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

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Abstract

Plant invasions may alter disease 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*), its preeminent host white-tailed deer (*Odocoileus virginianus*), 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 relative humidity, yielding a lower vapor pressure deficit (VPD) that likely reduced tick desiccation. The observational study showed similar average tick abundance in native and invaded plant communities and no difference in wildlife host (white-tailed deer) activity between plant communities. However, there was 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 are the dominant driver of tick abundance in invaded areas, while tick abundance in native-dominated areas may be promoted, at least in part, by white-tailed deer activity. Our results demonstrate that plant invasions can affect multiple, potentially counteracting mechanistic pathways that contribute 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 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 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 modifying either habitats that alter host abundance or microclimate conditions that promote or inhibit tick survival (Allan et al. 2010a, Williams and Ward 2010, Stewart et al. 2021) (Figure 1). Entomological metrics of exposure risk include measures of tick abundance (e.g., density of ticks), pathogen infection prevalence, or

their product (e.g., density of infected ticks) (Fischhoff et al. 2019). Vector abundance often is used as a proxy for tick exposure risk, indicating a human's likelihood of encountering a tick upon entering a particular habitat (Barbour and Fish 1993, Fischhoff et al. 2019). While there has been research on how these pathways individually affect tick abundance, studies that simultaneously address multiple pathways are needed to improve understanding of complex processes by which invasive plants may alter tick exposure risk, and thus infectious disease.

Collectively, evidence for mechanisms that influence tick-borne disease in invaded areas is sparse and inconsistent, and varies by tick species, invasive plant species, and habitat conditions, among other factors (Civitello et al. 2008, Allan et al. 2010a, Williams and Ward 2010, Mack and Smith 2011, Racelis et al. 2012, Adalsteinsson et al. 2016). Plant invaders have been shown to increase habitat use by small mammals (Guiden and Orrock 2019), and white-tailed deer (Elias et al. 2006, Allan et al. 2010a), leading to greater abundance of ticks (Elias et al. 2006) and pathogen-infected ticks (Allan et al. 2010a) compared to native areas. Plant invasions may also increase tick abundances relative to native plant dominated areas by providing favorable microclimate conditions (i.e., higher humidity, lower temperature, or lower vapor pressure deficit) that reduce tick desiccation (Williams and Ward 2010, Racelis et al. 2012, Brunner et al. 2023). However, the few studies comparing the abiotic mechanisms affecting tick survival in invaded and native areas show either no difference (Allan et al. 2010a) or lower tick survival (Civitello et al. 2008) in invaded compared to native plant dominated communities. Given the ongoing introduction and spread of both invasive plants (Seebens et al. 2017), and ticks (Ostfeld and Brunner 2015), there is a critical need to better understand how invasive plants affect host habitat use (Stewart et al. 2021) as well as the abiotic factors that influence tick survival.

Here, we measured differences in tick abundance in native and invaded plant communities, and how these may be attributable to tick survival and host activity, which are the two main pathways that determine tick abundance (Figure 1), in the two plant community types. Specifically, we used field experiments and observational field studies to compare microclimate conditions and tick survival (lone star tick, *Amblyomma americanum*) in native plant dominated areas compared to areas invaded by cogongrass (*Imperata cylindrica*). We also measured relative activity of a key host, white-tailed deer (*Odocoileus virginianus*), in invaded and native areas, and evaluated how tick abundance was related to host activity. White-tailed deer serve as an important host for all three life stages of *A. americanum* (Bloemer et al. 1986).

First, in a field experiment, we measured survival of lab-reared ticks in native plant communities and adjacent invaded areas while concurrently measuring temperature and relative humidity (RH) to calculate vapor pressure deficit (VPD), a measure of the strength of atmospheric desiccation (Grossiord et al. 2020). Second, we evaluated relative white-tailed deer activity (via camera traps) and abundances of host-seeking ticks (via CO_2 trapping) in native and invaded sites in a field survey. Because the invader creates much denser stands compared to native plant communities (Appendix S1: Figure S1), we hypothesized that invaded areas would have lower temperatures and higher relative humidity, yielding lower vapor pressure deficit, which would be more favorable for tick survival relative to native areas (Alba et al. 2017). 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 cover from predators, as documented with small mammals in experimental *Imperata*-invaded plots (Borden et al. 2022), which would in turn be linked to 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 most costly 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 enhanced fire induced tree mortality (Flory et al. 2022). *Imperata* has also been shown to change microclimate conditions, including greater 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 desiccation (i.e., loss of water through the cuticle) (Needham and Teel 1991) the primary cause of off-host tick mortality (Ostfeld and Brunner 2015). 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

158 80-82% relative humidity for adult *A. americanum* (Hair et al. 1975, Knülle and Rudolph 1982).
159 While desiccation is primarily driven by low relative humidity (at or below CEH), higher
160 temperatures lead to more water molecules escaping the cuticle due to kinetic energy (Sauer and
161 Hair 1986). For *A. americanum,* temperatures in excess of 35 ºC can contribute to desiccation
162 and mortality (Sauer and Hair 1971), while all terrestrial arthropods, including ticks, lose their
163 capacity to retain moisture at temperatures in excess of 40 ºC (Londt and Whitehead 1972).
164 Relative humidity and temperature can be converted to vapor pressure deficit (VPD) using the
165 formula from Murray (1967). The daily hazard of tick mortality has been shown to increase
166 drastically with increasing levels of daily maximum VPD (e.g., > 2 kPa) of tick species such as
167 *Ixodes scapularis* and *Ixodes ricinus* (Herrmann and Gern 2010, Brunner et al. 2023). Increases
168 in daily maximum VPD has also been associated with a reduction in tick counts and limiting
169 questing activity for *Ixodes* spp. (Sambado et al. 2024) and has shown to be an important
170 predictor of unsuitable habitat for *A. americanum* (Rochlin et al. 2023). Tick abundance,
171 including local abundance of *A. americanum,* can also be regulated by host activity (Paddock and
172 Yabsley 2007, Rochlin et al. 2022). White-tailed deer (*Odocoileus virginianus*) serve as key
173 hosts for all three life stages of *A. americanum* (Bloemer et al. 1986), and are important reservoir
174 hosts for multiple pathogens transmitted by *A. americanum* (Allan et al. 2010b).

175 *Field experiment: Tick survival and microclimate conditions*

176 To test if ticks survived longer in *Imperata*-invaded areas, we established an experiment
177 in a planted longleaf pine (*Pinus palustris*) stand with fine sandy soils near La Crosse, FL
178 (29.897° N, -82.420° W) that had distinct *Imperata*-invaded and native plant dominated areas
179 (Appendix S1: Figure S2, S3). The invaded area was highly invaded by *Imperata* and spanned
180 approximately 6300 m^2, while the surrounding area was not invaded and dominated by native

181 plant species. The native plant community was typical of a longleaf pine stand, with *Aristida*
182 *stricta* (wiregrass), *Rubus flagellaris* (common dewberry), *Carya sp.* (hickory), and *Andropogon*
183 spp. There was no recent chemical or mechanical management in either the invaded or native
184 areas, and the native plant community included no other non-native plant species. Because we
185 conducted our experiment within a forest stand with distinct invaded (*Imperata*) and native areas
186 in close proximity that shared the same overstory structure, we expected any differences in
187 microclimate conditions to be due to invasion, not other underlying factors (see Results).
188 We established 24 plots (1m x 1m), 12 in invaded habitat and 12 in native plant
189 dominated habitat. Plots were randomly established along two transects, one in each plant
190 community type, with at least 10m spacing. At the center of each plot, a 300-micron 10 cm x 20
191 cm nylon mesh bag (Skimz, Singapore) containing 10 nymph and 10 adult (5 female and 5 male)
192 *A. americanum* obtained from the National Tick Research and Educational Resource
193 (Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, OK)
194 was placed in a 50 cm tall cylindrical wire mesh exclosure to deter wildlife interference
195 (Appendix S1: Figure S2). We used lab-reared instead of wild-caught ticks to control for tick age
196 (within life stage) and to standardize the range of tick exposure to environmental conditions prior
197 to the experiment. Each mesh bag containing ticks was oriented vertically to facilitate natural
198 diurnal tick questing (i.e., host seeking behavior) and, although there was no substrate within the
199 bags, the bags remained in contact with the soil surface to allow for ticks to seek refuge below
200 the leaf litter to avoid desiccation stress (Schulze and Jordan 2003, Ostfeld and Brunner 2015)
201 throughout the experiment (Appendix S1: Figure S2).
202 The start date of the survival experiment (June 21, 2018) coincided with typical off host
203 periods (between blood meals) for *A. americanum* in the region (Davidson et al. 1994, Gleim et

al. 2014). During these long non-parasitic phases, ticks seek refuge in areas with microclimates that promote water balance (Knülle and Rudolph 1982, Davidson et al. 1994). Mesh bags were examined every 7-10 days for the first month and then every 10-14 days afterward to determine days survived for both nymph and adult ticks. During each visit, bags were removed from the cages but not opened, and survival status of each individual tick was determined by assessing the response of the tick to CO_2 stimulation from human breath (Steullet and Guerin 1992). Number of days survived for individual ticks was determined by the time between the start of the survival experiment and the date when the tick was observed not responding to CO_2 stimulation. Visits continued to the site until May 23, 2019, when all ticks had died.

To assess plant community structure and abiotic conditions in invaded and native plant dominated areas, at the start of the survival experiment we collected understory herbaceous plant height and standing biomass, light availability at the soil surface, and overstory canopy cover at each plot. Plant height was measured as the tallest point of living leaf tissue from soil surface. We collected aboveground biomass by clipping at the soil surface in 25 cm x 25 cm quadrats and dried at 60 ºC to a constant mass and weighed (± 0.01g). The 25 cm quadrats were placed adjacent to each 1 m experimental plot, in an area representative of the plant communities in the experimental plots and far enough away (~1-2m) to not alter microclimate conditions in the experimental plot. 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). To determine if the pine tree overstory was similar in native and invaded areas and was not a confounding factor with invasion, overstory canopy cover was estimated using a concave spherical densiometer (Forestry Suppliers Inc., Jackson, MS, USA) by taking the average of four readings facing each cardinal direction above each plot.

227 Throughout the experiment we recorded ground-level microclimate conditions
228 (temperature and relative humidity) at five-minute intervals immediately adjacent to each
229 enclosure containing the mesh bags using HOBO U23 Pro v2 loggers (Onset Computer
230 Corporation, Bourne, MA). Each logger was housed in a capped 18-inch length of 3.8 cm
231 diameter PVC pipe to protect it from rainfall and direct sunlight. Holes were drilled on four sides
232 six inches apart along the length of the pipe to allow for airflow and better reflect ambient
233 temperature and relative humidity (see Appendix S1: Figure S2a-b). We used the temperature
234 and relative humidity data at each five-minute interval to calculate VPD (Murray 1967).

235 *Statistical analysis: Site conditions*

236 We conducted our statistical analysis of the tick survival field experiment in several
237 phases. First, we conducted analyses to determine a) if *Imperata* invaded plant communities had
238 different characteristics that might influence microclimate conditions and b) if *Imperata* invasion
239 altered tick survival over time. We used multivariate analysis of variance (MANOVA) to test the
240 hypothesis that *Imperata* was associated with different plant community characteristics (i.e.,
241 vegetation height, standing biomass, light availability at soil surface, and overstory canopy
242 cover). We also plotted microclimate conditions (i.e., lower average daily maximum VPD,
243 higher average daily minimum relative humidity, and lower average daily maximum
244 temperature) over time to test the hypothesis that microclimates differed between native plant
245 dominated and invaded plots. These analyses were done using the "car" package (Fox and
246 Weisberg 2018, R Core Team 2020) in R version 3.6.1.

247 *Statistical analysis: Tick survival and microclimate conditions*

248 We used linear models using general least squares regression to assess how the number of
249 days survived for individual *A. americanum* of each life stage was related to the plant community

250 and VPD (daily maximum VPD). The general linear mixed effects model on number of days
251 survived for adult or nymph life stage ticks included the fixed effect terms of treatment (native),
252 maximum daily VPD experienced prior to mortality, and their interaction. Maximum daily VPD
253 prior to mortality was recorded as the maximum daily VPD measured at each plot between
254 survival checks (i.e., maximum VPD between the time when the tick was last observed alive and
255 when it was observed as dead). If data loggers failed or malfunctioned, then data from that time
256 interval was omitted from analyses. We included plot as a random effect as well as a compound
257 symmetry covariance structure based on BIC to account for repeated measures over time. Since
258 nymphs are generally more susceptible to desiccation due to their higher surface:volume ratio
259 and lower biomass energy reserves compared to adult ixodid ticks (Knülle and Rudolph 1982,
260 Needham and Teel 1991), we fit models for nymph and adult life stage ticks separately using the
261 "nlme" package (Pinheiro et al. 2025). Degrees of freedom were calculated using "lmertest"
262 (Kuznetsova et al. 2017) in R 3.6.1 (R Core Team 2019).

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

264 To examine the relationship between *Imperata* invasions and white-tailed deer activity
265 and tick abundance, we conducted field surveys in invaded and native dominated plant
266 communities across eight sites in north central Florida (Appendix S1: Figure S3). Invaded plots
267 were selected if the *Imperata* invasion covered a minimum of 500 m^2, and native plant
268 dominated plots were selected if they had visually similar overstory tree canopy structure to that
269 of the invaded plots. Since we encountered many large invasions with few comparable native
270 plant communities, at some sites we sampled multiple invaded plots per site. We sampled a total
271 of 34 plots, 22 plots in *Imperata* invaded areas and 12 in native plant dominated areas. Due to
272 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 S1). 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 S2). Corresponding pairs of native and invaded plots that were resampled were chosen haphazardly and revisited after a minimum of three weeks from the previous sampling event (Appendix S1: Table S2). Within a site, invaded and native plant dominated 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.

We placed two motion-activated cameras (Primos 12MP Proof Cam 02 HD, Primos Hunting, Flora, MS) in each plot to monitor wildlife activity. We focused our analysis on white-tailed deer activity only due to the tall vegetation in invaded areas limiting detection of smaller wildlife hosts with camera traps (Appendix S1: Figure S1). All cameras were set to take a burst of three photos on a 30 second delay, meaning that after the cameras were motion activated there would be a 30 second delay before the cameras were able to be activated again. From the burst of three photos, we analyzed only one photo to count occurrences. In the rare event that an individual or multiple deer were activating the camera by staying in frame for longer than 30 seconds, the deer in these photos were recorded as one occurrence. We made no effort to correct for particular individuals as we were interested in measuring white-tailed deer activity per day rather than number of unique hosts. Cameras were placed simultaneously at native and invaded plots so that deer activity could be calculated across the same time frame. At the end of the experiment photos were examined by three individuals for presence of white-tailed deer

296 (Appendix S1: Table S1). Cameras were positioned on opposite sides of the plot at a distance
297 between 10 m and 15 m from the center of the plot and approximately 1.5 m aboveground
298 (Appendix S1: Figure S4). Cameras were positioned so that their fields of view did not overlap,
299 maximizing the total area of the plot being sampled. Cameras were active from 11 April to 1
300 June 2019, which coincided with questing activity for nymph and adult *A. americanum* in the
301 region (Davidson et al. 1994, Gleim et al. 2014). In each field site we also recorded ground-level
302 microclimate conditions (temperature and relative humidity) from 13 June to 1 August 2019 at
303 five-minute intervals using HOBO U23 Pro v2 logger and PVC housing as described in the field
304 experiment above.

305 While the cameras were deployed, we concurrently estimated tick abundance for each
306 plot using carbon dioxide-baited traps (hereafter CO_2 trap). The CO_2 trap is one of the most
307 effective means of sampling *A. americanum* nymph and adult life stage ticks (Schulze et al.
308 1997) and is less biased by different vegetation structures (e.g., a plant invasion) than drag
309 sampling (Kensinger and Allan 2011). The CO_2 traps consisted of a mini cooler mounted on a
310 sheet of plywood (45 cm x 60 cm) with vent holes drilled along the sides of the cooler near the
311 base to disperse gaseous CO_2 from sublimating dry ice (Appendix S1: Figure S5). For each
312 sampling event, double-sided carpet tape was placed around the perimeter of the plywood to
313 capture ticks attracted by the CO_2. Each trap was filled with approximately 2 kg of dry ice and
314 left in the field for 24 hours before ticks were collected. We placed four CO_2 traps per plot, and
315 traps were placed at least 10m apart from each other within a plot. CO_2 traps can attract ticks that
316 are within a 5m radius of the trap (Kensinger and Allan 2011). When plots were resampled, traps
317 were placed in new locations that were greater than 5m from the previous sampling location.
318 This sampling approach maximized the area of the 10m radius plot that could be sampled with

319 CO_2 traps (Appendix S1: Figure S4). In total there were 51 tick sampling events, and with four
320 CO_2 traps per sample, there were 204 trap nights in the study. Traps were purposefully not
321 placed in plot centers to ensure that new areas of the plot were examined during each sampling
322 event. Ticks ensnared on the tape were counted and preserved in 70% ethanol for identification
323 and to determine life stage.

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

325 Relative white-tailed deer activity was estimated and standardized by dividing the
326 number of camera trap photos containing deer by the number of days (total hours / 24) the
327 camera was deployed and operating. This approach provided data in units of deer photos/day and
328 allowed for comparison of data from cameras with different lengths of operable deployment. Our
329 approach was intended to detect relative differences in activity by white-tailed deer in invaded
330 and native areas, not to estimate white-tailed deer population sizes.

331 We fit a negative binomial general linear mixed model to examine the relationship
332 between white-tailed deer activity and concurrent estimates of tick abundance from 11 April to 1
333 June 2019 in native and invaded plant communities. We fit a model of tick abundance (nymph +
334 adult ticks) using plant invasion status (native vs. invaded), white-tailed deer activity, and their
335 interaction, as fixed-effect terms and site as a random effect term to account for repeated
336 measures. Tick abundance includes both nymph and adult life stage ticks, because white-tailed
337 deer serve as an important host for both life stages of *A. americanum* (Bloemer et al. 1986).
338 Models were fit using the "lme4" package in R 3.6.1 (Bates et al. 2014, Team 2019). Two sided
339 t-test was also used to test for differences in relative host activity and in tick abundance between
340 native and invaded plant communities.

341

342 **Results**

343 *Field experiment: Site conditions*

344 There was a significant difference between the native and invaded plant community types
345 on the combined dependent variables average plant height, plant biomass, light availability at the
346 soil surface, and overstory canopy cover (MANOVA; Pillai's Trace $_{1,22}$ = 0.922; $p < 0.0001$). In
347 separate one-way ANOVAs, average plant height was 268% higher ($F_{1,22} = 179.83$; $p < 0.001$)
348 and plant biomass was 408% greater in invaded than native areas ($F_{1,22} = 29.29$; $p < 0.001$)
349 (Appendix S1: Figure S6a, b), which corresponded to 91% less light availability at the soil
350 surface in invaded areas ($F_{1,22} = 21.22$; $p = < 0.001$) (Appendix S1: Figure S6c). However, there
351 was no difference in overstory canopy cover in invaded and native areas ($F_{1,22} = 0.15$; $p =$
352 0.706), indicating differences in plant communities and understory light availability were likely
353 driven by presence of *Imperata* and not differences in overstory canopy cover (Appendix S1:
354 Figure S6d).

355 *Field experiment: Microclimate conditions and tick survival*

356 Throughout the survival experiment, average daily maximum VPD was approximately
357 70% lower in invaded (mean ± SE: 0.99 ± 0.04 kPa) compared to native (1.7 ± 0.07, Figure 2a)
358 areas. Average daily minimum relative humidity was approximately 16% greater in invaded
359 (mean ± SE: 79.21% ± 0.79) compared to native (67.98% ± 0.87) (Appendix S1: Figure S7a).
360 Average daily maximum temperature was approximately 13% lower in invaded (mean ± SE:
361 27.20°C ± 0.34) compared to native (31.29 °C ± 0.40) (Appendix S1: Figure S7b).

362 Regardless of sex or life stage, ticks survived longer in invaded compared to native plant
363 communities (Figure 2 c, d). Time to 100% mortality per plot was, on average, 57% longer for
364 nymphs and 45% longer for adults in the invaded compared to native dominated plots (Figure 2

365 c, d). Mean ± SE nymph survival was 130 ± 5.4 days in invaded areas versus 80.5 ± 5.0 days in
366 native vegetation, while mean adult survival was 256 ± 4.8 and 140 ± 7.3 days in invaded and
367 native areas, respectively. For nymph life stages, daily maximum VPD (kPa) was significantly
368 related to fewer days survived in both native and invaded plant communities (Figure 3a)
369 (Appendix S1: Table S3). Daily maximum VPD (kPa) was significantly related to fewer days
370 survived for adult life stage ticks in the native plant dominated community (Figure 3b)
371 (Appendix S1: Table S3). However, in invaded areas there was a significant, positive
372 relationship between daily maximum VPD and days survived (Figure 3b) (Appendix S1: Table
373 S3).

374 *Field survey: Microclimate, white-tailed deer activity, and tick abundance*

375 Across the eight field sites, microclimate conditions (vapor pressure deficit, relative
376 humidity and maximum temperature) in invaded and native plant communities were similar to
377 what was observed at the field experiment site, though over a much shorter time period
378 (Appendix S1: Figure S8). Mean ± SE of daily maximum VPD (kPa) was 0.4 ± 0.03 in invaded
379 areas and 1.8 ± 0.07 in native areas, minimum relative humidity (%) was 91.4 ± 0.7 in invaded
380 areas and 67.5 ± 1.0 in native areas, while average daily maximum temperature (ºC) was 30.0 ±
381 0.1 and 34.00 ± 0.2 in invaded and native areas, respectfully (Appendix S1: Figure S8).

382 There were no differences in relative white-tailed deer activity between native and
383 invaded plots (t_{44} = 1.01, p = 0.318) (Appendix S1: Figure S9). There were also no differences in
384 average tick abundance (nymph [t_{43} = -0.713, p = 0.480]; adult [t_{43} = -1.031, p = 0.308] life
385 stage ticks) between native and invaded areas (Appendix S1: Figure S10). In native
386 communities, tick abundance increased with white-tailed deer activity (deer photos/day)
387 (estimate = 0.6 ticks per deer photo/day; 95% CI = 0.1 – 1.1) (Figure 4, Appendix S1: Table S4),

388 while in invaded habitats, white-tailed deer activity was not related to tick abundance (estimate =
389 -0.4 ticks per deer photo/day; 95% CI = -0.9 – 0.1). For plots where no white-tailed deer were
390 detected (i.e., intercept term), invaded plant communities had positive tick abundances (estimate
391 = 1.4 ticks; 95% CI = 0.2 – 2.5) (Figure 4, Appendix S1: Table S4). There was one plot with
392 both the highest tick abundance and highest deer activity that could have strongly influenced the
393 results, so we ran the analysis using the same linear mixed effects model but with that data point
394 removed. Omitting that one data point resulted in no association between white-tailed deer
395 activity and tick abundance (estimate = -0.4 ticks per deer photo/day; 95% CI = -0.9 – 0.1)
396 (Appendix S1: Table S5), but there was a significant intercept term (estimate = 1.3 ticks; 95% CI
397 = 0.1 – 2.6) (Appendix S1:Table S5), indicating that tick abundance was greater in invaded plant
398 communities even when no white-tailed deer were detected.
399
400 **Discussion**
401 These results contribute to a growing understanding that introductions of non-native species may
402 have a myriad of indirect effects on ecological communities (Pejchar and Mooney 2009, Linders
403 et al. 2019). We documented that the invasive plant species cogongrass was associated with
404 greater tick survival time, which could maintain tick abundances even though invaded areas may
405 have less activity by the common host white-tailed deer. Consistent with our hypothesis about
406 differences in microclimate due to invasion, there was greatly prolonged tick survival in invaded
407 areas, which had lower vapor pressure deficit corresponding to both lower temperatures and
408 higher humidity. We had also hypothesized that invaded areas would have greater tick
409 abundance than native-dominated areas because of longer tick survival times and greater white-
410 tailed deer activity. Contrary to this hypothesis, we observed no overall difference in white-tailed

411 deer activity between native and invaded areas and detected no difference in average tick
412 abundance between the two areas during the time period of peak tick abundance (Davidson et al.
413 1994, Gleim et al. 2014). There was a weak positive relationship between tick abundance and
414 white-tailed deer activity, though only in native-dominated areas, and the pattern was driven by
415 one of the eight sites (Figure 4). Together, these results suggest the invasive plant is influencing
416 multiple, potentially counteracting, mechanistic pathways contributing to tick exposure risk.
417 Our results show that tick abundances in *Imperata*-invaded plant communities may be
418 maintained even with relatively low white-tailed deer activity due to more favorable
419 microclimate conditions that prolong off-host tick survival. Exploration of the relationship
420 between tick mortality and VPD revealed that survival of nymphal ticks in both vegetation types
421 and adult ticks in native vegetation declined with increasing VPD. Conversely, adult tick
422 survival in invaded habitats was prolonged by increasing VPD. We posit that this
423 counterintuitive result stems from the physiological buffering provided by *Imperata*, where
424 invaded sites rarely exhibited conditions that have been shown to produce rapid mortality for
425 other tick species in laboratory conditions (i.e., VPD > 2 kPa) (Herrmann and Gern 2010).
426 Instead, adult ticks in invaded habitats lived long enough that they eventually died as a result of
427 loss of metabolic reserves (Alasmari and Wall 2021) or other stressors that were not measured.
428 More generally, invasive plant buffering of microclimate conditions that would otherwise be
429 stressful for ticks suggests that invasions may facilitate tick survival under the hotter and drier
430 conditions expected with climate change (McDowell et al. 2022).
431 Deer are widely considered a key contributing factor to abundances of several North
432 American tick species but the shape of this relationship is often difficult to detect (Kugeler et al.
433 2016, Hofmeester et al. 2017). Other studies have emphasized the complexity of this

434 relationship, detecting either a weak positive relationship (Ostfeld et al. 2018) or no association
435 between deer abundance and tick abundance (Hofmeester et al. 2017). We essentially found the
436 same pattern: in our analysis of data from all eight field sites, we detected a weak positive
437 relationship between deer and tick abundance in native plant communities but no relationship
438 when an influential site was removed (Figure 4). In contrast to previous studies (Williams et al.
439 2009, Allan et al. 2010a), we did not find a relationship between tick abundance and deer activity
440 in invaded plant communities; however, both of those studies evaluated non-native invasive
441 shrubs, which may promote deer activity by providing forage or cover. Although other species
442 are known to use *Imperata* invaded areas for refuge, e.g., wild turkey (*Meleagris gallopavo,*
443 Cabrera et al. 2021) and cotton rats (*Sigmodon hispidus*, Borden et al. 2022), we found no
444 difference in abundance of white-tailed deer based on camera trap detections in *Imperata*
445 invasions compared to native plant communities.

446 Climate change is predicted to facilitate the spread of *Imperata,* expanding its range from
447 southeastern Gulf States to as far north as Virginia along the eastern USA seaboard (Bradley et
448 al. 2010). As *Imperata* spreads northward, it is likely to interact with other tick species, including
449 the blacklegged tick *Ixodes scapularis,* the primary vector for Lyme disease in the United States,
450 which could increase tick-borne disease risk (Steere et al. 2004). The geographic distribution of
451 the black-legged tick is also expanding, with an increase in the number of USA counties
452 reporting its presence from 1996-2005 (Eisen et al. 2016) facilitated by ongoing landscape
453 change (Gardner et al. 2020). The blacklegged tick has similar physiological thresholds to *A.*
454 *americanum* (Berger et al. 2014), suggesting it too may benefit from the low vapor pressure
455 deficit generated by *Imperata* invasions.

456 This study uniquely demonstrated how differences in abiotic conditions in invaded areas
457 can be associated with differences in tick abundance and thus disease exposure risk. Despite the
458 duration and precision of the survival assay and the scale of the field study, there were
459 limitations. For example, although we documented much longer tick survival in invaded areas,
460 and evidence for microclimate conditions driving that pattern, additional studies replicated across
461 a larger environmental gradient of invasion would be useful for validating this result. In addition,
462 including sites that vary in invader density or biomass could inform management of highly
463 invaded areas to reduce tick-borne exposure risk. While we found evidence for microclimate
464 driven survival, we found less support for increases in host habitat use within invaded plant
465 communities. We focused on white-tailed deer activity, in part because of invader height and
466 difficulty camera trapping rodents or other hosts with our methods; however, quantifying other
467 hosts (small- and medium-sized mammals, birds, etc.) in invaded areas that are known to
468 influence tick-borne disease risk could resolve the relative influence of host abundance and
469 microclimate-driven survival on tick abundance (Greiner et al. 1984, Clark 2004, Ostfeld et al.
470 2018). Additionally, since CO_2 traps only capture host-seeking ticks, actual tick abundance could
471 be greater in invaded areas if *Imperata* improves microclimate to the point where ticks might be
472 more selective about when they expend energy to pursue a host.
473 The dense herbaceous structure of *Imperata* invasions differ drastically from that of the
474 woody and grassy invaders that have been studied previously, making comparisons across
475 species and systems difficult. For example, studies evaluating the effects of woody invasive
476 plants on tick abundance (*Lonicera maackii*, *Berberis thunbergia, Rosa multiflora*) in the
477 Midwest or Northeast US (Williams et al. 2009, Allan et al. 2010a, Adalsteinsson et al. 2016)
478 have found that woody invasive plants alter tick abundance predominately by providing host

habitat rather than creating more favorable microclimates for tick survival (but see Williams and Ward 2010). By contrast, tick survival assays conducted using the invasive grass *Microstegium vimineum* found that the invader created less favorable microclimate conditions and reduced survival time for off-host ticks (Civitello et al. 2008). Impacts of plant invasions on tick abundance will likely differ by location and species studied, thus there is a need to address how invasive plants impact tick abundance through changes to host activity as well as how tick survival is altered by invader-driven changes in microclimate.

Consistent with Wei et al. (2020), our findings suggest that invaded plant communities play an important, but relatively underappreciated, indirect role in altering human vector-borne disease risk. Specifically, we provide evidence for how tick exposure risk may be driven by different mechanistic pathways in invaded and native plant communities. Invasive plant species have a wide variety of traits that could differentially affect off-host tick survival and host activity. While measurement 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.

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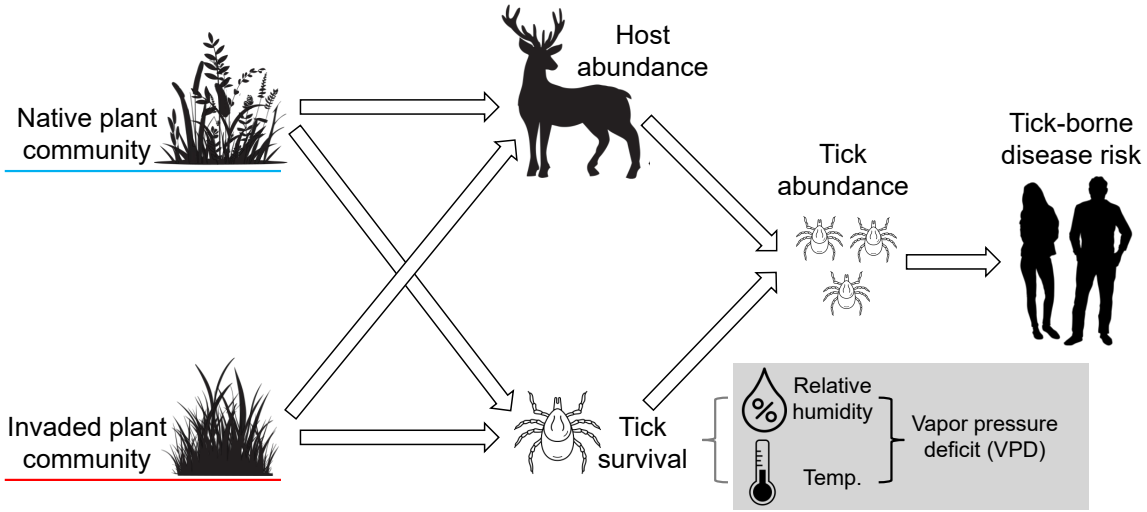
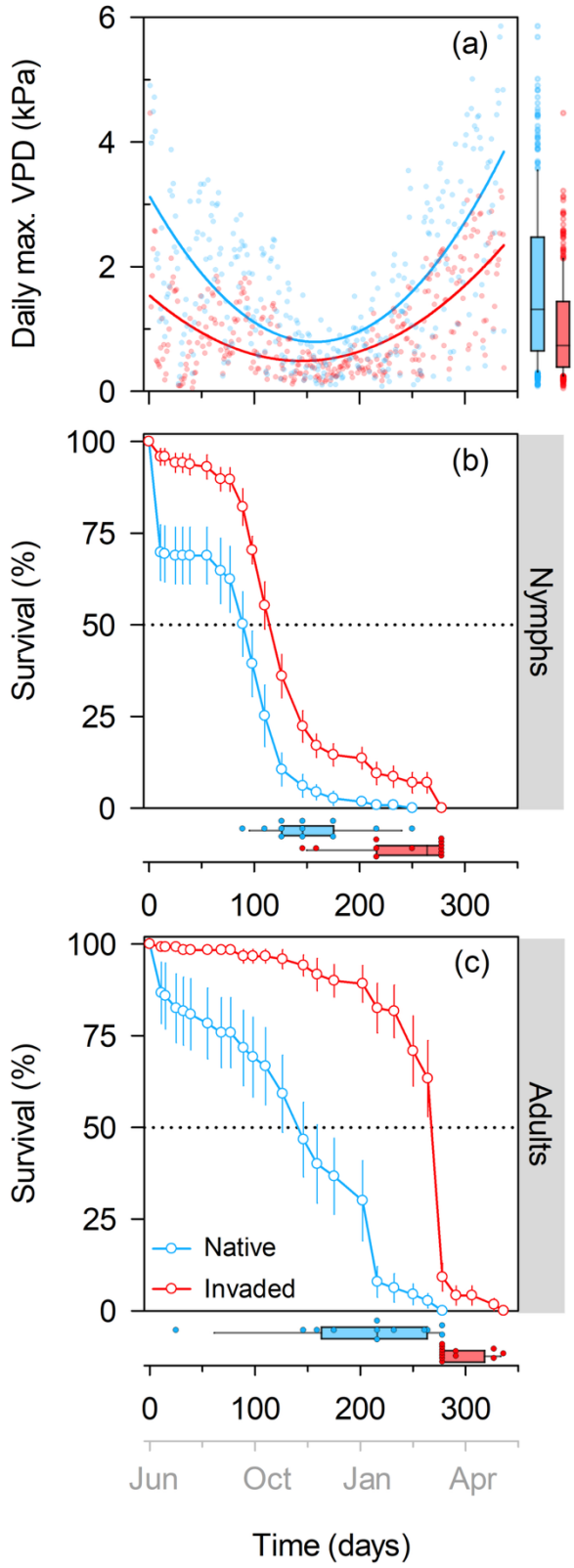


Figure 1. Conceptual diagram of two pathways that contribute to tick-borne disease risk. Native and invaded plant communities may have different effects on both host (e.g., deer, rodent) abundances and tick survival, which together determine tick abundance and, in turn, influence human tick exposure and tick-borne disease risk. Differences between invaded and native areas in microhabitat variables such as relative humidity and temperature, which determine vapor pressure deficit (VPD), can affect off-host tick survival. Vector graphics are copyright-free images obtained from stock.adobe.com via the University of Florida's enterprise license.


(a)
Daily max. VPD (kPa)
6
4
2
0
(b)
Survival (%)
100
75
50
25
0
Nymphs
0
100
200
300
(c)
Survival (%)
100
75
50
25
0
Adults
Native
Invaded
0
100
200
300
Jun
Oct
Jan
Apr
Time (days)

743

744 **Figure 2.** Microclimate conditions and tick survival per plot in native and invaded areas.
745 Average daily maximum vapor pressure deficit (VPD, kPa) (a), points are the average of
746 maximum daily VPD across all plots in each plant community type (n = 12). Solid lines in panel
747 (a) indicate best fit quadratic polynomials for native (blue) and invaded (red) areas. Box plots to
748 the right of panel (a) indicate the median and 25th and 75th percentile, with 10th and 90th
749 percentile whiskers for daily maximum VPD (kPa). Percent survival (mean ± SE) of (b) nymph
750 and (c) adult *Amblyomma americanum* in native (blue) and invaded (red) plots over time; the
751 second x-axis shows the month of the year. Box plots below panels (b) and (c) are distributions
752 of time to 100% mortality across the 12 plots showing the median and 25th and 75th percentile,
753 with 10th and 90th percentile whiskers.
754

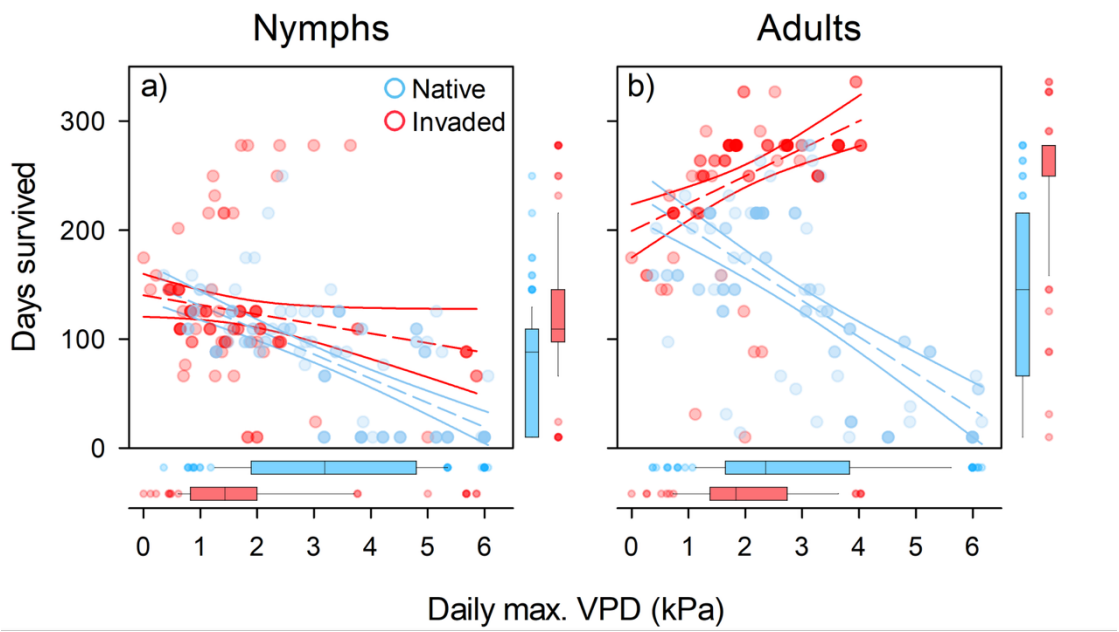
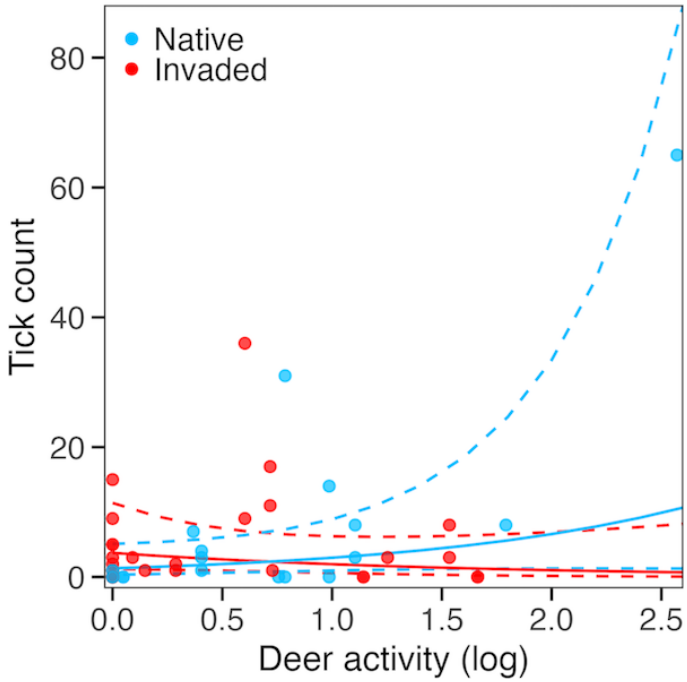


Figure 3. Number of days survived for individual nymph (a) and adult (b) life stage ticks and the daily maximum VPD experienced in native (blue) and invaded (red) plots between survival checks (the time interval when the tick was last seen alive and when it was recorded dead). Best fit lines (dashed) with 95% confidence interval (solid) 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 daily maximum VPD experienced by individual ticks prior to mortality in each treatment (x-axes).



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765

766 **Figure 4.** Relationship between deer activity (deer photos/day) and tick abundance (nymph and

767 adult ticks per plot) in native (blue) and invaded (red) plant communities. Best fit lines (solid)

768 from linear mixed effect models with 95% confidence interval (dashed).