of this particular species, as well as basic processes underpinning animal invasions and species coexistence.

This is the first study to investigate the roles of competition and predation in the invasion of *A. japonicus japonicus* into the range of *A. albopictus* and *T. rutilus*. This study found evidence that intraspecific aggregation is likely to provide refuge from competition for *A. japonicus japonicus*, and facilitate the invasion of this exotic mosquito into North America. There was no support for keystone predation by *T. rutilus*, and direct predation impacts may be a stronger impediment to the invasion of *A. japonicus japonicus* than the competition in containers where all three species co-occur. However, *T. rutilus* were rare in the field. Future research should focus on the relationship between *A. japonicus japonicus* with N, and the ability of *A. japonicus japonicus* to escape competition by early seasonal emergence relative to competitors.

Acknowledgments We thank B. Kesavaraju; L. McCuiston, Center of Vector Biology; S. A. Juliano, Illinois State University; R. Pozzatti, I. Terry, K. Iwata, N. Kirchoff, and D. Bodner, for useful discussion, for providing us with eggs, for experiment maintenance, or for data collection. We thank S. A. Juliano, S. LaDeau, and B. H. Momen for statistical advice, and two anonymous reviewers for excellent comments. This research was funded by a Maryland Agriculture Experimental Station grant MD-ENST-5739 to P. T. L. and the Washington Biologists Field Club grant to P. T. L. and T. Z. F.

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