

Exotic Grass Invasion Reduces Survival of *Amblyomma americanum* and *Dermacentor variabilis* Ticks (Acari: Ixodidae)

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ABSTRACT Exotic plants often invade areas of high human activity, such as along trails, roads, and forest edges, and in disturbed riparian areas. These same habitat types are also favored by ticks. This convergence suggests that habitat modifications caused by exotic plant invasions may mediate disease vector habitat quality, indirectly affecting human disease risk at the local spatial scale. We tested the hypothesis that experimental invasions of Japanese stiltgrass, *Microstegium vimineum* (Trin.) A. Camus, alter soil surface microclimate conditions, thereby reducing habitat quality for ticks. *Microstegium* is an exotic annual grass that is highly invasive throughout the eastern United States where the vector ticks *Amblyomma americanum* (Linnaeus) and *Dermacentor variabilis* (Say) occur. Ticks ($n = 100$ per species) were introduced into experimentally invaded and native vegetation control plots ($n = 5$ per treatment). *D. variabilis* mortality rate increased 173% and *A. americanum* mortality rate increased 70% in the invaded plots relative to those in control plots. *Microstegium* invasion also resulted in a 13.8% increase in temperature and an 18.8% decrease in humidity, which are known to increase tick mortality. We predict that areas invaded by *Microstegium* will have lower densities of host-seeking ticks and therefore reduced human disease risk. Our results emphasize the role of invasive species in mediating disease vector populations, the unpredictable consequences of biological invasions, and the need for integrative management strategies that can simultaneously address exotic plant invasions and vector-borne disease.

KEY WORDS *Amblyomma americanum*, *Dermacentor variabilis*, *Microstegium vimineum*, invasion, habitat quality

Exotic plant invasions can reduce the productivity and diversity of native plant communities by altering the availability of resources and displacing resident plants (Mack et al. 2000, Blossey et al. 2001, Meiners 2001, Alvarez and Cushman 2002, Merriam and Fiel 2002). Furthermore, changes in the abundance or diversity of plants can alter the physical structure and complexity of habitats and reduce quality for species at higher trophic levels such as birds, reptiles, arthropods, and amphibians (Brown et al. 2006, Ortega et al. 2006, Valentine et al. 2007, Wilkie et al. 2007). Separate from their negative effects on ecologically, economically, or culturally important resident species, plant invasions may have unexpected benefits if the affected species are disease vectors.

Exotic plants often invade areas of high human activity, such as along trails, roads, and forest edges, and in disturbed riparian areas (Brothers and Spingarn 1992, Tyser and Worley 1992, With 2002, Gelbard and Belnap 2003, Flory and Clay 2006). These same habitat types are also associated with increased human risk of zoonotic diseases (Jackson et al. 2006a, b), because of elevated human activity (Horobik et al. 2006) and/or

increased disease vector and reservoir densities (Ginsberg and Ewing 1989, Brown et al. 2005). Hard ticks (Family: Acari) represent a major disease vector that transmit a diverse group of viral, bacterial, and protozoan disease agents (Goodman et al. 2005). Tick-borne diseases are complex zoonoses that emerge and persist where the appropriate habitat (Lubelczyk et al. 2004, Elias et al. 2006), abiotic conditions (Bertrand and Wilson 1996, Randolph and Storey 1999), tick species, vertebrate host communities, and human activity coincide (Barbour and Fish 1993). Thus, plant invasions may mediate disease vector habitat quality, indirectly affecting human disease risk at the local spatial scale.

The exotic annual grass *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass) is rapidly invading many habitats throughout the eastern United States. It was introduced from southeast Asia in the early 1900s and currently occurs in at least 21 states (USDA–NRCS 2005), where it can decrease native plant productivity, reduce plant species diversity, and suppress forest regeneration (Oswalt et al. 2007, S.L.F. unpublished data). *Microstegium* produces abundant seed (Tu 2000) and is dispersed by water, animals, and humans. It is commonly found in the understory of

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bottomland hardwood forests and riparian areas (Winter et al. 1982, Barden 1987, Redman 1995, Cole and Weltzin 2004) and also invades wildlife openings, recent timber harvest areas, and along roads, trails, and streams (Fairbrothers and Gray 1972). Recent acarological studies have noted the cooccurrence of ticks and *Microstegium* (Carroll 2003, Carroll and Cyr 2005).

The goal of this study was to determine whether *Microstegium* invasions alter tick habitat quality given their ecological overlap and prior reports of potential impacts of invasive plant species on tick populations (Lubelczyk et al. 2004, Elias et al. 2006). Specifically, we studied the survival responses of the lone star tick, *Amblyomma americanum* (Linnaeus), and American dog tick, *Dermacentor variabilis* (Say), to *Microstegium* invasion by monitoring cohorts of ticks introduced into experimental plots of native vegetation either invaded or uninvaded by *Microstegium*. These ticks transmit agents of several emerging and established diseases such as human monocytotropic ehrlichiosis (vectored by *A. americanum*) and Rocky Mountain spotted fever (vectored by *D. variabilis*) (Brown et al. 2005). Both species coexist in a wide range of habitats. In southern Indiana, *A. americanum* are more common in drier, open habitats and *D. variabilis* tend to numerically dominate in ecotones and shadier, moist habitats.

We hypothesized that the suppression of the native plant community by *Microstegium* would result in drier and hotter soil surface conditions, which are unfavorable for questing ticks (Bertrand and Wilson 1996, Randolph and Storey 1999). Accordingly, we hypothesized that *Microstegium* invasion would reduce tick survival.

Materials and Methods

Experimental Invasion. The study site was located in Bloomington, IN, at the Indiana University Research and Teaching Preserve, Bayles Road site (39°13'9" N, 86°32'29" W). In September 2005, 10 plots (5.25 by 5.25 m) were arranged in an ≈60 by 60-m forest opening at 2.5-m spacing. The field was surrounded on all sides by mature trees including box elder (*Acer negundo*), tulip poplar (*Liriodendron tulipifera*), and sycamore (*Platanus occidentalis*). Each plot was surrounded by 60-cm-tall silt fence buried 10 cm deep to prevent movement of seeds among plots. All plots were planted with 12 native woodland herbaceous species (≈seeds/m²) corresponding to recommended seeding rates for natural area restoration: *Andropogon gerardii* (60), *Asclepias incarnata* (15), *Aster novae-angliae* (35), *Calamagrostis canadensis* (56), *Carex vulpinoidea* (42), *Elymus virginicus* (71), *Helenium autumnale* (33), *Panicum virgatum* (41), *Senna hebecarpa* (7), *Scirpus atrovirens* (49), *Scirpus cyperinus* (109), and *Verbena hastata* (33; seeds collected in Indiana by Heartland Restoration Services, Ft. Wayne, IN). Nine native tree species were also planted (seeds/plot): *Quercus macrocarpa* (40), *Quercus alba* (22), *Quercus palustris* (28), *Carya laciniosa*

(20), *Liquidambar styraciflua* (1,470), *Fraxinus pennsylvanica* (190), *Platanus occidentalis* (1,855), *Juglans nigra* (34; seeds purchased from Vallonia State Tree Nursery, Vallonia, IN). Large-seeded species were planted in a grid and small-seeded species were randomly scattered throughout the plots. Tree seeding rates were adjusted to account for unequal germination rates.

One half ($n = 5$) of the otherwise identical plots were sown with locally collected *Microstegium* seed at a rate of ≈690 seeds/m², corresponding to observed seedling densities in locally invaded sites (S.L.F., unpublished data).

Tick Survival. One hundred female questing lone star and 100 dog ticks were collected with cloth flags at Young's Creek Marsh, Hoosier National Forest (38°26'38" N, 86°31'31" W) on 22 June 2007 and stored in a humidity chamber. On 23 June 2007, 18 mo after the experimental invasion plots were established, ticks were confined individually to nylon mesh bags (30 by 60 mm, mesh size: 1 mm). Mesh bags were sewn on three sides, closed with a metal binder clip on the fourth side, and pinned to the ground with a wire flag threaded through the clip. The bags were placed directly on the soil surface below any leaf litter at 10 randomly chosen locations in the plots ≈1 m from the perimeter. Thus, each plot contained 20 bags (10 bags for each species) with one tick per bag. Tick survival was evaluated twice weekly from 26 June to 3 August 2007, coinciding with the natural local adult tick host-seeking season (Eisen 2007).

Environmental Conditions. Air temperature, humidity (digital hygrometer; VWR, West Chester, PA), and light penetration (AccuPAR Linear PAR/LAI ceptometer; Decagon Devices, Pullman, WA) were measured at the soil surface below the litter layer at five tick locations per plot on 28 June and 18 July 2007. The height of the tallest vegetation within 10 cm of each tick location was also measured on these dates. Plot means for each variable were analyzed individually using repeated-measures analysis of variance (ANOVA) (von Ende 1993).

Survival Analysis. We analyzed the tick survival data with univariate marginal Cox proportional hazards regressions using the "survival" package in R (Cox 1972, R Development Core Team 2008, Therneau and Lumley 2008). This analysis accounts for the clustering present by plot in the experimental design and estimates the population averaged proportional risk associated with the covariate (Therneau and Grambsch 2000). The hazard rate for the i th individual (λ_i) was calculated as a function of the baseline hazard rate (λ_0) and the exponentiation of the product of the covariate value (X_i) and its Cox proportional hazard regression coefficient (β) (Cox 1972).

$$\lambda_i = \lambda_0 \exp(\beta X_i)$$

We report hazard ratios (HR), which represent the proportional change from the baseline hazard rate that accompanies a single unit increase in the covariate:

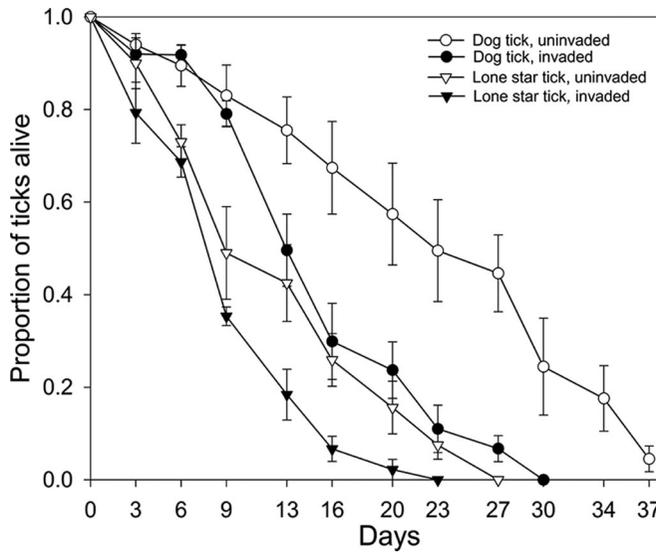


Fig. 1. Mean (\pm SE) survival of dog and lone star ticks in uninverted and *Microstegium*-invaded plots (10 ticks per species per plot, $n = 5$ per treatment) over the 37-d experiment.

$$HR = \frac{\lambda_{x+1}}{\lambda_x} = \exp(B)$$

This is equivalent to the exponentiation of the Cox proportional hazards regression coefficient.

In the analyses that follow, the single units are invasion status (0 or 1), 1°C, 1% RH, 1% light penetration, and 1-m vegetation height. Hazard ratios associated with these covariates were calculated for each tick species individually.

We first tested for the effect of *Microstegium* invasion for each tick species individually. Next, we tested the explanatory power of the environmental covariates by assigning the plot average environmental measure to each individual in that plot. The environmental variables were highly collinear with pairwise linear correlation coefficients ranging from 0.521 to 0.973. We nevertheless tested the explanatory power of each environmental variable individually. Twenty-three of the 200 ticks (11.5%) were lost during the 37-d trial. Data from these individuals were treated as censored observations in the Cox regression model (Cox 1972). No more than three individuals per species were lost from any single plot. Randomization tests performed by resampling the data without replacement (1,000 iterations each) were used to confirm that the analyses were robust to the structure of the data.

Results

Tick Survival. Survival of both tick species was significantly reduced in the *Microstegium*-invaded plots (Fig. 1). Dog tick and lone star tick mortality rates increased by 173 (HR = 2.73, $z = 3.62$, $df = 1$; $P = 0.00029$) and 70% (HR = 1.70, $z = 2.94$, $df = 1$; $P = 0.0033$), respectively, in invaded plots relative to control plots. Dog tick mortality significantly increased with increasing temperature and light penetration and

significantly decreased with increasing humidity and vegetation height. Lone star tick mortality significantly increased with light penetration and decreased with vegetation height, but there was no significant effect of temperature or humidity (Table 1). The results of the randomization tests were consistent with the interpretation of each statistical analysis (results not shown).

Environmental Conditions. There were significant differences in soil surface microclimate conditions between invaded and uninverted plots on both measurement dates. *Microstegium*-invaded plots were on average 13.8% hotter (Fig. 2A; $F = 15.40$, $df = 1,8$; $P = 0.0044$) and 18.8% less humid (Fig. 2B; $F = 12.65$, $df = 1,8$; $P = 0.0074$) than uninverted plots. In parallel, there was a 33.4% reduction in overall vegetation height on average (Fig. 2C; $F = 27.38$, $df = 1,8$; $P = 0.0008$) and a 136% increase in soil surface light penetration (Fig. 2D; $F = 13.95$, $df = 1,8$; $P = 0.0057$) in invaded plots. The invasion treatment had a stronger effect on light penetration on 28 June 2007 than on 18 July 2007 (date \times invasion, $F = 13.40$, $df = 1,8$; $P = 0.0064$), but no other significant date \times invasion interactions were detected.

Table 1. Results of the marginal Cox proportional hazard regression analyses on the environmental covariates for *A. americanum* and *D. variabilis* survival

Tick species	Predictor	HR	95% CI	P
<i>A. americanum</i>	Temperature	1.04	0.987-1.10	0.13
	Humidity	0.986	0.960-1.01	0.10
	Light penetration	1.09	1.01-1.17	0.025
	Vegetation height	0.399	0.149-0.773	0.01
<i>D. variabilis</i>	Temperature	1.2	1.09-1.32	0.0002
	Humidity	0.945	0.917-0.973	0.0002
	Light penetration	1.25	1.16-1.35	<0.0001
	Vegetation height	0.0903	0.0283-0.288	<0.0001

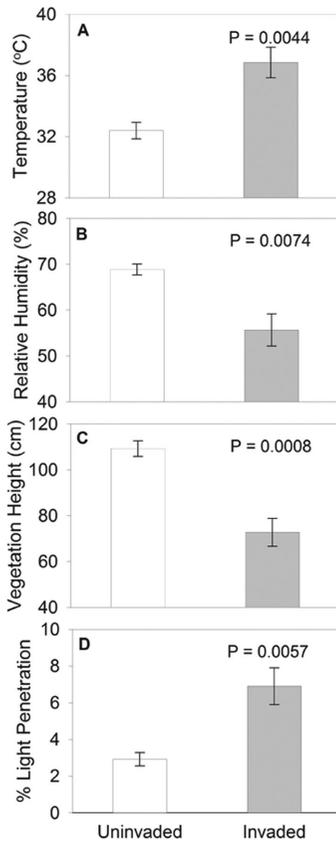


Fig. 2. Mean (\pm SE) temperature (A), relative humidity (B), tallest green vegetation (C), and percent light penetration (D) at the soil surface in uninvaded (white bars) and *Microstegium*-invaded (gray bars) plots averaged over two sampling dates.

Discussion

Microstegium invasion significantly reduced survival rates of lone star and dog ticks compared with ticks in uninvaded control plots, indicating that invasion reduced tick habitat quality. Invasion resulted in more adverse abiotic conditions (i.e., decreased relative humidity and increased temperature, Bertrand and Wilson 1996, Randolph and Storey 1999), likely caused by decreased vegetation height and increased light penetration at the soil surface. These changes, in turn, likely resulted from the suppressive effects of *Microstegium* growth during the previous year (2006). Furthermore, the extant *Microstegium* was at an early developmental stage (June–July 2007) that did not yet create dense shade, as it does later in the growing season. Although not quantified here, native vegetation was clearly less abundant in the invaded plots. These results indicate an unexpected consequence of an exotic plant invasion: reduced human exposure to disease-vectoring ticks in invaded areas.

The microclimate conditions measured in this study were better predictors of dog tick than lone star tick survival. The strong association of microclimate variation with dog tick survival confirms the importance

of these conditions for their survival. The lack of a similarly strong signal in the lone star tick survival analyses suggests the importance of other unmeasured environmental conditions (e.g., depth of the litter layer, Schulze et al. 2002). Alternatively, it may reflect a lesser response of lone star ticks to the observed range of temperature and humidity.

Tick questing behavior is limited in part by desiccation tolerance (Bertrand and Wilson 1996, Randolph and Storey 1999). When not questing, ticks reside at the soil surface, in crevices, or under leaf litter to minimize water loss and replenish water content (Needham and Teel 1991). However, such behavior reduces questing time, decreasing the density of active ticks and therefore human disease risk. Housing ticks in mesh bags constrained their use of these microrefugia but made repeated sampling possible and possibly facilitated tick rehydration at night (Padgett and Lane 2001). Thus, our approach provided a conservative approximation of the conditions that actively questing ticks encounter in each habitat type and allowed us to accurately quantify survival in response to invasion.

The results of the survival analysis presented here could be extended in the future by censusing tick densities in naturally invaded and uninvaded areas (as in Elias et al. 2006). We predict that resident ticks in *Microstegium*-invaded areas would seek hosts less frequently, disperse, or die. Any of these outcomes reduces human disease risk by decreasing the density of questing ticks in invaded areas. Observational studies may also provide insights into the consequences of invasion over the entire life cycle of the tick. For example, changes in vertebrate host community composition or tick infection frequency in response to invasion could also be quantified. We have no quantitative data on small mammal use of *Microstegium* patches but have noted substantial vole (*Microtus* spp.) activity in our experimental plots. These studies should also incorporate experiments such as described here to determine the relative importance of distinct environmental factors affecting disease risk. For example, shifts in plant or vertebrate host communities can alter disease risk by changing rates of tick survival, reproduction, infection, and pathogen strain diversity (LoGiudice et al. 2003, Brisson et al. 2008).

Recent studies have shown that plant invasions can alter the abundance of other disease vectors. For example, blacklegged tick (*Ixodes scapularis* Say) densities were greater in areas invaded by exotic shrubs in Maine (Lubelczyk et al. 2004, Elias et al. 2006). Additionally, the dominance of cattails, *Typha domingensis*, after anthropogenic nutrient input increased habitat suitability for the vector mosquito *Anopheles vestitipennis* in northern Belize (Rejmankova et al. 1998, Grieco et al. 2006). The significant impact of invasive plants on disease vector population dynamics reinforces the need for integration of invasive plant management into existing strategies for minimizing disease risk. Natural areas managers should be informed about local tick-borne disease risk and the consequences of invasive plant species for habitat

modifications for vector and reservoir communities. The identification of specific habitat modification mechanisms will aid in the development of integrative management strategies.

Under the observed conditions and time frame of this study, *Microstegium* invasion reduced habitat quality. However, *Microstegium* also invades shaded areas in the forest interior. Our study does not replicate those conditions, which must at least create reduced light penetration because of the forest canopy. Carroll and Cyr (2005) found severely depressed blacklegged tick densities among forest understory areas dominated by *Microstegium*. However, larval blacklegged tick survival did not significantly differ between white pine plantations invaded or uninvaded by *Microstegium* (Carroll 2003). The developmental timing of *Microstegium* as a warm season grass may also lead to differential effects of the invasion on different tick life stages. During the peak period of adult activity, *Microstegium* is in a juvenile preflowering stage (<20 cm tall). In late summer and early fall, mature *Microstegium* tillers can reach 2 m in height. Additionally, tillers fall flat, creating a dense mat that may alter soil surface humidity. *Microstegium* invasions could therefore affect larvae or nymphs differently than adults. Effects on juvenile life stages may be exacerbated by reduced dispersal capacity relative to adults (Sonenshine 2005). In such cases, adverse abiotic conditions may alter the timing or duration of diapause.

In summary, habitats commonly invaded by exotic plants such as *Microstegium* are often those favored by host-seeking ticks and by humans (e.g., trails, roadsides, disturbed areas). Because of frequent human activity in these habitats, small changes in vector density may have a relatively large impact on overall disease incidence. Habitat modifications caused by dominant invasive plants can dramatically affect disease vectors. Positive (Elias et al. 2006, Grieco et al. 2006) or negative (this study) effects on disease vectors may enhance or disrupt zoonotic disease maintenance. The effects of invasive plant species on disease vectors should be studied in other systems. More generally, our results emphasize the complex consequences of biological invasions. These may be beneficial to humans depending on the characteristics of the habitats replaced and created by invasive plants. This study highlights the role of invasive plant species in mediating local changes in human disease vectors and calls for integrative research to improve understanding of the direct and indirect consequences of plant invasions on zoonotic disease.

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