Mechanistic pathways of tick exposure risk in native and invaded plant communities

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Running title: < Plant invasion effects on ticks >

Keywords: *Amblyomma americanum, Imperata cylindrica*, tick survival, disease ecology, invasion, indirect effects

Statement of authorship:
DH, WD, BA, MD, and SLF conceived the idea and designed the experiment. DH, WD, and SC carried out the experiment. DH, WD, SC, and AG performed the analyses. DH wrote the first draft of the manuscript and all authors contributed substantially to revisions.

Data accessibility (Open Research Statement):
All data and code supporting these results has been archived via data dryad.
https://doi.org/10.5061/dryad.mpg4f4r2k

Section length:
Abstract: 238/ 350 words
Manuscript length: 31 pages
Number of references: 62
Number of figures: 4
Number of tables/ textboxes: 0

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Abstract

Plant invasions may alter vector abundance by several mechanistic pathways, including modifying microclimates that influence vector survival or changing habitats to influence host use. Here, we used a field experiment and observational data to evaluate multiple mechanistic pathways (tick survival and host abundance) by which plant invasions may alter vector-borne disease risk using the common disease vector lone star tick (*Amblyomma americanum*) and the widespread invasive cogongrass (*Imperata cylindrica*) in the southeastern USA. In the field experiment, ticks survived over 50% longer in areas dominated by the invasive plant compared to those with only native plant species. Invaded areas had lower temperatures and higher humidity that likely reduced tick desiccation. The observational study showed greater average tick abundance in native plant communities and no difference in wildlife host (white-tailed deer) activity between plant communities. There was also a positive relationship between tick abundance and white-tailed deer activity, but only in native areas. Together, these results suggest that more favorable microclimate conditions resulting in greater tick longevity is the dominant driver of tick abundance in invaded areas, while tick abundance in native-dominated areas is promoted, at least in part, by white-tailed deer activity. Our results demonstrate that plant invaders affect multiple, potentially off-setting mechanistic pathways contributing to tick exposure risk. The complexity of these relationships highlights the need for better understanding of how invasive species and other global change drivers influence abundance of disease vectors and, ultimately, disease transmission.

Introduction

Human-mediated introductions of species to non-native ranges have resulted in widespread biological invasions, which are a key driver of global environmental change (Vitousek et al. 1996). Accumulating evidence demonstrates that invasive species can have direct effects on ecological communities by altering, for example, biodiversity, nutrient cycling, and disturbance regimes (Vilà et al. 2011, Pyšek et al. 2012). However, they can also elicit indirect effects that may be larger than their direct effects, such as through changes to habitat structure and microclimate (Linders et al. 2019). These indirect effects can have cascading impacts on humans by affecting food production, recreation, and climate mitigation (Pejchar and Mooney 2009). Invasive species may also indirectly influence human health if they alter interactions among species that transmit diseases to humans (Rai and Singh 2020), however, to our knowledge such effects have been rarely explored.

Infectious pathogens transmitted from animals to humans via arthropod vectors such as mosquitoes and ticks place a major burden on global health (Morens et al. 2004, Jones et al. 2008). Tick-borne disease transmission to humans results from complex species interactions that are mediated by impacts of plant communities on tick growth, survival, dispersal, questing, and reproduction (Ostfeld et al. 2018, Morand and Lajaunie 2021) and host habitat conditions that affect the frequency and duration of host use (Elias et al. 2006, Allan et al. 2010a, Guiden and Orrock 2019). Plant invasions can alter multiple mechanistic pathways that affect tick abundance and infectious disease exposure for humans by either modifying host habitats that alter host abundance or by changing microclimate conditions that promote or inhibit tick survival (Allan et al. 2010a, Williams and Ward 2010, Mackay et al. 2016, Stewart et al. 2021) (Figure 1). Entomological metrics of exposure risk include metrics of tick abundance (e.g. density of ticks),

87 pathogen infection prevalence, or their product (e.g. density of infected ticks) (Fischhoff et al.
88 2019). Vector abundance often is used as a proxy for tick exposure risk, or a human's likelihood
89 of encountering a tick upon entering a particular habitat. While there has been research on how
90 these pathways individually affect tick abundance, studies that simultaneously address multiple
91 pathways are needed to improve understanding of complex processes by which invasive plants
92 may alter tick exposure risk, and thus infectious disease.

93 Collectively, evidence for mechanisms that influence tick-borne disease risk in invaded
94 areas is sparse and inconsistent. The limited evidence for invasive plant effects on tick-borne
95 disease varies by tick species, invasive plant species, and habitat conditions, among other factors
96 (Civitello et al. 2008, Allan et al. 2010a, Williams and Ward 2010, Mack and Smith 2011,
97 Racelis et al. 2012, Adalsteinsson et al. 2016). Plant invaders have been shown to increase host
98 habitat use (Guiden and Orrock 2019), leading to greater abundance of ticks (Elias et al. 2006)
99 and pathogen-infected ticks (Allan et al. 2010a) compared to native areas. Invasive plants may
100 also increase tick abundances relative to native plant dominated areas by providing favorable
101 microclimate conditions (i.e., higher humidity and/or lower temperature) that reduce tick
102 desiccation (Williams and Ward 2010, Racelis et al. 2012). However, the few studies comparing
103 the abiotic mechanisms affecting tick survival in invaded and native areas show either no
104 difference (Allan et al. 2010a) or lower tick survival (Civitello et al. 2008) in invaded compared
105 to native plant dominated communities. Given the ongoing introduction and spread of both
106 invasive plants (Seebens et al. 2017), and ticks (Ostfeld and Brunner 2015), there is a critical
107 need to better understand how invasive plants affect host habitat use (Stewart et al. 2021) as well
108 as the abiotic factors that influence tick survival.

Here, we measured effects of plant invasion on tick survival and host activity to determine if these pathways were predictive of tick abundance. Specifically, we combined field experiments and observational field studies to evaluate how an invasive plant (cogongrass; *Imperata cylindrica*) affected microclimate conditions and tick survival (lone star tick; *Amblyomma americanum*) compared to native species dominated areas, and how differences in relative host activity (i.e., white-tailed deer, *Odocoileus virginianus*) between invaded and native areas were related to tick abundance (Figure 1). We measured temperature, relative humidity (RH), and survival of lab-reared ticks in invaded and nearby native communities in a field experiment over 11 months and we evaluated relative white-tailed deer activity (via camera traps) and abundances of host-seeking ticks (via CO_2 trapping) in paired invaded and native sites in a field survey. Because the invader creates much denser stands compared to native plant communities, we hypothesized that invaded areas would have lower temperatures and higher relative humidity, which would be favorable for tick survival relative to native areas. We also hypothesized that relative white-tailed deer use would be greater in invaded communities because dense cover created by the invader would provide perceived protection from predators, as documented with small mammals in cogongrass (Borden et al. 2022), which would in turn result in greater tick abundance.

Methods

Study system

One of the most widely distributed invasive plant species in the southeastern USA is *Imperata cylindrica,* (L.) Beauv. (cogongrass; hereafter *Imperata*), (Estrada and Flory 2015) and it is one of the top five costliest terrestrial invasive plants to manage in Florida (Hiatt et al.

2019). *Imperata* can invade a wide variety of habitats due in part to its greater trait plasticity (Hiatt and Flory 2020), and drought tolerance (Fahey et al. 2018) compared to co-occurring native plant species. *Imperata* invasions can alter the structure of southern pine forests by producing greater fire intensity compared to native plant communities (Dillon et al. 2021) leading to fire induced tree mortality (Flory et al. 2022). *Imperata* has also been shown to alter microclimate conditions, including higher soil moisture and relative humidity, and lower temperatures at ground level compared to native plant communities due to its higher stem density and greater leaf area (Alba et al. 2017, Cabrera et al. 2021).

Lone star ticks (*Amblyomma americanum*) are hard ticks in the family Ixodidae (Keirans and Litwak 1989) that can transmit pathogens, including the causative agents of human ehrlichiosis, Rocky Mountain spotted fever, and tularemia (Childs and Paddock 2003). Time between blood meals (off-host), either seeking hosts to parasitize, digesting blood meals, or dormant, comprises over 90% of an Ixodid tick's life cycle, making the primary cause of off-host tick mortality desiccation (i.e., loss of water through the cuticle) (Needham and Teel 1991). Maintaining a constant water balance is one of the most important processes that influence off-host survival and, ultimately, tick population size (Knülle and Rudolph 1982, Needham and Teel 1991, Perret et al. 2000, Maldonado-Ruiz et al. 2020). Ticks will begin to desiccate when they are below their critical equilibrium humidity (CEH), which is 80-82% relative humidity for adult *A. americanum* (Hair et al. 1975, Knülle and Rudolph 1982). While desiccation is primarily driven by low relative humidity (at or below CEH), increased temperature leads to an increase in water molecules escaping the cuticle due to kinetic energy (Sauer and Hair 1986). For *A. americanum* temperatures in excess of 35 ºC can contribute to desiccation and mortality (Sauer and Hair 1971), while all terrestrial arthropods, including ticks lose their capacity to retain

155 moisture at temperatures in excess of 40 ºC (Londt and Whitehead 1972). While tick abundance
156 is influenced by microclimate, local abundance of *A. americanum* can also be regulated by host
157 activity. White-tailed deer (*Odocoileus virginianus*) serve as key hosts for all three life stages of
158 *A. americanum* (Bloemer et al. 1986), and are important reservoir hosts for multiple pathogens
159 transmitted by *A. americanum* (Allan et al. 2010b).

160 *Field experiment: Tick survival and microclimate conditions*

161 To examine the effect of *Imperata* invasion on tick survival, we established an
162 experiment in a planted longleaf pine (*Pinus palustris*) stand with fine sandy soils near La
163 Crosse, FL (29.897° N, -82.420° W) that had distinct *Imperata*-invaded and -uninvaded areas
164 (Appendix S1: Figure S1, S2). The invaded area was highly dominated by *Imperata* and spanned
165 approximately 6300 m^2, while the surrounding area was uninvaded, native understory. The plant
166 community of the native area was typical of a longleaf pine stand, with *Aristida stricta*
167 (wiregrass), *Rubus flagellaris* (common dewberry), *Carya sp.* (hickory), and *Andropogon* spp.
168 There was no recent chemical or mechanical management in either the invaded or native areas,
169 and the native understory included no other non-native plant species. Because we conducted our
170 experiment within a forest stand with distinct invaded (*Imperata*) and native areas in close
171 proximity that shared the same overstory structure, we expected any differences in microclimate
172 conditions to be due to invasion, not other underlying factors (see Results).

173 We established 24 plots (1m x 1m), 12 in invaded habitat and 12 in native habitat, with at
174 least 10m between plots. Plots were established every 10m along two transects, one in each plant
175 community; plots were then randomly placed along each transect by in areas that were
176 representative of each plant community. At the center of each plot, a 300-micron 10 cm x 20 cm
177 nylon mesh bag (Skimz, Singapore), containing 10 nymph and 10 adult (5 female and 5 male) *A.*

178 *americanum* obtained from the National Tick Research and Educational Resource (Department
179 of Entomology and Plant Pathology, Oklahoma State University, Stillwater, OK) were placed in
180 50 cm tall cylindrical wire mesh exclosures to deter wildlife interference. To control for age of
181 ticks (within life stage) and standardize the prior range of exposure to environmental conditions,
182 we used lab-reared instead of wild-caught ticks. Each mesh bag containing ticks was oriented
183 vertically to facilitate natural diurnal tick questing (i.e., host seeking behavior) and, although
184 there was no substrate within the bags, the bags remained in contact with the litter layer to allow
185 for ticks to seek refuge below the leaf litter to avoid desiccation stress (Schulze and Jordan 2003)
186 throughout the experiment (Appendix S1: Figure S1).

187 The start date of the survival experiment (June 21, 2018) coincided with typical off host
188 periods (between blood meals) for *A. americanum* in the region (Davidson et al. 1994, Gleim et
189 al. 2014). During these long non-parasitic phases, ticks seek refuge in areas with microclimates
190 that promote constant water balance (Knülle and Rudolph 1982, Davidson et al. 1994). Mesh
191 bags were examined frequently (every 7-10 days) for the first month and then every 10-14 days
192 afterward to determine days survived for both nymph and adult ticks. During each visit, bags
193 were removed from the cages but not opened, and survival status of each individual tick was
194 determined by assessing the response of the tick to CO_2 stimulation from human breath (Steullet
195 and Guerin 1992). Visits continued to the site until May 23, 2019 when all ticks had died.

196 To assess plant community structure and abiotic conditions in invaded and native areas,
197 at the start of the survival experiment we collected understory herbaceous plant height and
198 standing biomass, light availability at the soil surface, and overstory canopy cover at each plot.
199 Plant height was measured as the tallest point of living leaf tissue from soil surface. Standing
200 biomass was collected in 25 cm x 25 cm quadrats and dried at 60 ºC to a constant mass and

weighed (± 0.01g). Photosynthetically active radiation (PAR, i.e., light) was measured at ground level in each plot using an ACCUPAR LP-80 PAR/LAI ceptometer (Decagon Device Inc., Pullman, WA, USA). Overstory canopy cover was estimated using a concave spherical densiometer (Forestry Suppliers Inc., Jackson, MS, USA) by the average of four readings facing each cardinal direction.

Throughout the experiment we recorded ground-level microclimate conditions (temperature and relative humidity) at five-minute intervals immediately adjacent to each enclosure containing the mesh bags using HOBO U23 Pro v2 loggers (Onset Computer Corporation, Bourne, MA). Each logger was housed in a capped 18-inch length of 3.8 cm diameter PVC pipe to protect it from rainfall and direct sunlight. Holes were drilled on four sides six inches apart along the length of the pipe to allow for airflow and better reflect ambient temperature and relative humidity (see Appendix S1: Figure S1a-b).

Statistical analysis: Site conditions

We conducted our statistical analysis of the tick survival field experiment in several phases. First, we conducted two analyses to determine how *Imperata* affected plant community characteristics that might influence microclimate conditions and if *Imperata* invasion altered tick survival over time. We used multivariate analysis of variance (MANOVA) to test the hypothesis that *Imperata* changed plant community characteristics (i.e., vegetation height, standing biomass, and light availability at soil surface). Analysis of variance (ANOVA) was used to test if overstory canopy cover was similar in invaded and uninvaded areas (i.e., differences in understory plant community characteristics were due to invasion, not the tree canopy or other environmental factors). We also fit polynomial non-linear ordinary least squares regressions to test the hypothesis that *Imperata* invasions changed microclimate conditions (i.e., higher average

224 daily minimum relative humidity and lower average daily maximum temperature) during the
225 experiment. These analyses were done using the "car" package (Fox and Weisberg 2018, Team
226 2019) in R version 3.6.1, R Core (Fox and Weisberg 2018, Team 2019)).

227 *Statistical analysis: Tick survival and microclimate conditions*

228 We used linear regression models to assess how the number of days survived for
229 individual *A. americanum* of each life stage was related to the plant community and each
230 microclimate variable (hours per day under 80% relative humidity and daily maximum
231 temperature). The first set of mixed effects regression models on number of days survived for
232 adult or nymph life stage ticks included the fixed effects of treatment (native), hours per day
233 under 80% relative humidity (total hrs. below 80% relative humidity/ days survived), and their
234 interaction. The second set of mixed effects regression models for days survived for nymph or
235 adult life stage ticks included fixed effects of treatment (native), maximum temperature
236 experienced at mortality, and their interaction. Maximum temperature at mortality was recorded
237 as the maximum temperature measured at each plot between survival checks (i.e., maximum
238 temperature between the time when the tick was last observed alive and when it was observed as
239 dead). We included plot as a random effect in both models to account for repeated measures.
240 Models were fit for nymph and adult life stage ticks separately using the "lme4" package (Bates
241 et al. 2014), and degrees of freedom were calculated using "lmertest" (Kuznetsova et al. 2017) in
242 R 3.6.1 (R Core Team 2019). To further elucidate the effect of both relative humidity and
243 temperature on tick survival, we also used ordinary least squares linear regression to further
244 investigate the mechanistic effect of each respective microclimate variable on nymph and adult
245 survival time (days) (Appendix S1: Table S4). These models provide estimates of effect sizes of
246 maximum temperature or relative humidity on survival, irrespective of plant community. For

these models, we scaled the microclimate variables using a z-score standardization so that the effect of each variable could be compared on the same axis.

Field survey: White-tailed deer activity, tick abundance, and microclimate

To examine the impact of *Imperata* invasions on white-tailed deer activity and tick abundance, we conducted field surveys in invaded and native dominated plant communities across eight sites in north central Florida (Appendix S1: Figure S2). Invaded plots were selected if the *Imperata* invasion covered a minimum of 500 m^2, native plots were selected if they had similar overstory tree canopy structure to that of the invaded plots. Since we encountered many large invasions with few comparable native plant communities, at some sites we sampled multiple invaded plots per site. We sampled a total of 34 plots, 22 plots in *Imperata* invaded areas and 12 in native plant dominated areas. Due to limited supply of camera traps, a sub-set of the plots were sampled for white-tailed deer activity (28 plots total, 17 in *Imperata* invaded areas and 11 in native plant dominated areas, Appendix S1: Table S5). Plots were also sampled for tick abundance and some plots were sampled multiple times, yielding 51 tick sampling events, 32 in *Imperata* invaded areas and 19 in native plant communities (Appendix S1: Table S6). Within a site, invaded and native plots were located at least 20 m away from each other. *Imperata* invasions varied in size across sites but covered a minimum of 500 m^2 to more than 1 ha. We established plots (10 m radius) under similar overstory tree species and canopy cover between invaded and native plots, so the primary difference in habitats was presence or absence of the invader.

To estimate relative white-tailed deer use of invaded and native areas, we placed two motion-activated cameras (Primos 12MP Proof Cam 02 HD, Primos Hunting, Flora, MS) in each plot to monitor wildlife activity. All cameras were set to take a burst of three photos on a 30

270 second delay, meaning that after the cameras were motion activated there would be a 30 second
271 delay before the cameras were able to be activated again. We made no effort to correct for
272 particular individuals as we were interested in measuring white-tailed deer activity per day rather
273 than number of unique hosts. Cameras were placed simultaneously at paired native and invaded
274 plots so that deer activity could be calculated across the same time frame. At the end of the
275 experiment photos were examined by three individuals for presence of white-tailed deer
276 (Appendix S1: Table S5). Cameras were positioned on opposite sides of the plot at a distance
277 between 10 m and 15 m from the center of the plot and approximately 1.5 m aboveground.
278 Cameras were positioned so that their fields of view did not overlap, maximizing the total area of
279 the plot being sampled. Cameras were active from 11 April to 1 June 2019, which coincided with
280 questing activity for nymph and adult *A. americanum* in the region (Davidson et al. 1994, Gleim
281 et al. 2014). In each field site we also recorded ground-level microclimate conditions
282 (temperature and relative humidity) from 13 June to 1 August 2019 at five-minute intervals using
283 HOBO U23 Pro v2 logger and PVC housing as described in the field experiment above.
284 We concurrently estimated tick abundance for each plot using carbon dioxide-baited traps
285 (hereafter CO_2 trap). The CO_2 trap is one of the most effective means of sampling *A. americanum*
286 nymph and adult life stage ticks (Schulze et al. 1997) and is less biased by different vegetation
287 structures (e.g., a plant invasion) than drag sampling (Kensinger and Allan 2011). The CO_2 traps
288 consisted of a mini cooler mounted on a sheet of plywood (45 cm x 60 cm) with vent holes
289 drilled along the sides of the cooler near the base to disperse gaseous CO_2 from sublimating dry
290 ice. For each sampling event, double-sided carpet tape was placed around the perimeter of the
291 plywood to capture ticks attracted by the CO_2. Each trap was filled with approximately 2 kg of
292 dry ice and left in the field for 24 hours before ticks were collected. We placed four CO_2 traps

293 per plot, and traps were placed at least 10m apart from each other within a plot. CO_2 traps can
294 attract ticks that are within a 5m radius of the trap (Kensinger and Allan 2011). When plots were
295 resampled, traps were placed in new locations that were greater than 5m from the previous
296 sampling location. This sampling approach maximized the area of the 10m radius plot that could
297 be sampled with CO_2 traps (Appendix S1: Figure S3). In total there were 51 tick sampling
298 events, and with four CO_2 traps per sample, there were over 200 trap nights in the study. Traps
299 were purposefully not placed in plot centers to ensure that new areas of the plot were examined
300 during each sampling event. Ticks ensnared on the tape were counted and preserved in 70%
301 ethanol for identification and to determine life stage.

302 *Statistical analysis: Tick abundance and white-tailed deer activity*

303 We focused our analysis on white-tailed deer activity only due to the tall vegetation in
304 invaded areas limiting detection of smaller wildlife hosts with camera traps (Appendix S1:
305 Figure S4). White-tailed deer serve as an important host for all three life stages of *A.*
306 *americanum* (Bloemer et al. 1986). Relative white-tailed deer activity was estimated and
307 standardized by dividing the number of camera trap photos containing deer by the number of
308 days the camera was deployed and operating. This approach provided data in units of deer
309 photos/day and allowed for comparison of data from cameras with different lengths of operable
310 deployment. Our approach was intended to detect relative differences in activity by white-tailed
311 deer in invaded and native areas, not to estimate white-tailed deer population sizes.

312 We fit negative binomial general linear mixed effects model to examine the effect of
313 white-tailed deer activity on tick abundance from 11 April to 1 June 2019 in native and invaded
314 plant communities. We analyzed the fixed effects of plant invasion status (native vs. invaded),
315 white-tailed deer activity, and their interaction, on tick abundance (nymph + adult ticks). We

316 included site as a random effect in the model to account for repeated measures. White-tailed deer
317 activity was log-transformed to meet assumptions of normality. Models were fit using the "lme4"
318 package in R 3.6.1 (Bates et al. 2014, Team 2019). Negative binomial regression was also used
319 to test for differences in relative host activity and in tick abundance between native and invaded
320 plant communities.
321
322 **Results**
323 *Field experiment: Site conditions*
324 Average plant height, plant biomass, and light availability at the soil surface were
325 influenced by *Imperata* (MANOVA; $F_{3,20} = 74.48$; $p < 0.0001$). Average plant height was 268%
326 higher and plant biomass was 408% greater in invaded than native areas (Appendix S1: Figure
327 S5a, b), which corresponded to 91% less light availability at the soil surface in invaded areas
328 (Appendix S1: Figure S5c). There was no difference in overstory canopy cover in invaded and
329 native areas (ANOVA; $F_{1,22} = 0.146$; $p = 0.706$), indicating differences in plant communities and
330 understory light availability was driven by presence of *Imperata* (Appendix S1: Figure S5d).
331 *Field experiment: Tick survival and microclimate conditions*
332 Regardless of sex or life stage, ticks survived longer in invaded compared to native plant
333 communities (Figure 2 a, b). Time to 100% mortality per plot was, on average, 57% longer for
334 nymphs and 45% longer for adults in the invaded compared to uninvaded native plots (Figure 2
335 a, b). Throughout the experiment, there was greater relative humidity as well as lower maximum
336 temperatures in invaded areas (Figure 2 c, d). Average daily minimum relative humidity in
337 invaded areas was 79% at the start of the experiment (Appendix S1: Table S1, Intercept) and was
338 16% greater than native areas throughout the experiment (Appendix S1: Table S1, Invasion

339 effect). Average daily maximum temperature in the invaded area was 39 ºC at the start of the
340 experiment (Appendix S1: Table S1, Intercept) and remained roughly 6 ºC cooler compared to
341 native areas throughout the experiment (Figure 2 c, d; Appendix S1: TableS1, Treatment effect).
342 Across both life stages, individual tick survival was longer in invaded areas. Mean ± SE
343 nymph survival was 130 ± 5.4 days in invaded areas versus 80.5 ± 5.0 days in native vegetation,
344 while mean adult survival was 256 ± 4.8 and 140 ± 7.3 days in invaded and native areas,
345 respectively. For both nymph and adult life stages, exposure time (hours per day) to relative
346 humidity below 80% was significantly related to fewer days survived in native plant
347 communities (Figure 3a, b) (Appendix S1: Table S2). In invaded areas there was less exposure
348 time to relative humidity below 80% (1.9 h/day invaded vs 3.1 h/day native), and relative
349 humidity was not related to number of days survived for nymph or adult ticks. Maximum
350 temperature at mortality (i.e., maximum temperature between the time when the tick was last
351 observed alive and when it was observed as dead) was negatively correlated with survival time
352 for nymphal ticks, regardless of invasion (Figure 3c) (Appendix S1: Table S3). For adult ticks,
353 maximum temperature prior to mortality was negatively correlated with survival time for ticks in
354 native but not invaded plots (Figure 3d) (Appendix S1: Table S3).
355 Both microclimate variables had a negative effect on days survived, but maximum
356 temperature prior to observed mortality had a stronger effect than hours below the CEH
357 threshold for both life stages (Appendix S1: Table S4, Figure S6). For nymphs, maximum
358 temperature had a strong negative effect size on days survived (estimate = -46.9; 95% CI = -55.0
359 – -38.6; $p < 0.0001$), while hours below 80% relative humidity had a smaller, nonsignificant
360 effect size (estimate = -5.0; 95% CI = -14.0 – 4.1; $p < 0.254$). For adult ticks, maximum
361 temperature also had a strong negative effect size (estimate = -28.2; 95% CI = -38.3 – -19.6; $p <$

362 0.0001), and hours below 80% relative humidity had a smaller but still negative effect (estimate
363 = -14.6; 95% CI = -29.2 – 0.0; p = 0.052) on survival.

364 *Field survey: White-tailed deer activity, tick abundance, and microclimate*

365 There were no differences in relative white-tailed deer activity between native and
366 invaded plots ($t_{1,44}$ = 1.01; p = 0.318) (Appendix S1: Figure S7). There were also no differences
367 in average tick abundance (nymph [$t_{1,49}$ = 0.905; p = 0.370]; adult [$t_{1,49}$ = 1.298; p = 0.200] life
368 stage ticks) between native and invaded areas (Appendix S1: Figure S8). In native communities,
369 white-tailed deer activity (deer photos/day) was positively correlated with tick abundance
370 (estimate = 1.4; 95% CI = 0.1 – 2.8; p = 0.033) (Figure 4, Appendix S1: Table S7), while in
371 invaded habitats, tick abundance was not related to white-tailed deer activity (estimate = -0.6;
372 95% CI = -1.8 – 0.5; p = 0.273). For plots where no white-tailed deer were detected (i.e.,
373 intercept term), invaded plant communities had positive tick abundances (estimate = 1.3; 95% CI
374 = 0.6 – 2.8; p = 0.027) (Figure 4, Appendix S1: Table S7). There was one plot with both high
375 tick abundance and high deer activity that could have strongly influenced the results, so we ran
376 the analysis using the same linear mixed effects model but with that data point removed.
377 Omitting that one data point resulted in no correlation between white-tailed deer activity and tick
378 abundance (estimate = 0.8; 95% CI = -0.8 – 2.6; p = 0.349) (Appendix S1: Table S8), but there
379 was a significant intercept term (estimate = 1.3; 95% CI = -0.1 – 2.7; p = 0.036) (Appendix
380 S1:Table S8), indicating that tick abundance was greater in invaded plant communities even
381 when no white-tailed deer were detected.

382 Across the eight field sites, microclimate conditions (relative humidity and maximum
383 temperature) in invaded and native plant communities were similar to what was observed at the
384 field experiment site (Appendix S1: Figure S9). Mean ± SE of daily minimum relative humidity

385 (%) was 92.0 ± 0.6 in invaded areas and 68.4 ± 0.9 in native areas, while average daily
386 maximum temperature (ºC) was 30.0 ± 0.1 and 34.00 ± 0.2 in invaded and native areas,
387 respectfully (Appendix S1: Figure S9).
388
389 **Discussion**
390 These results contribute to a growing understanding that introductions of non-native species may
391 have a myriad of indirect effects on ecological communities (Pejchar and Mooney 2009, Linders
392 et al. 2019). We demonstrated that an invasive plant species increased survival time of human
393 disease vectors that may maintain tick abundances in less favorable wildlife host habitat. The
394 invasive grass *Imperata*, which is widespread in the southeastern USA, likely influences tick
395 exposure risk through multiple mechanistic pathways. Consistent with our hypothesis about
396 invader effects on microclimate, lower temperatures and higher humidity corresponded with
397 greatly prolonged tick survival in invaded areas. We also hypothesized that invaded areas would
398 have greater tick abundance than native-dominated areas because of longer tick survival and
399 greater white-tailed deer activity. Contrary to this hypothesis, we observed no overall difference
400 in white-tailed deer activity between native and invaded areas and detected no difference in
401 average tick abundance between the two areas during the time period of peak tick abundance
402 (Davidson et al. 1994, Gleim et al. 2014). However, there was a positive relationship between
403 tick abundance and white-tailed deer activity observed only in native-dominated areas. Together,
404 these results suggest the invasive plant is affecting multiple, potentially off-setting, mechanistic
405 pathways contributing to tick exposure risk.
406 Our results show that tick abundances in *Imperata*-invaded plant communities may be
407 maintained even with relatively low white-tailed deer activity due to more favorable

408 microclimate conditions that prolong off-host tick survival. In contrast, native plant communities
409 were less favorable for ticks because they had consistently lower humidity at or below the
410 critical equilibrium humidity (CEH). The cumulative stress of relative humidity at or below the
411 CEH predisposed ticks to mortality in native-dominated areas during persistently hotter periods
412 or rapid increases in temperature, which were buffered in invaded areas. Our field experiment
413 results also validate the thresholds of relative humidity and temperature for tick desiccation and
414 mortality described in foundational laboratory experiments (Sauer and Hair 1971, Hair et al.
415 1975).

416 Deer are widely considered a key contributing factor to abundances of several North
417 American tick species but the shape of this relationship is often difficult to detect (Kugeler et al.
418 2016, Hofmeester et al. 2017). Other studies have emphasized the complexity of this
419 relationship, detecting either a weak positive relationship (Ostfeld et al. 2018), or no correlation
420 between deer abundance and tick abundance (Hofmeester et al. 2017). In our analysis of data
421 from eight field sites, we detected a positive relationship between deer and tick abundance in
422 native plant communities (Figure 4). However, one site appears to be driving this relationship,
423 and when that site is removed from the analysis the effect is no longer significant. In contrast to
424 previous studies, we did not find a relationship between tick abundance and deer activity in
425 invaded plant communities (Williams et al. 2009, Allan et al. 2010a), however, both studies
426 evaluated non-native invasive shrubs, which may promote deer activity by providing forage or
427 cover. Although other species are known to use *Imperata* invaded areas for refuge, e.g., wild
428 turkey (*Meleagris gallopavo,* Cabrera et al. 2021) and cotton rats (*Sigmodon hispidus*, Borden et
429 al. 2022), our results suggest that *Imperata* invasions aren't preferred over native plant
430 communities by white-tailed deer.

431 Climate change is predicted to facilitate the spread of *Imperata,* expanding its range from
432 southeastern Gulf States to as far north as Virginia along the eastern USA seaboard (Bradley et
433 al. 2010). As *Imperata* spreads northward, it is likely to interact with other tick species, including
434 the blacklegged tick *Ixodes scapularis,* the primary vector for Lyme disease in the United States,
435 which could increase tick-borne disease risk (Steere et al. 2004). The geographic distribution of
436 the black-legged tick is also expanding, with an increase in the number of USA counties
437 reporting its presence from 1996-2005 (Eisen et al. 2016), and ongoing landscape change
438 facilitates this invasion (Gardner et al. 2020). The blacklegged tick has a similar CEH to that of
439 *A. americanum,* suggesting other tick species may benefit from the relatively high relative
440 humidity and low maximum temperature generated by *Imperata* invasions (Berger et al. 2014).
441 This study uniquely demonstrated how alterations of abiotic and biotic factors by
442 invasive plants can impact tick exposure risk. Despite the duration and precision of the survival
443 assay and the scale of the field study, there were limitations. For example, although we
444 documented much longer tick survival due to a plant invasion, and strong evidence for
445 microclimate driving that pattern, additional studies replicated across a larger environmental
446 gradient of invasion would be useful for validating this result. In addition, including sites that
447 vary in invader density or biomass could inform management of highly invaded areas to reduce
448 tick-borne disease risk. Finally, while we focused on white-tailed deer activity, in part because of
449 invader height and difficulty camera trapping rodents or other hosts, quantifying invader effects
450 on other hosts (small- and medium-sized mammals, birds, etc.) that are known to influence tick-
451 borne disease risk could help in resolving the relative influence of host abundance and
452 microclimate-driven survival on tick abundance (Greiner et al. 1984, Clark 2004, Ostfeld et al.
453 2018). Additionally, since CO_2 traps only capture host-seeking ticks, actual tick abundance could

454 be greater in invaded areas if cogongrass improves microclimate significantly where ticks might
455 be more selective about when they expend energy to pursue a host.
456 Other studies that have evaluated the effects of invasive plants on tick abundance have
457 focused on woody invaders (*Lonicera macckii*, *Berberis thunbergia, Rosa multiflora*) and were
458 conducted in the Midwest or Northeast US (Williams et al. 2009, Allan et al. 2010a,
459 Adalsteinsson et al. 2016). These studies have found that woody invasive plants alter tick
460 abundance predominately by providing host habitat rather than creating more favorable
461 microclimates for tick survival (but see Williams and Ward 2010). Tick survival assays
462 conducted using the invasive grass *Microstegium vimineum* found that the invader created less
463 favorable microclimate conditions and reduced survival time for off-host ticks (Civitello et al.
464 2008). The dense herbaceous structure of *Imperata* invasions differ drastically from that of *M.*
465 *vimineum* and the woody invaders that have been studied previously, making comparisons across
466 systems difficult. Impacts of plant invasions on tick abundance will likely differ by location and
467 species studied, thus there is a need to address how invasive plants impact tick abundance
468 through changes to host activity as well as how tick survival is altered by invader-driven changes
469 in microclimate.
470 Our findings demonstrate potential indirect effects of plant invasions on human health.
471 Specifically, we provide evidence for how tick exposure risk may be driven by different
472 mechanistic pathways in invaded and native plant communities. Consistent with Wei et al.
473 (2020), invaded plant communities appear to play an important, but relatively underappreciated,
474 role in altering human vector-borne disease risk. Invasive plant species have a wide variety of
475 traits that could differentially affect off-host tick survival and host activity. While measurement
476 of microclimate factors and tick survival are straightforward for field ecology research studies,

measurement of activity of large-bodied mammals with large home range sizes, such as white-tailed deer, is notoriously difficult. Thus, we encourage future work to explore these relationships among invasive plants, environmental conditions, ticks, and their hosts more generally across other invasive plant and tick species, and under different climates, landscape conditions, and disturbance regimes. Understanding the relative contribution of host use and microclimate across habitats invaded by different species will aid in our ability to determine current, and forecast future, impacts of plant invasions on tick-borne disease risk. More broadly, these findings highlight the complex and indirect mechanisms by which invasive species may impact species interactions.

Acknowledgements

We thank Taylor Clark for assistance with data collection, Tempest McCabe for feedback and assistance with statistical analysis, and members of the Flory Lab at the University of Florida for comments and feedback on figures and text.

Funding

This research was funded by the Strategic Environmental Research and Development Program (RC-2636).

The authors declare no conflict of interest

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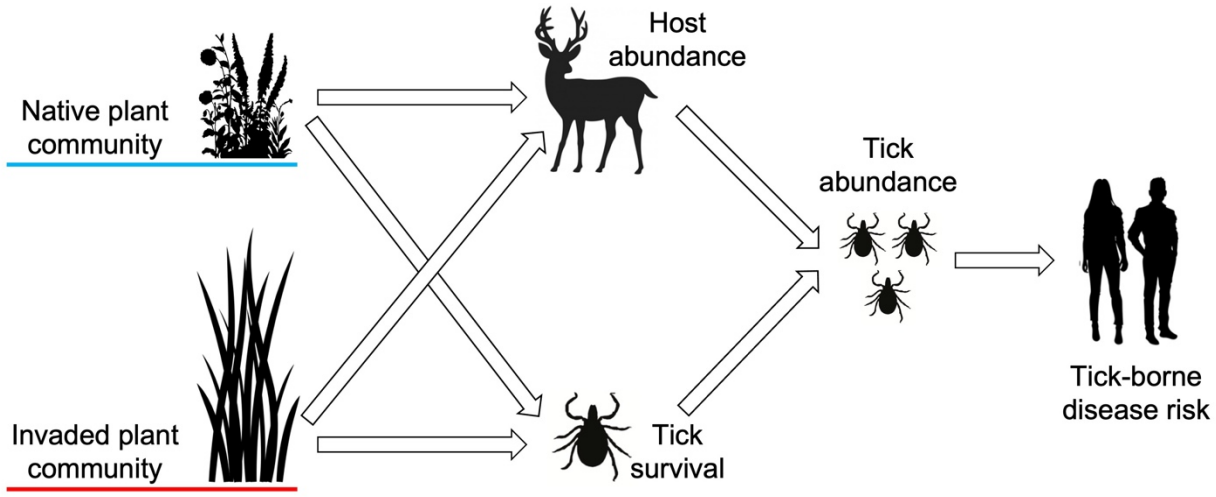

Figure 1. Conceptual diagram of two pathways that contribute to tick-borne disease risk. Native and invaded plant communities may have different effects on both host (e.g., deer, rodent) abundances and tick survival, which together determine tick abundance and, in turn, influence human tick exposure and tick-borne disease risk.

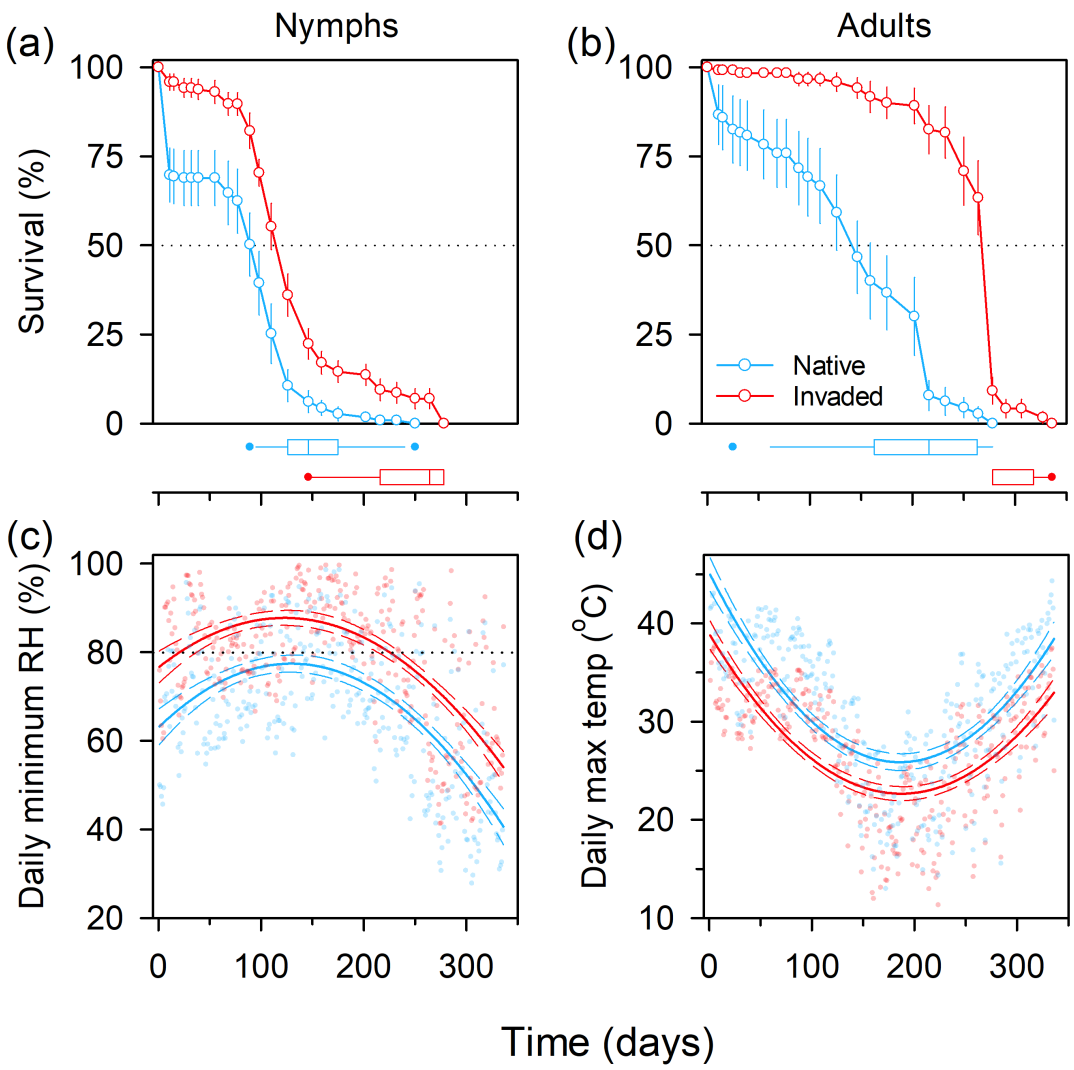

Figure 2. Tick survival per plot and microclimate conditions in native and invaded areas. Percent survival (mean ± SE) of (a) nymph and (b) adult Amblyomma americanum in native (blue) and invaded (red) plots over time (start date of experiment June 21, 2018). Box plots below panels (a) and (b) are distributions of time to 100% mortality across plots. Microclimate conditions: (c) average daily minimum relative humidity (RH) (%), dotted line indicates critical equilibrium humidity for Amblyomma americanum (80% RH), and (d) average daily maximum temperature (ºC). Points in (c) and (d) are daily averages across all plots (n = 12) in each treatment. Curved lines in panels (c and d) are polynomial non-linear least squares regression (solid) with 95% CI (dashed) for native (blue) and invaded (red) areas.

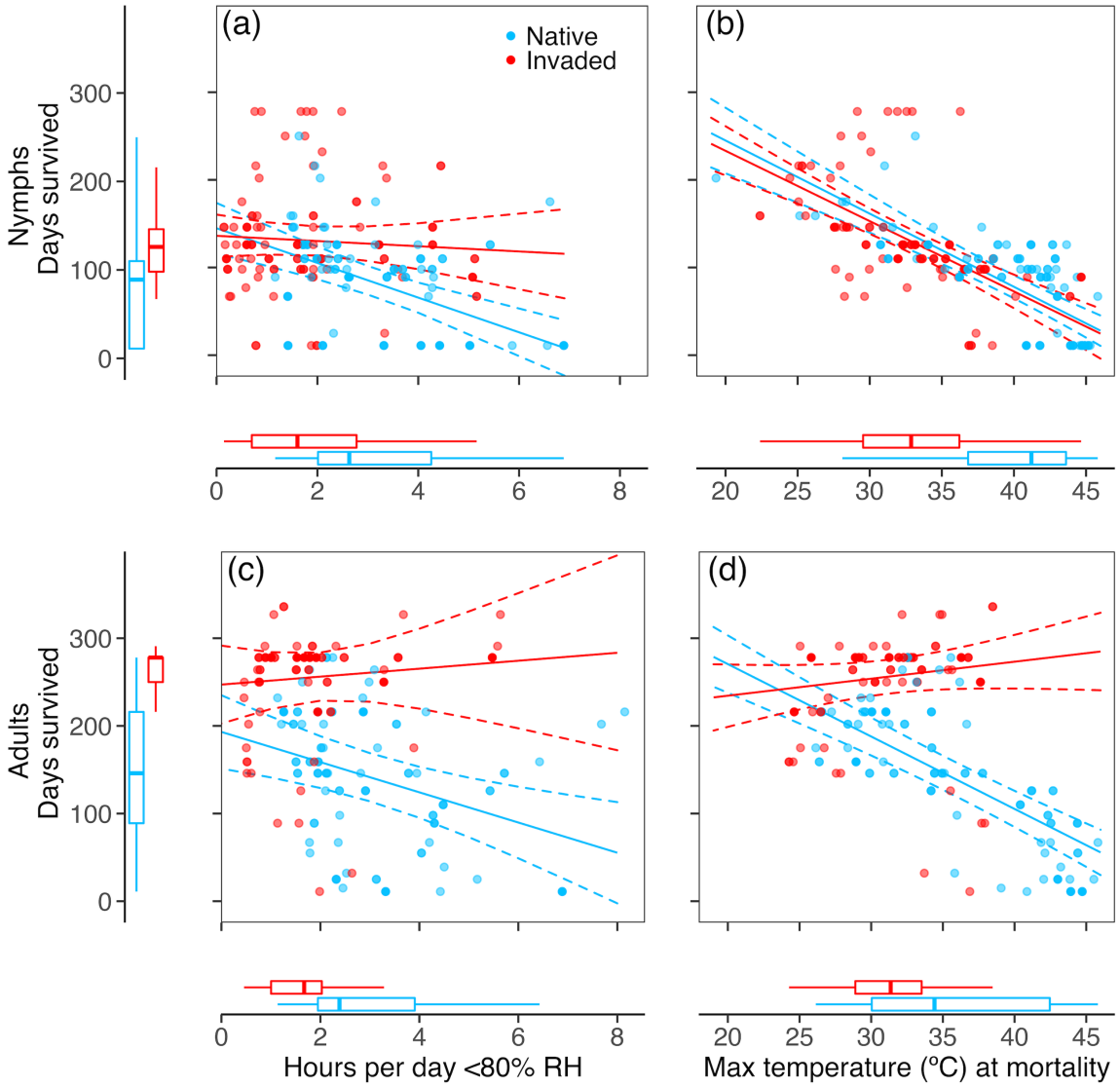

Figure 3. Number of days survived for individual nymph (a, b) and adult (c, d) life stage ticks and microclimate conditions that were experienced in native (blue) and invaded (red) plots. Relationship between days survived and hours per day below 80% RH, and the relationship between days survived and the maximum temperature that was experienced prior to mortality for nymphs (a, b) and adults (c, d). Best fit lines (solid) with 95% confidence interval (dashed) are from linear mixed effects models. Box plots indicate median and 25th and 75th percentile, with 10th and 90th percentile whiskers for days survived (y-axes) and microclimate conditions experienced by individual ticks in each treatment (x-axes).

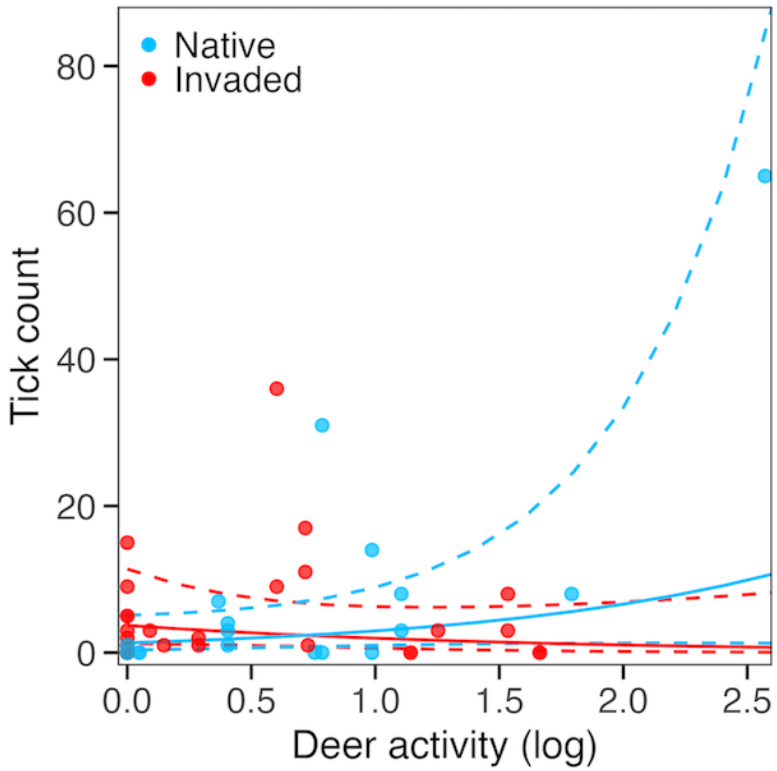

Figure 4. Relationship between host use (deer activity) and tick abundance (nymph and adult ticks per plot) in native (blue) and invaded (red) plant communities. Best fit lines (solid) from linear mixed effect models with 95% confidence interval (dashed).