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Invasive plant alters ability to predict disease vector distribution

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Abstract. Risk models for vector-borne diseases rely on accurate quantification of the relationship between vector abundance and habitat, but this relationship can be obscured if habitats are modified by invasive species in ways that alter vector behavior but are undetectable in remotely sensed data. At a forest in eastern Missouri we assessed whether the presence of an invasive shrub, Amur honeysuckle, *Lonicera maackii*, affects oviposition by treehole mosquitoes, *Aedes triseriatus*, a primary vector of La Crosse virus in the United States. Oviposition significantly decreased with increasing density of *L. maackii*. Moreover, our results indicate that *L. maackii* may hinder the efficacy of models that use remotely sensed data to predict vector abundance: there was a strong relationship between landscape composition around plots and oviposition, but only in plots not invaded by *L. maackii*. Overlooking potentially important but cryptic effects of invasive plants on habitat selection by vectors may undermine accurate forecasting of disease risk.

Key words: Aedes triseriatus; *disease vectors; invasive plant;* Lonicera maackii; *mosquito; oviposition.*

Introduction

The accurate identification of vector habitat is a key component of assessing and mitigating the risk of vector-borne diseases (Brownstein et al. 2002, Jackson et al. 2006, Kalluri et al. 2007). The accuracy of many disease risk models depends on the relationship between habitat features and vector abundance (Brownstein et al. 2002, Diuk-Wasser et al. 2006, Peterson et al. 2008, Rochlin et al. 2008). However, one of the most important pathways by which humans alter natural habitats is by the introduction of nonnative species into novel landscapes (Hobbs and Humphries 1995), and the distribution of many invasive species is linked to human disturbance and human population centers (Bartuszevige et al. 2006, Thuiller et al. 2006). Invasive species that transform habitat can have far-reaching impacts on ecosystems (Crooks 2002), but it remains unclear whether habitat modification by invasive plants alters habitat selection behavior of vectors in a way that compromises our ability to accurately characterize vector habitat. This may be particularly important given the widespread distribution of many invasive plant species and the frequent association of invasive plants with areas of high human population density (Lonsdale 1999, Reichard and White 2001, Barton et al. 2004). In this paper, we ask whether an invasive plant that alters forest understory structure (i.e., an ecosystem engineer; Jones et al. 1997) alters oviposition behavior of an important disease vector and test for differences in the habitat characteristics associated with oviposition in invaded and uninvaded forest.

In the United States, the eastern treehole mosquito, *Aedes triseriatus* (Say) (Diptera: Culicidae, synonym *Ochlerotatus triseriatus*), is the primary vector of La Crosse virus (Beaty and Thompson 1975) and experimental data suggest it may be a potential vector of yellow fever, eastern equine encephalitis (Jenkins and Carpenter 1946), and dengue (Freier and Grimstad 1983). The geographic range of *A. triseriatus* encompasses most of the eastern United States, from Maine to Montana in the north to Florida and Texas in the south (Jenkins and Carpenter 1946). Understanding the habitat preferences of *A. triseriatus* is important for assessing disease risk because, as a container-breeding mosquito that utilizes both abandoned tires as well as natural phytotelmata, it is frequently associated with habitats in close proximity to human habitation (Rochlin et al. 2008). Although such areas of high oviposition activity do not necessarily correlate directly with areas of high adult density (Ellis 2008), they remain important for understanding vector distribution because models of disease risk report strong correlations between distances from breeding habitat, biting intensity, and rates of disease transmission (Beaty and Thompson 1975, Smith et al. 2004, Le Menach et al. 2005). Because oviposition behavior is important for evaluating exposure risk for disease carrying mosquitoes, we use oviposition rate as our response metric for understanding invasive plant impacts on vector distribution (Turell et al. 2005, Ellis 2008).

Many disease forecasting models use remotely sensed habitat data to predict the risk of transmission to humans (Smith et al. 2004, Diuk-Wasser et al. 2006,

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Rochlin et al. 2008). However, if invasive species alter habitat selection behavior of disease vectors in ways that are undetectable using remote sensing methods, disease forecasting models may be vulnerable to substantial error associated with the cryptic impacts of invasive species. Amur honeysuckle, *Lonicera maackii*, is a shrub native to northeastern Asia that was brought to the United States as an ornamental plant in the late 19th century. It has since invaded much of the United States east of the Rocky Mountains and therefore overlaps with *A. triseriatus* in much of its invaded range. *Lonicera maackii* tends to be associated with habitat edges (Hutchinson and Vankat 1997, Bartuszevige et al. 2006, Watling and Orrock 2010) and its density is correlated with human activities at both local and regional scales (Hutchinson and Vankat 1997, Bartuszevige et al. 2006), increasing the potential for overlap with *A. triseriatus*. However, because *L. maackii* invades the forest understory (Collier et al. 2002), the occurrence and density of *L. maackii* may be undetectable in the remotely sensed images used in forecasting models. We hypothesized that high density forest may be more attractive to mosquitoes because of the abundance of resting places and increasing amounts of shade, resulting in invaded areas harboring more vectors than uninvaded forest. We made observations of *A. triseriatus* oviposition behavior in experimental phytotelmata located in forest plots that varied in *L. maackii* density and tested for associations between oviposition and local and regional habitat characteristics to understand the potential for an invasive plant to undermine remotely sensed models of vector distribution and disease risk.

METHODS

Study area

The study was conducted at the August A. Busch Memorial Conservation Area (BCA), St. Charles county, Missouri (38°45′ N, 91°21′ W), a 2827-ha protected area that consists of a mosaic of habitat types, including forest, croplands, grasslands, old fields, prairies, and wetlands. The heterogeneity of land use within BCA provides an opportunity to examine the effect of those habitats that frequently abut urban and suburban centers, and which are consequently of great concern for vector control. Our study took place in mixed oak–hickory deciduous forest, the most common habitat type at the BCA, covering approximately 47% of the reserve (81% of the forested area). Throughout the BCA, we established six study plots in areas invaded by *L. maackii* and six plots that were not invaded; all plots were separated by a minimum distance of 400 m.

Sampling methods

Mosquito oviposition.—Twelve oviposition traps were distributed along three parallel transects within each 30 × 30 m plot. Each trap consisted of a black plastic cup filled with 300 mL of tap water and a 5-inch (1 inch = 2.54 cm) presoaked wooden paddle as oviposition substrate; this trap design has been successfully used to monitor oviposition activity of container-breeding mosquitoes throughout the United States (Scholl and DeFoliart 1977, Beier et al. 1982, Edgerly et al. 1998). Each trap initially received approximately four leaves obtained from the ground in the immediate vicinity of the trap; litter in native plots was composed primarily of oak and hickory leaves, litter in invaded plots was composed of primarily oak, hickory, and *L. maackii*. Holes were punched at the waterline to prevent overflow in the event of rain. Traps were at least 10 m apart, and secured at 0–1 m above the ground, where *A. triseriatus* in the midwestern United States are most active (Scholl and DeFoliart 1977).

Oviposition activity was sampled weekly from 29 September to 28 October 2008, a time period that coincides with a seasonal peak in prevalence for *A. triseriatus* in the midwestern United States (Kitron et al. 1989). The wooden oviposition substrates were collected in individual plastic bags, and replaced with fresh presoaked paddles. Water levels were topped off to the 300-mL level as necessary. Raccoon activity at some plots resulted in the disturbance and loss of several samples. Disturbed cups were repaired or replaced as necessary. When possible, oviposition substrate was recovered from the forest floor and the eggs processed. When either substrate or trap had been severely compromised (substrate gone or buried, trap empty of water or upside down) the trap was considered to have been "unavailable" for oviposition for the previous week. Collected eggs were counted under a WILD M5A stereomicroscope (Wild Heerbrugg, Gais, Switzerland) at 500× magnification, identified to genus, placed in hatching medium, incubated, and emergent larvae were identified to species.

Landscape variables.—We differentiate between "local" habitat variables obtained from within plots where mosquito oviposition was measured and "landscape" variables describing the variation in land cover around each plot. Using ArcGIS (ESRI, Redlands, California, USA), the landscape context of each plot was characterized as proportional cover of eight land cover types (deciduous forest, evergreen forest, deciduous woodland, crops, grassland, woody wetland, urban, and concrete) in 200-m buffers around each plot using spatial data obtained from the Missouri Spatial Data Information Service 2005 land cover classification (*available online*).[5] Our selection of 200-m buffers is based on the estimated dispersal range of *A. triseriatus* (Turell et al. 2005). The distance from each plot to the nearest body of water was also included with regional habitat data.

Local habitat variables.—Local habitat variables were measured at each of the 12 oviposition traps and plot mean values for each variable were obtained by

[5] ⟨http://msdis.Missouri.edu⟩

averaging the 12 observations. The number of *L. maackii* stems within 1 m of each trap was recorded; plots that were devoid of *L. maackii* or had an average stem count of less than 0.2 were classified as "low" density plots, plots classified as "high" density contained *L. maackii* densities of 1.3–4.08 stems. Light readings were made at 1 m and at ground level using an Apogee Quantum sensor (Apogee Instruments, Logan, Utah, USA), averaging 10 measurements along a 70-cm unit. Measurements made at 1 m provide a proxy measure for the openness of the canopy, light readings made at 0 m provide a measure of the available light below the shrub canopy, and the difference between light readings taken at 1 m and ground level provided a measure of understory density. We measured the availability of cavity-forming trees (e.g., the occurrence of natural phytotelmata) by counting the number of woody stems with a diameter at breast height (dbh) greater than 20 cm within a 1-m radius of each trap. Previous surveys of second growth forest found cavities unlikely to be present in trees with dbh < 20 cm (Fan et al. 2003). Finally, each plot was surveyed for the presence of naturally occurring treeholes by visual identification of treeholes between ground level to a height of 3 m within a 1-m radius from each trap.

Data analysis

Weekly egg counts from each trap were summed to yield the total number of eggs oviposited at the trap over four weeks. The total egg count at each trap was divided by the number of weeks the trap was undisturbed to correct for differences in trap availability due to disturbance. Corrected count data were log transformed to meet assumptions of normality and homogeneity of variance. Because we were interested in obtaining a metric of oviposition for each study plot, and data analyses suggested that there was no spatial autocorrelation within invaded or uninvaded plots (A. Conley, *unpublished data*), adjusted count data from the 12 traps within each plot were summed together to create a single measure of the average weeklong oviposition activity within the entire plot.

Given the number of landscape and local variables and the potential for collinearity among variables, we used principal components analysis (PCA) to reduce the local and landscape variables to a smaller number of principal components encapsulating environmental variation across the 12 plots. Prior to PCA with landscape data, the land cover data was consolidated to reduce the 8 habitat classes into a smaller number of variables. We pooled pixels classified as woodland, deciduous forest, and evergreen forest into a single forest cover variable. Crops and grassland were pooled into a variable representing non-forest habitat. The remaining habitat classes (woody wetland, urban, concrete) occurred so rarely (between one and three plots) and in such a low proportion (0.06–9.00%) of each buffer, that they were not included in the analysis. The pooled forest and non-forest variables were included with distance to water, resulting in three landscape variables that were subjected to PCA. Local variables subjected to PCA consisted of the number of trees with dbh greater than 20 cm, the average tree dbh at the plot, the light availability at 1 m, light availability at 0 m, and the difference between light readings at 1 m and the ground. Following PCA, we retained principal components with eigenvalues greater than 1 (Everitt 2005).

The relationship between oviposition and the density of *L. maackii* was evaluated using general linear models. To evaluate how *L. maackii* might affect prediction of oviposition in light of local habitat characteristics and landscape characteristics, we construct separate models for both local and landscape variables; this approach also reflects the likely situation that managers seeking to model vector distribution will have only one of the data types at their disposal. For each model, the initial model included *L. maackii* density, local or landscape variables, and all possible two-way interactions; model terms were subsequently eliminated, using corrected AIC to compare models and guide selection of the most parsimonious model. Statistical analyses were conducted in R version 2.1.1 (R Development Core Team 2005).

RESULTS

Over four weeks of observation, 6504 eggs were collected, with the majority of eggs (84%) collected in the first two weeks. All eggs collected in the first three weeks (99% of all eggs collected) were flooded for subsequent larval species identification. Eggs laid by females late in the fall have already entered diapause and are resistant to flooding, which may have contributed to our low mean hatch rate of 11%. A total of 729 larvae were identified to species, of which 95.1% were positively identified as *A. triseriatus*, and 4.94% were identified as *A. albopictus*. *Aedes albopictus* comprised 5.4% of larvae in plots uninvaded by *L. maackii* and 3.9% of larvae from invaded plots. Eggs could not be visually identified to species.

The survey of natural treeholes found eight treeholes in five plots, three plots with low densities of *L. maackii* and two plots with high *L. maackii* densities. The number of treeholes present was not significantly correlated with levels of oviposition ($t = 0.66$, df = 10, Pearson's $r = 0.20$, $P = 0.52$). Aside from *L. maackii* density, there were no discernable differences between invaded and uninvaded plots; invaded plots did not significantly differ from native plots in their landscape context, light availability, natural treehole abundance, average tree dbh, or the number of trees with a dbh greater than 20 cm (t test, all $P > 0.15$).

Severe disturbances were experienced by 19% of the traps in our study; on average over four weeks there were 39.5 ± 2.1 (mean ± SE) of a possible 48 undisturbed traps in each plot invaded by *L. maackii* and 38.5 ± 3.2 in each uninvaded plot. Levels of disturbance were not significantly different between uninvaded and invaded habitats ($t = 0.27$, df = 8.6, $P = 0.80$).

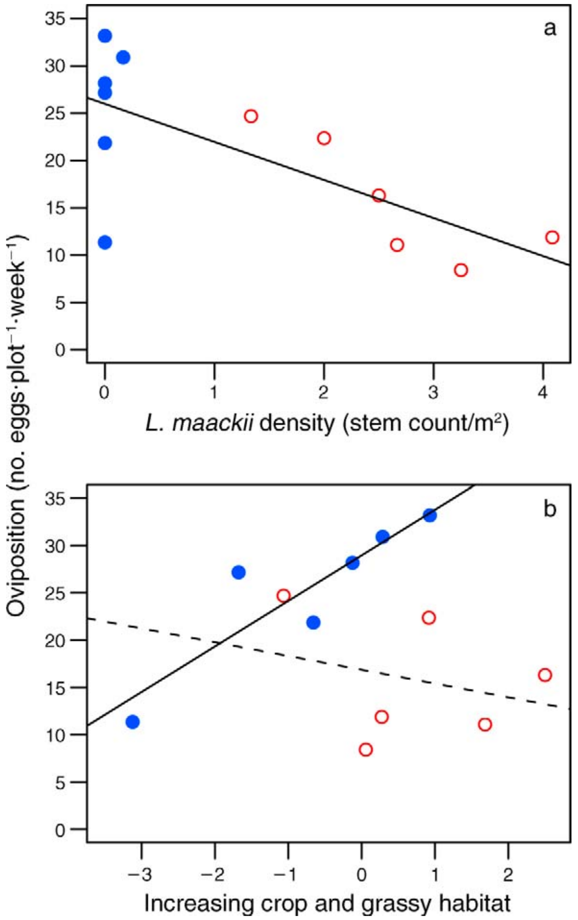

FIG. 1. (a) Relationship between *Lonicera maackii* density and *Aedes triseriatus* oviposition. Regression results showed a significant relationship between decreasing density of *L. maackii* and increasing average weeklong levels of oviposition ($r^2 = 0.45$, see *Results*). Open red circles represent plots with low densities of *L. maackii*; solid blue circles represent plots with high densities. (b) Relationship between *A. triseriatus* oviposition and landscape variables produced by principal components analysis. Regression results in uninvaded habitats show a significant relationship (solid line; $r^2 = 0.75$, $F_{1,4} = 16.13$, $P = 0.02$), but not in invaded habitats (dashed line; $r^2 = -0.15$, $F_{1,4} = 0.34$, $P = 0.59$). Open red circles represent plots with low densities of *L. maackii*; solid blue circles represent plots with high densities.

Effect of L. maackii *on mosquito oviposition*

There was a significant linear relationship between *L. maackii* density and oviposition activity ($F_{1,10} = 10.15$, $r^2 = 0.45$, $P = 0.010$; Fig. 1a); plots with higher densities of *L. maackii* had lower levels of oviposition activity.

Lonicera maackii *and landscape variables*.—We retained two landscape variables created using PCA; together, these variables explained 95% of the variation in the original landscape data. The first landscape principal component explained 70% of the variation in the landscape data and described increasing crop and grass habitat ($r = 0.90$, $t = 6.73$, df = 10, $P < 0.001$), decreasing forest cover ($r = -0.94$, $t = -9.08$, df = 10, $P < 0.001$), and decreasing distance to water ($r = -0.62$, $t = -2.48$, df = 10, $P = 0.03$). The second landscape principal component explained the remaining 30% of variation and was largely associated with an increase in the distance to water ($r = 0.79$, $t = 4.02$, df = 10, $P < 0.003$). The final model with landscape variables included a significant effect of *L. maackii* density ($F_{1,8} = 11.28$, $P = 0.01$): there were 233.5 ± 80 eggs in high-density *L. maackii* plots, but 850.5 ± 174.9 eggs in low-density *L. maackii* plots. Although there was no significant main effect of the landscape-level principal component describing increasing crop and grass habitat and decreasing forest cover ($F_{1,8} = 2.67$, $P = 0.14$), there was a significant interaction between *L. maackii* density and this variable ($F_{1,8} = 5.55$, $P = 0.046$). In high-density *L. maackii* plots, there was no relationship between this principal component and oviposition rates, whereas there was a significant positive relationship when *L. maackii* density was low (Fig. 1b).

Lonicera maackii *and local variables*.—We retained three local variables that explained 94% of the variation in the original data. The first local principal component explained 39% of the variation in the local data and described increasing difference in light between 1 m and 0 m ($r = 0.81$, $t = 4.32$, df = 10, $P < 0.002$) and increasing average tree diameter at breast height ($r = 0.87$, $t = 5.66$, df = 10, $P < 0.001$). The second local principal component explained 35% of the variation in the local data and was associated with an increase in light at 1 m ($r = 0.93$, $t = 7.87$, df = 10, $P < 0.001$) and light at 0 m ($r = 0.68$, $t = 2.97$, df = 10, $P = 0.014$). The third local principal component explained 20% of the variation in the local data and was associated with the number of large trees ($r = 0.65$, $t = 2.75$, df = 10, $P = 0.02$). Like the model with regional data, the final model that included local variables created with principal components analysis included a significant effect of *L. maackii* density ($F_{1,8} = 8.43$, $P = 0.02$). There was no significant main effect of the local principal component describing increasing average tree diameter and increasing difference between light at 1 m and 0 m ($F_{1,8} = 0.05$, $P = 0.83$). However, there was a significant interaction between *L. maackii* density and this local principal component ($F_{1,8} = 7.79$, $P = 0.023$): there was a trend of increased oviposition with increasing tree density and light attenuation in invaded plots ($r = 0.77$, $t = 2.43$, df = 4, $P = 0.07$), but not in study plots without *L. maackii* ($r = -0.65$, $t = -1.71$, df = 4, $P = 0.16$).

DISCUSSION

We found that an invasive shrub significantly impacts vector breeding behavior, with oviposition activity decreasing with increasing densities of *L. maackii* (Fig. 1a). When invaded and uninvaded areas are analyzed separately, they reveal very different relationships between oviposition rate and landscape habitat variables. In uninvaded forest, greater oviposition rate is associated with plots surrounded by larger proportions of grassland or cropland. This positive association between vector distribution and open habitat (Fig. 1b), is supported by observations in other container-breeding species. The best predictive model of adult *Culex pipiens* abundance was based on an inverse relationship with forest cover (Diuk-Wasser et al. 2006). Mark–recapture experiments with lab-reared *A. triseriatus* in the northeastern United States found that female distributions were significantly associated with dense ground (<1 m) vegetation (Ellis 2008). Likewise, studies in heterogeneous suburban landscapes in North Carolina also found a significant association between *A. albopictus* oviposition density and open-grass-shrub cover. (Richards et al. 2006). In contrast, *A. triseriatus* oviposition rates in invaded forest are not linked to the availability of open habitat within a 200 m radius (Fig. 1b).

One pathway by which *L. maackii* may alter vector distribution is through modification of habitat structure (Gould and Gorchov 2000, Hartman and McCarthy 2008). We found that *A. triseriatus* oviposition responded differently in invaded plots to local variables describing the abundance of large trees and the density of the understory within a plot; with a trend of greater oviposition on invaded plots with denser understories and larger trees. The importance of larger trees (i.e., greater dbh) in invaded study plots may also indicate that changes in the quality of leaf input are responsible for contributing to the differences in *A. triseriatus* oviposition that we observed, as *A. triseriatus* oviposition is known to be affected by the kinds of leaf litter available in a study from Florida (Reiskind et al. 2009). If *L. maackii* leaf litter provides a low-quality substrate, then oviposition would be expected to increase in invaded habitats where native trees provide a greater relative amount of leaf litter (i.e., invaded study plots with large trees). Leachate from invasive plants can affect survival and performance of amphibian larvae (Maerz et al. 2005; J. I. Watling et al., *in press*) and aquatic invertebrates (Canhoto and Laranjeira 2007); our work suggests that differences in *L. maackii* leaf litter may also affect the oviposition of aquatic *A. triseriatus* larvae. Finally, although our study was conducted during a time of year when *L. maackii* was not flowering, it is also possible that the prodigious flower production of *L. maackii* affects mosquito oviposition by providing nectar resources used by juvenile mosquitoes (Foster 1995), as flowering *L. maackii* has been shown to affect pollinator visitation (McKinney and Goodell 2010).

In the early fall, the eggs laid by *A. triseriatus* are already in diapause, and will emerge in the spring; in this manner, our data set captures the ability of an invasive shrub to indirectly influence the emerging distribution of adult mosquitoes the following spring. From our sample we are unable to examine to the influence *L. maackii* may have on oviposition earlier in the season, when *A. triseriatus* are competing with the invasive Tiger mosquito, *Aedes albopictus*. *Lonicera maackii* may influence oviposition in a variety of ways, including decreasing the availability of sugar sources for foraging adults and releasing chemicals from decomposing leaves that interfere with oviposition cues, but our data do not speak to that mechanism. The geographic ranges of both *L. maackii* and *A. triseriatus* are so extensive that it is also possible that the same species, in different habitats, such as southern forests where *A. triseriatus* tend to oviposit at greater altitudes, may interact in completely different ways. Given the pervasive spread of *L. maackii*, this is an area which may warrant further study.

Invasion by *L. maackii* alters the relationship between vector distribution and remotely sensed habitat data. Although not all mosquito stages are associated with the same suite of environmental characteristics (e.g., correlates of oviposition rates are not necessarily associated with the number of emergent mosquitoes; Yee et al. 2010), our results support the hypothesis that an invasive plant can alter vector behavior in a way that may undermine the effectiveness of disease risk models. Disease control programs rely upon the association between environmental features and vector distributions; a relationship connected by vector behavior (Kalluri et al. 2007). Our data suggest that habitat modification by *L. maackii* may disrupt such a relationship with *Aedes triseriatus*. More generally, our work adds to the increasing evidence that invasive *L. maackii* can alter the behavior and abundance of native animals, such as pollinators (McKinney and Goodell 2010), vertebrates (Mattos and Orrock 2010; H. P. Dutra, *unpublished manuscript*), and ticks (Allan et al. 2010). Because the cryptic effects of plant invasion may be difficult to detect in remotely sensed images, and the effects of invasive plants on native ecosystems are expected to increase in the future, disease models that ignore the capacity for invasive species to alter habitat selection behavior may be less capable of accurately predicting risk for future populations.

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