Impacts of plant invasions on tick-borne disease risk

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Abstract

Under global change, plant invasions may alter tick-borne disease (TBD) exposure risk. The direction and magnitude of changes in TBD risk resulting from invasions remain poorly understood because research has often been species-specific or insufficient to quantify mechanisms. In this overview, we describe how invasive plant functional traits can mediate microclimates, how tick survival and abundance vary under altered environmental conditions created by invasive plants, and how invasive plants can impact blood meal host activity and pathogen prevalence. These findings are synthesized within a One Health framework that considers climate, landscape, and disturbance to ultimately predict TBD risk. We then discuss modeling approaches for predicting TBD risk amidst global change, and identify research gaps and future directions, including quantification of invader functional traits, assessment of plant invasion effects on TBD risk, and the potential for plant invasions to facilitate geographic expansions of ticks, hosts, and pathogens.

Introductions of species to non-native ranges have resulted in widespread biological invasions, which are a key driver of global environmental change (Paini et al. 2016, Trumbore et al. 2015). Accumulating evidence demonstrates that invasive species (*sensu* Richardson et al. 2000) can have direct effects on ecological communities by altering, for example, biodiversity, nutrient cycling, and disturbance regimes (Pyšek et al. 2012). However, invaders can also elicit indirect effects that may rival their direct effects, such as through impacts on habitat structure and microclimates (Alba et al. 2017). An increasingly explored but still understudied indirect effect of plant invaders is their impact on pathogen transmission (Goss et al. 2020), including vector-borne pathogens transmitted by ticks and other arthropods to humans. This issue is of critical importance given that the incidence of tick-borne diseases (TBDs) is increasing globally (Rochlin and Toledo 2020), particularly in the northern hemisphere, due to expanding distributions of tick species and their associated pathogens (Sonenshine 2018). In the U.S., from 2019-2022, 184,459 cases of TBDs were reported to the Centers for Disease Control and Prevention (CDC, 2024). Even these high and increasing numbers are known to be underreported due to COVID-19 impacts to all disease surveillance records, under-recognition of TBDs, and point-of-care reporting pipeline complexity for under-resourced health areas (Sambado and Ryan 2024). This increasing problem may be further exacerbated by introductions of novel disease vectors. For example, the newly introduced Asian longhorned tick (*Haemaphysalis longicornis*) is invading rapidly in the eastern U.S., can use multiple native small and medium sized mammalian host species for blood meals (Ferreira et al. 2023), and threatens human and animal health (Schappach et al. 2020, Yabsley and Thompson 2023).

Invasive plants may alter TBD exposure risk by altering habitat structure and microclimate (Civitello et al. 2008). Change in TBD exposure risk is defined here as any difference in probability of encountering an infected tick due to altered tick density or pathogen infection prevalence. Environmental tick abundance is influenced by tick survival and availability of tick blood meal hosts (e.g., deer, rodents, among many taxa – we refer to these blood meal hosts simply as ‘hosts’ from here forward) for completion of the tick life cycle (Ostfeld et al. 2006). Many of the ixodid tick species responsible for transmission of pathogens to humans feed on a different host individual in each of the three blood-feeding life-stages (i.e., hosts may vary considerably in their suitability as blood meal sources and in their capacity to transmit pathogens to feeding ticks), thus host species capable of transmitting pathogens serve as pathogen 'reservoirs' (Ostfeld et al. 2006). In between blood meals, ticks may drop off hosts to accomplish important physiological processes, including digesting blood meals, molting, egg laying in the case of gravid females, and in temperate climates, over-wintering (Needham and Teel 1991). Off-host ticks often make use of vegetation or leaf litter to provide protection against extremes in environmental conditions.

Microclimate, specifically temperature and humidity, is the primary determinant of off-host tick survival (Hiatt et al. 2024) and is directly influenced by climate. However, microclimate can be mediated by landscape characteristics (e.g., slope, aspect, elevation, tree cover) and disturbance (e.g., land use change, extreme weather) as well as local-scale composition and traits of vegetation (Diuk-Wasser et al. 2021, Mathisson et al. 2021). Host abundance and activity are, in turn, strongly affected by habitat structure, such as plant diversity and composition, and relative abundance of plant species. Habitat can vary based on plant species functional traits (i.e., measurable characteristics that can influence survival, growth, and reproduction), including quantitative traits such as stem density and categorical traits like growth form (e.g., grass, shrub, tree). Altogether, TBD risk is driven by complex interactions involving ticks, hosts, plants, and their environment (Morand and Lajaunie 2021, Ostfeld et al. 2018), all of which can be altered by plant invasions through shifts in microclimate and host habitat structure across environmental contexts (Fig. 1).

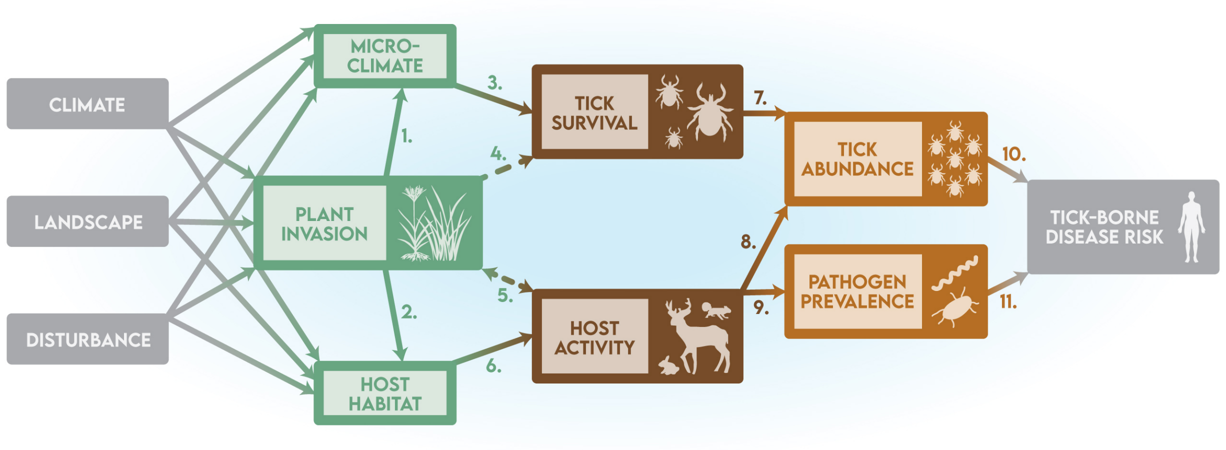

Figure 1. A One Health framework depicting the pathways by which plant invasions can be influenced by climate, landscape characteristics, and disturbance, which can then affect microclimate and host habitat, ticks and pathogens, and TBD risk. Plant invasions can influence microclimate and host habitat directly (solid lines), and each of these factors may directly or indirectly (dashed lines) change tick survival and host activity. Consequently, tick abundance can be altered by tick survival or host activity and pathogen prevalence can change through host activity. Ultimately, risk of exposure to TBDs for humans is determined by the abundance of ticks and pathogen prevalence. Each numbered arrow relates to a specific hypothesis explained in the text. The boxes indicating the effects of climate, landscape, and disturbance on plant invasions are gray because they have been reviewed extensively elsewhere. The need to better understand TBD exposure risk for humans is highlighted below in the section on research gaps and future directions.

Documented effects of plant invasions on microclimates, tick survival, and hosts

Invasive plants may affect disease risk by altering microclimates that affect off-host tick survival or by modifying habitat conditions that affect host abundance or activity (Box 1). Over 90% of an ixodid tick's life is spent off host, thus desiccation is one of the primary causes of tick mortality between blood meals (Needham and Teel 1991). To limit desiccation, ticks need microclimates that are above their critical equilibrium humidity (e.g., 80-82% relative humidity for adult lone star ticks, *Amblyomma americanum*, Hair et al. 1975, Knulle and Rudolph 1982); desiccation and mortality can also occur under temperatures greater than 35ºC (Sauer and Hair 1971). Field studies demonstrating higher tick abundances in areas invaded by Japanese barberry (*Berberis thunbergia*) and giant reed (*Arundo donax*) attribute greater tick abundances to favorable microclimates that reduce off-host tick desiccation, including lower temperatures or higher humidity (Racelis et al. 2012, Williams and Ward 2010). Yet, the few published tick survival experiments in invaded habitats show no effect on tick survival from Amur honeysuckle (*Lonicera maackii*, Allan et al. 2010a) or lower tick survival with stiltgrass (*Microstegium vimineum,* Civitello et al. 2008*)* in invaded compared to native areas. Conversely, a recent study demonstrated that invasive cogongrass (*Imperata cylindrica*) greatly enhanced plant cover, reduced temperature, and increased humidity, which reduced vapor pressure deficit (VPD) and was associated with greater longevity of lone star ticks (Fig. 2, Hiatt et al. 2024).

Studies on tick wildlife hosts, which can include deer, small mammals, birds, mesocarnivores, and other animals (Halsey et al. 2018), have shown that invasive shrubs, including Japanese barberry and Amur honeysuckle, increased habitat use by white-footed mice (*Peromyscus leucopus*) and/or white-tailed deer (*Odocoileus virginianus*), leading to greater abundances of ticks (Elias et al. 2006) and pathogen-infected ticks (Allan et al. 2010a). When management strategies included removal of invasive shrubs, disease risk was reduced to levels comparable to areas with only native vegetation (Allan et al. 2010a). While pointing to potential directional impacts of plant invasions on the overall transmission chain for TBDs, most studies thus far have fallen short of identifying the precise mechanism underlying impacts of plant invaders on tick survival and host habitat use, such as the role of plant functional traits in driving microclimate differences (see Box 1 for expanded explanations and evidence). Building on the evidentiary to evaluate generalizability of the effects of plant invasions on TBD exposure risk is an important next step.

Box 1: Documented mechanisms by which plant invasions have directly or indirectly impacted ticks and tick-borne pathogens (all images from Creative Commons).

Mechanism 1: Changes in Tick Survival

Plant invasions increase tick survival

Williams et al. (2009) found more blacklegged (*Ixodes scapularis*) larval ticks on white-footed mice (*Peromyscus leucopus*) and adult ticks questing in Japanese barberry (*Berberis thunbergii*), and Williams & Ward (2010) showed that Japanese barberry plots had more infected blacklegged ticks than when Japanese barberry was managed or absent. Intact Japanese barberry plots had higher humidity and lower vapor pressure deficit, potentially increasing tick survival. Linske et al. (2018) found more blacklegged ticks per mouse in full Japanese barberry stands compared to no barberry and controlled barberry stands but no difference in mouse abundance, suggesting Japanese barberry increases opportunities for questing ticks to find a host. Racelis et al. (2012) found that cattle tick (*Rhipicephalus microplus*) survival increased in giant reed (*Arundo donax*) invasions due to lower temperatures than buffelgrass (*Pennisetum ciliare*) invaded pastures and closed canopy forests. Hiatt et al. (2024) showed that lone star tick (*Amblyomma americanum*) survival increased under cogongrass (*Imperata cylindrica*) invasion due to lower vapor pressure deficit (VPD, i.e., the result of higher humidity and lower temperatures).

Plant invasions decrease tick survival

Civitello et al. (2008) showed that lone star tick and American dog tick (*Dermacentor variabilis*) survival decreased with stiltgrass (*Microstegium vimineum*) invasion due to lower humidity and higher temperature. Malo et al. (2013) found lower castor bean tick (*Ixodes ricinus*) abundance in common rhododendron (*Rhododendron ponticum*) invasions despite higher wood mouse (*Apodemus sylvaticus*) abundance, possibly due to effects of polyphenols and cyanidin in leaf litter on tick survival. Adalsteinsson et al. (2016) identified lower blacklegged tick abundance in forest fragments invaded by multiflora rose (*Rosa multiflora*) due to reduced leaf litter which decreased tick survival.

Plant invasions have no effect on tick survival

Allan et al. (2010a) found no difference in nymph or adult lone star tick survival where Amur honeysuckle (*Lonicera maackii*) was intact versus eradicated.

Berberis thunbergii

Arundo donax

Imperata cylindrica

Microstegium vimineum

Rhododendron ponticum

Mechanism 2: Changes in Host Activity/Abundance

Plant invasions increase host activity/abundance

Elias et al. (2006) found blacklegged tick abundance was positively associated with white-tailed deer (*Odocoileus virginianus*) and white-footed mouse activity in habitats invaded by understory shrubs. Allan et al. (2010a) showed a positive correlation between white-tailed deer activity and abundance of *Ehrlichia*-infected lone star ticks in Amur honeysuckle invasion. Wei et al. (2020) found that tick infestations on rodents were higher in *Leucaena leucocephala* invaded habitats compared to agricultural or residential habitats. Mandli et al. (2021) found that tick tubes treated with permethrin paired with removal of invasive Amur honeysuckle and buckthorn (*Rhamnus* spp.) decreased infestation of blacklegged ticks on white-footed mice. Noden et al. (2021) found more *Ehrlichia*- and *Rickettsia*-infected lone star ticks in eastern redcedar (*Juniperus virginiana*) invaded plots, providing indirect evidence of an increase in reservoir host activity in invaded areas. D'Antonio et al. (2023) found more blacklegged ticks and white-footed mice in Japanese barberry-invaded plots, which provide protection from predators and greater opportunities for questing ticks.

Plant invasions decrease host activity/abundance

Parker et al. (2017) found that as non-native shrubs increased, infestation of multiple tick species on migratory birds decreased, likely because invasive plant fruit attractive to avian hosts were located above the height where questing ticks are expected to be active.

Plant invasions have no effect on host activity/abundance

Busala et al. (2024) found no difference in relative abundance of white-footed mice between forest patches invaded versus uninvaded by non-native shrubs, although mice were larger in patches with more invasive shrubs. Hiatt et al. (2024) found no relationship between cogongrass invasion and white-tailed deer activity on lone star tick abundance.

Mechanism 3: Cascading Indirect Effects

Swei et al. (2011) found a positive correlation between western blacklegged (*Ixodes pacificus*) nymph densities and sudden oak death (caused by invasive fungus *Phytophthora ramorum*), possibly due to vertebrate host increase following oak death. Vaicekonyte & Keesing (2012) showed that garlic mustard (*Alliaria petiolata*) removal promoted entomopathogenic soil fungi, potentially lowering blacklegged tick survival.


Rosa multiflora


Leucaena leucocephala


Lonicera maackii


Rhamnus cathartica


Alliaria petiolata

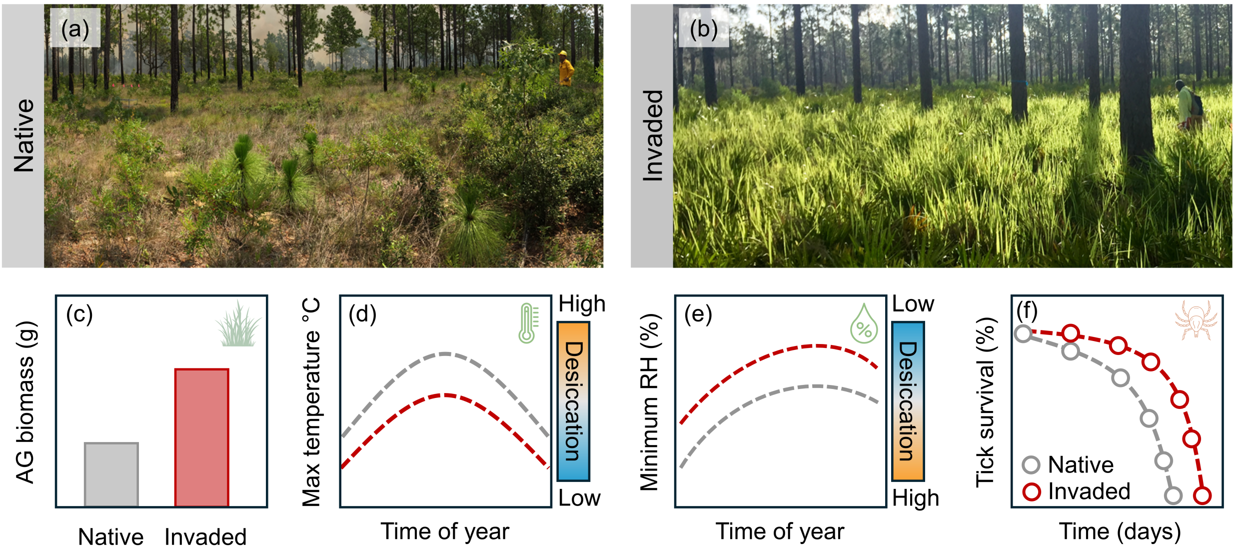

Figure 2. Differences in native and invasive plant functional traits can reduce tick desiccation and increase tick survival. Landscape photos showing a native longleaf pine savanna with a diverse native understory (a), and the same ecosystem invaded by cogongrass (*Imperata cylindrica,* b). Invaded plant communities had significantly greater aboveground (AG) biomass per area (c), lower daily max temperature °C (d), and higher daily minimum relative humidity (%, e), than native plant communities. Tick survival was prolonged in invaded areas over time (f), likely because of reduced desiccation in invaded areas. Panels c-f depict the general patterns documented in Hiatt et al. 2024. Photos by Drew Hiatt. Vector graphics in panels c-f are copyright-free images obtained from stock.adobe.com via the University of Florida's enterprise license.

Framework to integrate plant invasion effects on TBD risk

It is evident that non-native plant invasions can affect tick survival and host habitat, with potential to facilitate or inhibit infectious disease risk for humans (Allan et al. 2010a, Mack and Smith 2011, Stewart et al. 2021). However, the extent of current knowledge on plant invasions and TBD risk is limited and seemingly inconsistent, in part because studies are typically focused on one or a few invasive plant and tick species combinations and on individual mechanisms. The range of evidence on abiotic versus biotic mechanisms underlying invasive plant effects on TBDs may be explained by differences in invasive plant functional traits, landscape characteristics, seasonality, or climate. While there has been research on how different pathways may individually affect tick abundance or survival, studies that simultaneously address multiple pathways are lacking but urgently needed to improve TBD risk predictions and mitigation.

Here, we present an integrative One Health framework for predicting invasive plant impacts on TBD risk under an overarching hypothesis that invasions affect microclimate and host habitat, which, in turn, alter tick survival and encounters with wildlife hosts. As a result, these factors may change tick abundance or pathogen prevalence, ultimately determining human TBD exposure risk (Fig. 1). We expect that these interconnected drivers are subject to contextual factors including climate, landscape cover and configuration, and disturbance history, resulting in variations in TBD risk across landscapes, which may be further compounded by the dynamics of a changing climate. We do not explicitly address the role of these broader factors in altering TBD risk here, but we emphasize the need to understand how plant invasions may impact TBD risk across various landscape and environmental contexts.

Each numbered arrow in Figure 1 represents a unique hypothesis that may contribute to understanding interactions between invasive species and factors that affect TBD risk. We expound on these hypotheses by delineating important research needs that would enhance our understanding of the multifaceted interactions between invasion and TBD risk. We characterize how functional traits of invasive plants affect microclimates, describe evidence for tick survival and abundance under plant invasion altered microclimates, and review effects of invasive plants on blood meal host activity and pathogen prevalence. This framework spans local microclimates to regional scales, provides a roadmap to investigate how climate, landscape characteristics, invasive plants, and their interactions under global change influence TBD risk, and provides essential research directions for addressing this critical ecological and public health issue.

In proposing a One Health framework to investigate effects of plant invasions on TBD risk, we provide a roadmap for future research that encourages scientists to investigate interactions between different plant invasions and different ticks and pathogens under the unifying concept that plant functional traits are likely to dictate outcomes. This approach facilitates comparisons across systems to promote better understanding of specific mechanisms in future synthesis of this literature. It also enables outreach and communication about the effects of plant invasions on public health, allowing managers to more effectively message with the public about invasive plant management and TBD mitigation.

A. Impacts of invasive plant functional traits on microclimates

We hypothesize that invasive plants have measurable and unique effects on microclimates compared to native species, and that these effects can be predicted by invader functional traits (Fig. 1, arrow 1). Plant traits can influence microclimate by altering solar radiation absorption, transpiration and evaporation rates, quantity and structure of the litter layer, and air circulation, among other factors (Chapin III 2003, Ehrmann et al. 2017). Potentially important plant traits in this context include biomass, height, stem density, basal area, leaf mass per unit leaf area, and leaf mass ratio. Invasive species can exhibit novel traits compared to native species in a community (Mathakutha et al. 2019, Van Kleunen et al.

2010), and they can have more extreme values of common traits, such as exceptionally dense growth, higher biomass, taller stature, or greater leafiness, all of which might alter microclimate (Fig. 2,3, e.g., Alba et al. 2017). Non-native plants may exhibit extreme values of traits due to enemy release or other factors that contribute to their success in novel habitats. Moreover, invaders can have different growth forms, which is a categorical functional trait, compared to most native species in an ecosystem. For example, stiltgrass is a highly shade tolerant warm season annual grass that creates dense and widespread invasions in forest understories throughout the eastern U.S. (Flory and Clay 2010, Flory et al. 2015, Warren et al. 2011) where there are few native warm season annual grass species. Likewise, cogongrass is a perennial rhizomatous grass that invades pine forests in the southeastern U.S. where most native grass species are bunchgrasses that provide much less ground cover at lower biomass (Fig. 2, Hiatt and Flory 2020, Hiatt et al. 2024). Finally, community species composition, which can be altered by highly abundant, dense, and dominant invasive plant species can also significantly influence microclimate (Chapin III 2003). Altogether, the functional traits of plant invaders may exert a unique influence on microclimate conditions compared to native plant species.

A limitation of current research on plant invasion impacts on ticks lies in contrasting and non-generalizable inferences derived from individual invasive plant species. Functional traits may provide a common currency to quantify and predict effects of invasive plants (and co-occurring dominant native species) on microclimates. Certain functional traits could be quantified across native and invasive species per unit individual or per unit area depending on growth form. We hypothesize that functional traits of invaders such as relatively high stem density or high biomass, or more broadly, greater invasive plant cover in a community, will decrease the diurnal range of temperature and humidity (i.e., will buffer microclimate extremes) relative to habitats without the invader but with dominant native species. Greater invasive plant cover and specific functional traits may also reduce days with extreme microclimate conditions (i.e., very hot or cold) within a season compared to native plant dominated habitats (Fig. 2). Conversely, if an invader has a unique growth form with an open canopy and replaces a more densely growing native species, microclimate temperature or humidity extremes may increase, both within daily contexts and at a seasonal timescale.

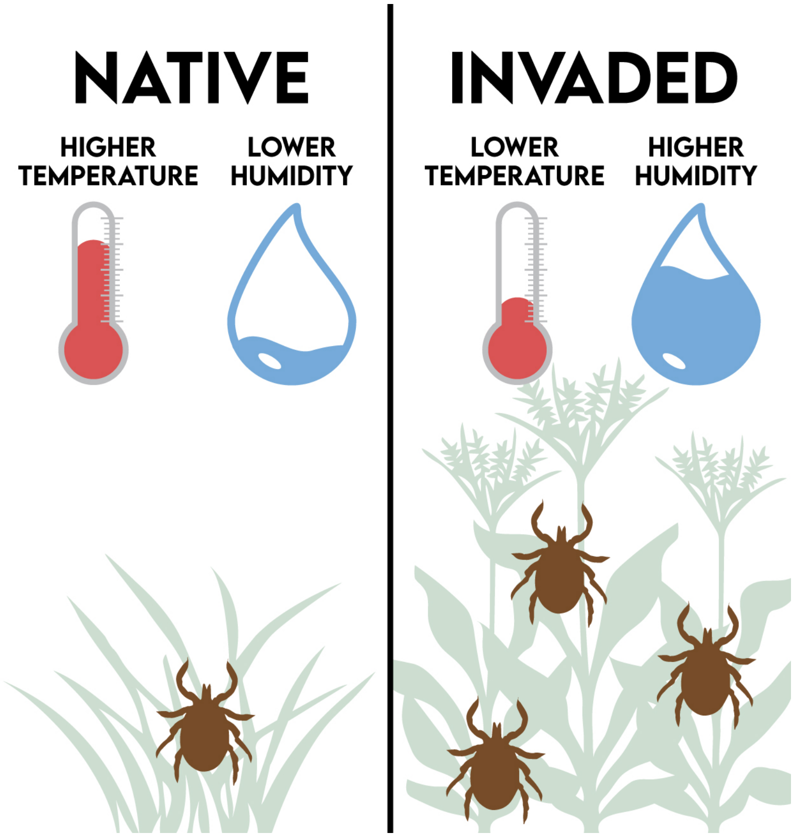

Figure 3. Invasive plants can alter microclimate conditions and enhance tick abundance. Here, the shorter statured native grass species is being replaced by a tall, densely growing invasive forb species. As a result, the invaded area has a lower temperature and higher humidity than the native plant dominated area, potentially leading to higher off-host tick survival.

B. Tick survival and abundance under altered microclimates

Previous research on a limited number of tick species under specific conditions has shown that temperature and humidity can significantly influence off-host tick survival (Bertrand and Wilson 1996, Stafford III 1994). High temperature and low relative humidity are stressors that disrupt water balance regulation and prompt changes in physiological, behavioral and developmental responses in individual ticks, which may translate to population level responses (Duffy and Campbell 1994). Characterizing this response is important given tradeoffs between behaviors enabling tick longevity (e.g., burrowing in leaf litter) versus energetically costly host-seeking (e.g., "questing") behaviors (Nielebeck et al. 2023). Questing, when ticks climb vegetation and seek to attach to passing hosts, prompts water loss and physiological stress (Needham and Teel 1991). Thus, one hypothesis is that invaders that generate microclimates with high humidity and low temperature promote optimal hydration status for ticks between questing bouts and enhance survival (e.g., see Fig. 2). Climate conditions outside optimal temperature and humidity ranges could limit costly behaviors such as questing for blood meals and might compromise survival as conditions become more extreme.

We hypothesize that plant invasions indirectly impact tick survival (Fig. 1, arrow 4) through alteration of microclimate conditions (Fig. 1, arrows 1,3). Specifically, we expect that 1) tick longevity will be greater when unfavorable microclimate conditions (e.g., high temperature, low humidity) are buffered (Van Gestel et al. 2022) by densely growing, high biomass, or otherwise functionally unique invasive plant species compared to native plant species that would otherwise occur at the site, and 2) effects of invasive plants on microclimate and tick survival will be mediated by the larger environmental context, including macroclimate, landscape characteristics (e.g., elevation, canopy coverage), and disturbance patterns (Fig. 1). While microclimate likely has a positive impact on survival and host-seeking activities, it could also impose negative impacts, or even different impacts on different parts of the tick life cycle (e.g., higher larval survival but lower nymph survival depending on how phenology of plant species correspond to phenology of tick species, Civitello et al. 2008). Finally, changes in tick survival may not always translate to differences in tick abundance (Fig. 1, arrow 7) depending on other biotic factors such as blood meal host availability.

C. Invasive plant effects on host habitat and activity

Ticks can feed on a range of animals, across multiple taxa, both wild and domestic (including humans). These blood meals maintain tick survival and additionally serve as pathogen transmission routes, where the tick may become infected by feeding on an infected host and subsequently pass the pathogen to a new host (De la Fuente et al. 2017). The vector competence of ticks for the wide array of pathogens they are associated with is outside the scope of this piece, but is an important component of the transmission pathway, and thus of 'risk' for human disease. There is even some evidence for infection status of ticks changing their questing behavior (Richardson et al. 2022) which, if mediated by altered habitat in the presence of invasive plants, would have onward implications for TBD exposure risk.

Invasive plants can indirectly alter host activity (Fig. 1, arrow 5) through changes in habitat suitability and food availability (Fig. 1, arrows 2, 6). Changes in conditions that influence host habitat preference and patch-use may lead to changes in availability and density of blood meal hosts required for the life cycle of the tick, consequently impacting tick reproductive success and tick population dynamics, density, or abundance (Fig. 1, arrow 8, Fig. 4). Hosts may utilize invaded habitats for protection from predators (Borden et al. 2022, Orrock et al. 2010), because of better environmental conditions (Cheeseman et al. 2019), or they may use them as food sources in their foraging landscape (Cheeseman et al. 2018). All three hypothesized mechanisms for host use of invaded areas can promote host activity and potentially tick abundance. For example, blacklegged tick abundance was positively correlated with white-tailed deer and white-footed mouse abundances in dense Japanese barberry invasions, which the authors attributed to the physical protection provided by Japanese barberry (D'Antonio et al. 2023). However, in another recent study, lone star tick abundance was not correlated with host activity in cogongrass invasion, while there was a positive relationship between host activity and tick abundance in native areas (Hiatt et al. 2024). Additionally, higher tick burdens have been documented on wildlife hosts in invaded habitats, suggesting invasive plants may concentrate ticks and hosts into shared habitats and increase the probability of a tick encountering and feeding upon a reservoir host species even when there is no change in host abundance (e.g., Linske et al. 2018). These differences highlight the need to better understand the ecological mechanisms by which blood meal hosts respond to plant invasions and the complexity of drivers of TBD risk.

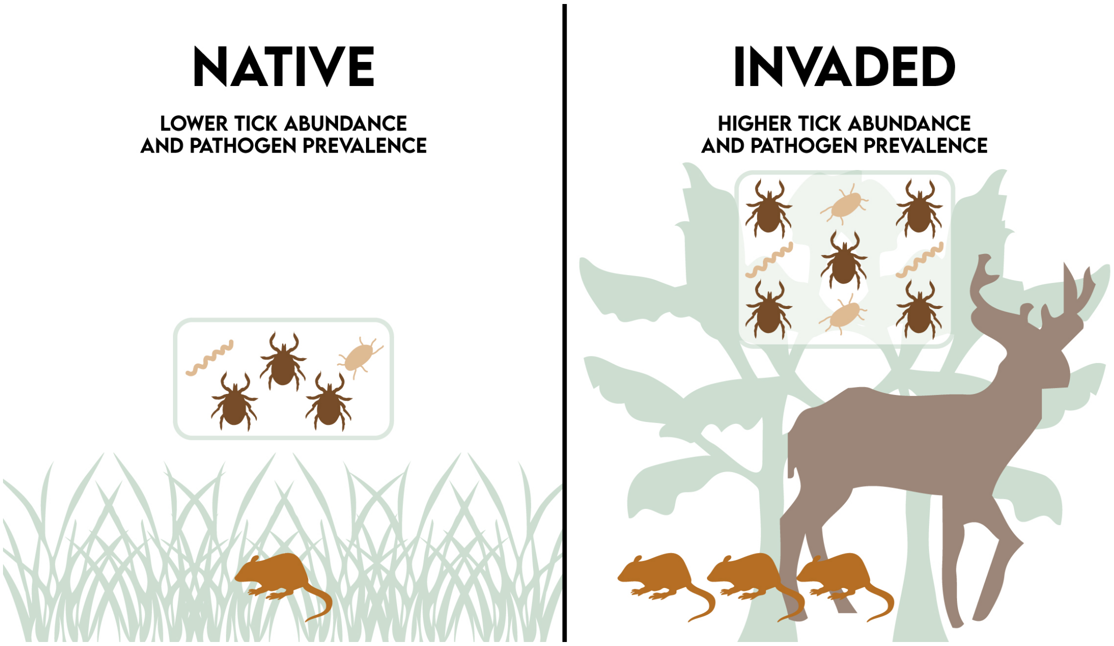

Figure 4. Invasive plants may provide better host habitat and increase tick abundance and pathogen prevalence. In this example, a shrub invasion improves host habitat by providing better cover or forage, thereby increasing reservoir host abundance. As a result, there is greater tick abundance and higher pathogen prevalence compared to the native plant dominated area.

D. Plant invasion impacts on pathogen prevalence

Greater host activity (habitat utilization) can impact pathogen prevalence in ticks, and among hosts (Figure 1, arrow 9), in a process of amplification, depending on the reservoir competence of host species for the transmission of pathogens. As a result, some studies have demonstrated a positive relationship between abundance of pathogen-infected ticks and the presence of invasive plant species. For example, Amur honeysuckle invaded plots had a higher prevalence of the *Ehrlichia chaffeensis* – infected lone star nymphs (Allan et al. 2010a) due to greater activity by white-tailed deer, an important host for lone star ticks and a pathogen reservoir for *E. chaffeensis*, one of the causal bacterial pathogens of ehrlichiosis in humans (Allan et al. 2010b). Similarly, there was a higher prevalence of blacklegged nymphs infected with the Lyme disease causing *Borrelia burgdorferi* in multiflora rose (*Rosa multiflora*) invaded plots, which was attributed to more favorable understory structure for white-footed mice, a highly competent reservoir for this pathogen (Adalsteinsson et al. 2018). Overall, relatively few studies have connected plant invasions to the prevalence of tick-borne pathogens, and to our knowledge, none have extended the full chain of interaction to human infections (Fig. 1, arrows 10, 11), which is the ultimate outcome of a far greater chain of events in this One Health system (Sambado and Ryan 2024).

Integrating (micro) climate into models of TBDs: caveats abound

Few fully parameterized mechanistic models exist that directly link empirical microclimate data and potentially mitigating effects of vegetation cover to tick survival, likely owing to the time and resource-intensive nature of data collection required to inform such models (Boehnke et al. 2017). A few studies have explored relationships across scales, for example, between local habitats and broad scale climatologies to compare functional impact of habitat features on seasonality (Estrada-Peña et al. 2004, MacDonald et al. 2020, Ogden et al. 2008, Randolph et al. 2002). To understand how microclimate, mediated by plant invasions, is described by larger scale climate measurements, models must accommodate inputs from multiple spatial scales. Adopting a variety of modeling approaches with appropriately scaled data inputs will allow for exploration of trade-offs between modeling with large scale climate layers, versus localized climate and microclimate measures to capture sub-annual seasonal impacts on tick survival hypothesized to be influenced by invasive plants.

The scale of a question, whether explicitly spatial (a delineated area, a pixel size) or described as a scale of ecological function (e.g., the microclimate under one plant, Fig. 1, arrow 1 to inform arrow 3, or the range of an entire species, Fig. 1 arrow 2 to inform arrows 5,6) will necessarily be constrained by data collection logistics and availability of corresponding covariate measurements at appropriate scale and frequency. More specifically, when we incorporate measured climate and environmental drivers using sensors of many kinds into models, we are often also limited by the scale and frequency of that data acquisition. From temperature/humidity loggers to Earth Observation System (EOS) imagery, or gridded data such as regional to global scale interpolated surfaces or projected climate models, it is important to keep in mind which environmental data products are appropriate and how data must be prepared, aggregated, and modeled.

Microscale data have the advantage of capturing very fine scale relationships. For example, the immediate questing habitat of an off-host tick is sensitive to the microclimate and is likely involved in human TBD pathogen transmission. Larger scales may thus either aggregate microscale measured impacts or may instead reflect different types of data measurements. For example, we may incorporate multiple temperature and humidity logger outputs to capture the variability of microscale climatologies across a larger landscape, perhaps comparing invaded and uninvaded native plant dominated areas of a site.

The availability of coarser temporal scale (e.g., 16-day aggregates) or coarser spatial scale, but longer-term data (e.g., 1 km^2 over a decade) measurements from EOS data, and descriptors of landcover types or greenness indices to capture phenology (e.g., NDVI Pettorelli et al. 2011, Pettorelli et al. 2005), allows for rapid, large scale, observation data acquisition. This approach allows for exploring relationships with environmental drivers that can be replicated across multiple sites in a landscape but may be too coarse to capture the microscale variability relevant to the scale of the question addressed.

How microclimates scale to the macroscale is an active field of research (Lembrechts and Lenoir 2020) but still relies on the availability of microclimate data to create reliable and validated generalizable products (Lembrechts et al. 2021). Adequate data collection at the microscale to inform generalizable models at larger scales is resource-intensive and time consuming. Yet, it is generally at the macroscale that we can start to incorporate the impacts of broader scale patterns of global change such as human-environment modifications, including agricultural conversion, processes of urbanization such as an increase in impervious surfaces, and processes that increase tick encounters such as patterns of settlement (Combs et al. 2022, Gregory et al. 2022). For example, the U.S. urban-suburbanization and sprawl pattern, a proxy for disturbance history, has resulted in increased edge habitat, where plant invasions are promoted by availability of gaps in primary habitat and invasive species may comprise a significant proportion of primary and secondary successional species. At this macroscale, the configuration of environment types and descriptions of landscape fragmentation may become additionally important to understand landscape processes and TBD exposure (Diuk-Wasser et al. 2021, Kache et al. 2022, VanAcker et al. 2024).

At present, models describing how ticks and TBDs exist in the environment are mostly confined to specific locations, and models of ticks on those landscapes usually assume stationarity of vegetation composition and phenology (for reviews, see Lippi et al. 2021a, Lippi et al. 2021c). Modeling approaches applied to larger landscapes, such as ecological niche modeling (ENM) or species distribution modeling (SDM, e.g., Flenniken et al. 2022, Lippi et al. 2023b, Lippi et al. 2021b), retain similar assumptions. These models rest on the assumption that the environment, modeled as a function of input data layers, has shaped the presence of the species in that location.

An important question to address when modeling TBDs on landscapes is whether the environmental history of a location shaped the presence of the pathogen, the human encounter, the tick, or the tick's host. For some exploration of these concepts in the context of SDM/ENM models see Lippi et al. (2023a) and Lippi et al. (2021b). Recent work by Estrada-Pena and de la Fuente (2024) also found that across a suite of SDM/ENM model approaches, which they refer to as machine learning algorithms, the addition of land use and landcover variables greatly improved evaluations of risk of tick-borne pathogens in Europe, beyond climate-only driven models. While a full review of SDM/ENM models of TBDs is outside of scope of this overview, this issue presents a conundrum about the inclusion of dynamic plant invasions into current approaches. Peterson et al. (2005) presented a time-specific niche modeling approach to dengue cases and consistently captured mosquito surveillance data to create monthly landscape level models using a suite of stationary variables (e.g., slope, aspect, elevation) and one key EOS derived dynamic vegetation greenness product, the Normalized Difference Vegetation Index (NDVI). With sufficient fine-scale and high frequency data, a similar approach (using appropriate environmental variable measurements) could capture year-on-year impacts of invasions on the distribution of ticks or TBD cases. To our knowledge, this modeling approach has not yet been undertaken for TBDs or even tick or host distributions, separately.

Research gaps and future directions

As a result of invader effects on microclimate and host habitat, plant invasions have been shown to sometimes change tick survival and abundance, pathogen prevalence, or host activity. Thus, invasive plants may indirectly influence human health if they modify interactions among species in ways that ultimately alter pathogen transmission to humans. To date, transmission of TBDs has been described primarily as interactions of humans, animals, and pathogens in a landscape. However, the additional driving dynamics of how plant invasions mediate these interactions have received far less attention and yet may be critically important. Future research should include comparisons among multiple invasive plant and tick species to identify the underlying mechanisms of TBD risk under global change. We encourage the use of previous theory, existing data from field surveys, field and lab experiments, and EOS data; thereby leveraging existing infrastructure and extensive datasets to effectively address the issues presented here. We highlight four primary research priorities to better understand the impacts of plant invasions on TBD exposure risk.

1. Measure invasive plant functional traits related to microclimate impacts

Evidence synthesized from studies to date suggest non-native plant invasions may alter TBD exposure risk through both direct and indirect mechanistic pathways. The direction and magnitude of these effects so far appear variable. However, the potential role of plant functional traits, phenology, or form of subsidy provided to wildlife hosts (e.g., shelter, food), has not been captured fully to date in previous studies. Additionally, different tick species can be adapted to different habitats (Mathisson et al. 2021), such as grassland versus forest ecosystems, which may lead to differing interactions with invasions by non-native plant species. Focusing on invader functional traits may facilitate development of a generalizable and predictive approach that links traits to microclimate, host activity, and tick abundance, thus advancing understanding and predictions of how plant invasions may alter TBD risk (Fig. 1). Future studies should attempt to quantify not only the mechanisms by which plant invasions alter the risk of TBD but also report key differences in the role of functional traits of native and invasive plant species within study sites.

2. Identify specific mechanisms by which plant invasions affect tick-borne disease risk

Several of the studies reviewed here suggested that plant invaders affected tick survival, and a few field-based studies have been performed comparing tick survival in invaded and native plant dominated habitats. However, a variety of metrics are used across studies to measure changes in microclimate suitability, including mean, minimum or maximum of temperature, humidity, or vapor pressure deficit, hindering comparisons across studies. Furthermore, it remains unknown whether changes in tick survival are driven by long-term, gradual changes in abiotic conditions, or due to ticks being subjected to short-term extreme conditions that rapidly alter mortality rates. It also remains largely unknown whether changes in tick survival or other life history parameters meaningfully impact disease-causing pathogen transmission (Fig. 1, arrow 11), and even the fitness costs of infections in ticks. This part of the larger framework may be best addressed by incorporating differences in survival rates into mathematical models of tick population dynamics and infection. Similarly, several of the studies reviewed here indicated that plant invaders affected host activity or abundance, yet most studies do not test directly whether this is due to plant invasions causing changes in availability of food, refuge from predators, or environmental suitability for hosts. Understanding the specific mechanisms will aid in developing a general predictive framework for effects of plant invasion on tick-borne disease risk.

3. Assess plant invasion effects on reported tick-borne disease incidence

A high priority across many aspects of vector-borne disease ecology is to connect environmental change not only to risk of exposure to pathogen-infected vectors but also changes in human disease incidence (Keesing et al. 2022). For reportable diseases such as several of the TBDs in the U.S., including Lyme and ehrlichiosis, it may be possible to connect plant invasions to changes in human case rates using spatial distribution data. We can start to identify and quantify connections between plant invasions and human cases with sufficient spatially and temporally resolved geospatial data on human case reports, tick surveillance records (which are sparse, but improving, e.g., Foster et al. 2023), vegetation surveys, and remotely sensed classified imagery describing landcover change and known plant invasions. Human behavior is another understudied facet of how changes in exposure risk may influence disease incidence. Plant invasions may alter human behavior in the outdoors, for example, by causing people to avoid dense invasions of thorny plant species such as Japanese barberry. Conversely, when plant invasions are close to trails, humans may come in closer contact with these invasions. This phenomenon has received little research attention, although Elias et al. (2024) demonstrated that removal of Japanese barberry along hiking trails in Maine did not reduce the abundance of questing blacklegged ticks.

4. Explore the potential of plant invasions to facilitate geographic expansion of ticks and pathogens

Globally, numerous tick species and their associated pathogens are expanding in geographic distribution, imperiling human and animal health (Sonenshine 2018). Examples include the blacklegged tick and Lyme disease in the northeastern and midwestern U.S. (Eisen and Eisen 2023), the lone star tick and associated pathogens in the central and southern U.S. (Springer et al. 2014), and ongoing introductions of *Hyalomma* spp. ticks, which vector Crimean-Congo hemorrhagic fever virus, to Europe (Vial et al. 2016). Expanding distributions of ticks are frequently attributed to factors including climate change (Ostfeld and Brunner 2015), landscape change (Gardner et al. 2020), and novel introductions (Schappach et al. 2020). Moreover, hosts that disperse ticks may also disperse associated tick-borne pathogens through transporting infected ticks or by infectious hosts introducing pathogens to newly established tick populations (Tsao et al. 2021).

Due to the interactions between anthropogenic change and wildlife movements in contributing to expanding geographic ranges of ticks and tick-borne pathogens, this presents another challenge requiring the One Health lens. However, the role of non-native plant invasions in altering dispersal or habitat suitability for tick and pathogen invasions has received scant attention. We predict that when invaded habitats serve to attract dispersing wildlife, plant invasions may increase geographic dispersal of ticks and pathogens by enhancing wildlife host movements. Additionally, if invaded habitats offer more suitable microclimates for tick survival, plant invasions may increase tick establishment success during dispersal to new areas. Thus, considering the ongoing geographic range expansion of numerous tick and tick-borne pathogen species, along with ongoing range expansion of many invasive plant species (Clements and Ditommaso 2011), determining if and to what extent plant invasions alter dispersal and establishment probabilities is an urgent research priority.

Conclusions

Global change, including shifts in climate and land use and changing disturbance regimes, is contributing to plant invasion, with implications for both direct effects on native species and ecosystem functions, but also significant potential for enhanced or altered TBD exposure risk. The knock-on effects of plant invasions in landscapes on potential tick hosts, such as increasing or decreasing suitable habitat or potential tick host availability, may in turn be affected by management decisions aimed at preserving imperiled native hosts or restoring ecosystem functions. Moreover, these management efforts are occurring in landscapes with disturbance histories mediated by humans, which speaks to the larger interconnected One Health framework needed to investigate the interplay of multiple interacting drivers (Fig. 1). Whether humans living, working, or recreating in areas with greater prevalence of non-native plant invasions experience higher rates of infection by TBDs is an urgent research priority. The framework and research priorities outlined here should improve predictions of TBD exposure risk in invaded landscapes, such as through better quantification of invader functional traits linked to microclimate and habitat host use. Moreover, as many TBDs are expanding in geographic distribution, understanding the role plant invasions may play in affecting tick or pathogen dispersal or establishment in new areas can both illuminate a factor that is contributing to changes in distribution and offer a relatively tractable management approach. If controlling plant invasions limits tick and pathogen range expansion and reduces TBD risk, those who live, work, or recreate in natural areas may benefit from this win-win solution that addresses both pressing environmental challenges.

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References

Adalsteinsson SA, D'Amico V, Shriver WG, Brisson D, Buler JJ. 2016. Scale-dependent effects of nonnative plant invasion on host-seeking tick abundance. Ecosphere 7:e01317.

Adalsteinsson SA, Shriver WG, Hojgaard A, Bowman JL, Brisson D, D'Amico V, Buler JJ. 2018. Multiflora rose invasion amplifies prevalence of Lyme disease pathogen, but not necessarily Lyme disease risk. Parasites & vectors 11:1–10.

Alba C, NeSmith JE, Fahey C, Angelini C, Flory SL. 2017. Methods to test the interactive effects of drought and plant invasion on ecosystem structure and function using complementary common garden and field experiments. Ecology and evolution 7:1442–1452.

Allan BF, Dutra HP, Goessling LS, Barnett K, Chase JM, Marquis RJ, Pang G, Storch GA, Thach RE, Orrock JL. 2010a. Invasive honeysuckle eradication reduces tick-borne disease risk by altering host dynamics. Proceedings of the National Academy of Sciences 107:18523–18527.

Allan BF, Goessling LS, Storch GA, Thach RE. 2010b. Blood meal analysis to identify reservoir hosts for *Amblyomma americanum* ticks. Emerging Infectious Diseases 16:433.

Bertrand MR, Wilson ML. 1996. Microclimate-dependent survival of unfed adult *Ixodes scapularis* (Acari: Ixodidae) in nature: life cycle and study design implications. Journal of Medical Entomology 33:619–627.

Boehnke D, Gebhardt R, Petney T, Norra S. 2017. On the complexity of measuring forests microclimate and interpreting its relevance in habitat ecology: the example of *Ixodes ricinus* ticks. Parasites & vectors 10:1–14.

Borden JB, San Antonio KM, Tomat-Kelly G, Clark T, Flory SL. 2022. Invasive grass indirectly alters seasonal patterns in seed predation. Biology Letters 18:20220095.

Busala GM, Phillips PM, Behm JE. 2024. Variation in forest patch habitat quality for white-footed mice driven by invasive plants in an urbanizing landscape. Ecosphere 15:e70068.

CDC Office of Public Health Data S, and Technology. 2024. 2022 Annual Tables of Infectious Disease Data. (https://www.cdc.gov/nndss/data-statistics/infectious-tables/index.html).

Chapin III FS. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. Annals of Botany 91:455–463.

Cheeseman AE, Cohen JB, Ryan SJ, Whipps CM. 2019. Determinants of home-range size of imperiled New England cottontails (*Sylvilagus transitionalis*) and introduced eastern cottontails (*Sylvilagus floridanus*). Canadian Journal of Zoology 97:516–523.

Cheeseman AE, Ryan SJ, Whipps CM, Cohen JB. 2018. Competition alters seasonal resource selection and promotes use of invasive shrubs by an imperiled native cottontail. Ecology and evolution 8:11122–11133.

Civitello D, Flory S, Clay K. 2008. Exotic grass invasion reduces survival of *Amblyomma americanum* and *Dermacentor variabilis* ticks (Acari : Ixodidae). Journal of Medical Entomology 45:867–872.

Clements D, Ditommaso A. 2011. Climate change and weed adaptation: can evolution of invasive plants lead to greater range expansion than forecasted? Weed Research 51:227–240.

Combs MA, Kache PA, VanAcker MC, Gregory N, Plimpton LD, Tufts DM, Fernandez MP, Diuk-Wasser MA. 2022. Socio-ecological drivers of multiple zoonotic hazards in highly urbanized cities. Global Change Biology 28:1705–1724.

D'Antonio BE, Ehlert K, Pitt AL. 2023. The effects of varying degrees of Japanese barberry invasion on the abundance of blacklegged ticks and white-footed mice. Bios 94:12–19.

De la Fuente J, Antunes S, Bonnet S, Cabezas-Cruz A, Domingos AG, Estrada-Peña A, Johnson N, Kocan KM, Mansfield KL, Nijhof AM. 2017. Tick-pathogen interactions and vector competence: identification of molecular drivers for tick-borne diseases. Frontiers in cellular and infection microbiology 7:114.

Diuk-Wasser MA, VanAcker MC, Fernandez MP. 2021. Impact of land use changes and habitat fragmentation on the eco-epidemiology of tick-borne diseases. Journal of Medical Entomology 58:1546–1564.

Duffy DC, Campbell SR. 1994. Ambient air temperature as a predictor of activity of adult *Ixodes scapularis* (Acari: Ixodidae). Journal of Medical Entomology 31:178–180.

Ehrmann S, Liira J, Gärtner S, Hansen K, Brunet J, Cousins SA, Deconchat M, Decocq G, De Frenne P, De Smedt P. 2017. Environmental drivers of *Ixodes ricinus* abundance in forest fragments of rural European landscapes. BMC Ecology 17:1–14.

Eisen L, Eisen RJ. 2023. Changes in the geographic distribution of the blacklegged tick, *Ixodes scapularis*, in the United States. Ticks and tick-borne diseases 14:102233.

Elias SP, Lubelczyk CB, Rand PW, Lacombe EH, Holman MS, Smith Jr RP. 2006. Deer browse resistant exotic-invasive understory: an indicator of elevated human risk of exposure to *Ixodes scapularis* (Acari: Ixodidae) in southern coastal Maine woodlands. Journal of Medical Entomology 43:1142–1152.

Elias SP, Rand PW, Lubelczyk CB, McVety MR, Smith RP. 2024. Partial trailside Japanese barberry (Ranunculales: Berberidaceae) removal did not reduce the abundance of questing blacklegged ticks (Acari: Ixodidae). Environmental Entomology 53:417–424.

Estrada-Peña A, de la Fuente J. 2024. Machine learning algorithms for the evaluation of risk by tick-borne pathogens in Europe. Annals of Medicine 56:2405074.

Estrada-Peña A, Martinez J, Sanchez Acedo C, Quilez J, Del Cacho E. 2004. Phenology of the tick, *Ixodes ricinus*, in its southern distribution range (central Spain). Medical and Veterinary Entomology 18:387–397.

Ferreira FC, González J, Milholland MT, Tung GA, Fonseca DM. 2023. Ticks (Acari: Ixodida) on synanthropic small and medium-sized mammals in areas of the northeastern United States infested with the Asian longhorned tick, *Haemaphysalis longicornis*. International Journal for Parasitology 53:809–819.

Flenniken JM, Tuten HC, Rose Vineer H, Phillips VC, Stone CM, Allan BF. 2022. Environmental drivers of Gulf Coast tick (Acari: Ixodidae) range expansion in the United States. Journal of Medical Entomology 59:1625–1635.

Flory S, Clay K. 2010. Non-native grass invasion suppresses forest succession. Oecologia 164:1029–1038.

Flory S, Clay K, Emery S, Robb J, Winters B. 2015. Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. Journal of Applied Ecology 52:992–1000.

Foster E, Maes SA, Holcomb KM, Eisen RJ. 2023. Prevalence of five human pathogens in host-seeking *Ixodes scapularis* and *Ixodes pacificus* by region, state, and county in the contiguous United States generated through national tick surveillance. Ticks and tick-borne diseases 14:102250.

Gardner AM, Pawlikowski NC, Hamer SA, Hickling GJ, Miller JR, Schotthoefer AM, Tsao JI, Allan BF. 2020. Landscape features predict the current and forecast the future geographic spread of Lyme disease. Proceedings of the Royal Society B 287:20202278.

Goss EM, Kendig AE, Adhikari A, Lane B, Kortessis N, Holt RD, Clay K, Harmon PF, Flory SL. 2020. Disease in invasive plant populations. Annual Review of Phytopathology 58:97–117.

Gregory N, Fernandez MP, Diuk-Wasser M. 2022. Risk of tick-borne pathogen spillover into urban yards in New York City. Parasites & vectors 15:288.

Hair J, Sauer J, Durham K. 1975. Water balance and humidity preference in three species of ticks. Journal of Medical Entomology 12:37–47.

Halsey SJ, Allan BF, Miller JR. 2018. The role of *Ixodes scapularis*, *Borrelia burgdorferi* and wildlife hosts in Lyme disease prevalence: a quantitative review. Ticks and tick-borne diseases 9:1103–1114.

Hiatt D, Flory SL. 2020. Populations of a widespread invader and co-occurring native species vary in phenotypic plasticity. New Phytologist 225:584–594.

Hiatt D, Dillon WW, Gardner A, Cabrera S, Dietze M, Allan BF, Flory SL. 2024. Mechanistic pathways of tick exposure risk in native and invaded plant communities. bioRxiv:2024.2011. 2019.624319.

Kache PA, Bron GM, Zapata-Ramirez S, Tsao JI, Bartholomay LC, Paskewitz SM, Diuk-Wasser MA, del Pilar Fernandez M. 2022. Evaluating spatial and temporal patterns of tick encounters using community science data submitted through a smartphone application.

Keesing F, Mowry S, Bremer W, Duerr S, Evans Jr AS, Fischhoff IR, Hinckley AF, Hook SA, Keating F, Pendleton J. 2022. Effects of tick-control interventions on tick abundance, human encounters with ticks, and incidence of tickborne diseases in residential neighborhoods, New York, USA. Emerging Infectious Diseases 28:957.

Knulle W, Rudolph D. 1982. Humidity relationships and water balance of ticks. Pages 43–70. Physiology of Ticks, Elsevier.

Lembrechts JJ, Lenoir J. 2020. Microclimatic conditions anywhere at any time! Global Change Biology 26:337–339.

Lembrechts JJ, Lenoir J, R Scheffers B, De Frenne P. 2021. Designing countrywide and regional microclimate networks. Global Ecology and Biogeography 30:1168–1174.

Linske MA, Williams SC, Ward JS, Stafford III KC. 2018. Indirect effects of Japanese barberry infestations on white-footed mice exposure to *Borrelia burgdorferi*. Environmental Entomology 47:795–802.

Lippi CA, Canfield S, Espada C, Gaff HD, Ryan SJ. 2023a. Estimating the distribution of *Oryzomys palustris*, a potential key host in expanding rickettsial tick-borne disease risk. Ecosphere 14:e4445.

Lippi CA, Gaff HD, Nadolny RM, Ryan SJ. 2023b. Newer surveillance data extends our understanding of the niche of *Rickettsia montanensis* (Rickettsiales: Rickettsiaceae) infection of the American dog tick (Acari: Ixodidae) in the United States. Vector-Borne and Zoonotic Diseases 23:316–323.

Lippi CA, Gaff HD, White AL, Ryan SJ. 2021a. Scoping review of distribution models for selected *Amblyomma* ticks and rickettsial group pathogens. PeerJ 9:e10596.

Lippi CA, Gaff HD, White AL, St. John HK, Richards AL, Ryan SJ. 2021b. Exploring the niche of *Rickettsia montanensis* (Rickettsiales: Rickettsiaceae) infection of the American dog tick (Acari: Ixodidae), using multiple species distribution model approaches. Journal of Medical Entomology 58:1083–1092.

Lippi CA, Ryan SJ, White AL, Gaff HD, Carlson CJ. 2021c. Trends and opportunities in tick-borne disease geography. Journal of Medical Entomology 58:2021-2029.

MacDonald AJ, McComb S, O'Neill C, Padgett KA, Larsen AE. 2020. Projected climate and land use change alter western blacklegged tick phenology, seasonal host-seeking suitability and human encounter risk in California. Global Change Biology 26:5459–5474.

Mack R, Smith M. 2011. Invasive plants as catalysts for the spread of human parasites. NeoBiota 9:13.

Malo AF, Godsall B, Prebble C, Grange Z, McCandless S, Taylor A, Coulson T. 2013. Positive effects of an invasive shrub on aggregation and abundance of a native small rodent. Behavioral Ecology 24:759–767.

Mandli JT, Lee X, Bron GM, Paskewitz SM. 2021. Integrated tick management in south central wisconsin: Impact of invasive vegetation removal and host-targeted acaricides on the density of questing *Ixodes scapularis* (acari: Ixodidae) nymphs. Journal of Medical Entomology 58:2358–2367.

Mathakutha R, Steyn C, le Roux PC, Blom IJ, Chown SL, Daru BH, Ripley BS, Louw A, Greve M. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. Journal of Vegetation Science 30:994–1006.

Mathisson DC, Kross SM, Palmer MI, Diuk-Wasser MA. 2021. Effect of vegetation on the abundance of tick vectors in the northeastern United States: a review of the literature. Journal of Medical Entomology 58:2030–2037.

Morand S, Lajaunie C. 2021. Outbreaks of vector-borne and zoonotic diseases are associated with changes in forest cover and oil palm expansion at global scale. Frontiers in veterinary science 8:230.

Needham GR, Teel PD. 1991. Off-host physiological ecology of Ixodid ticks. Annual Review of Entomology 36:659–681.

Nielebeck C, Kim SH, Pepe A, Himes L, Miller Z, Zummo S, Tang M, Monzón JD. 2023. Climatic stress decreases tick survival but increases rate of host-seeking behavior. Ecosphere 14:e4369.

Noden BH, Tanner EP, Polo JA, Fuhlendorf SD. 2021. Invasive woody plants as foci of tick-borne pathogens: eastern redcedar in the southern Great Plains. Journal of Vector Ecology 46:12–18.

Ogden N, Bigras-Poulin M, Hanincova K, Maarouf A, O'callaghan C, Kurtenbach K. 2008. Projected effects of climate change on tick phenology and fitness of pathogens transmitted by the North American tick *Ixodes scapularis*. Journal of Theoretical Biology 254:621–632.

Orrock JL, Baskett ML, Holt RD. 2010. Spatial interplay of plant competition and consumer foraging mediate plant coexistence and drive the invasion ratchet. Proceedings of the Royal Society of London B: Biological Sciences 277:3307–3315.

Ostfeld RS, Brunner JL. 2015. Climate change and *Ixodes* tick-borne diseases of humans. Philosophical Transactions of the Royal Society B: Biological Sciences 370:20140051.

Ostfeld RS, Canham CD, Oggenfuss K, Winchcombe RJ, Keesing F. 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. PLoS Biology 4:e145.

Ostfeld RS, Levi T, Keesing F, Oggenfuss K, Canham CD. 2018. Tick-borne disease risk in a forest food web. Ecology 99:1562–1573.

Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP, Thomas MB. 2016. Global threat to agriculture from invasive species. Proceedings of the National Academy of Sciences 113:7575–7579.

Parker CM, Miller JR, Allan BF. 2017. Avian and habitat characteristics influence tick infestation among birds in Illinois. Journal of Medical Entomology 54:550–558.

Peterson AT, Martínez-Campos C, Nakazawa Y, Martínez-Meyer E. 2005. Time-specific ecological niche modeling predicts spatial dynamics of vector insects and human dengue cases. Transactions of the Royal Society of Tropical Medicine and Hygiene 99:647–655.

Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jędrzejewska B, Lima M, Kausrud K. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Pettorelli N, Vik JO, Mysterud A, Gaillard J-M, Tucker CJ, Stenseth NC. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18:1725–1737.

Racelis A, Davey R, Goolsby J, De León AP, Varner K, Duhaime R. 2012. Facilitative ecological interactions between invasive species: *Arundo donax* stands as favorable habitat for cattle ticks (Acari: Ixodidae) along the US–Mexico border. Journal of Medical Entomology 49:410–417.

Randolph SE, Green R, Hoodless A, Peacey M. 2002. An empirical quantitative framework for the seasonal population dynamics of the tick *Ixodes ricinus*. International Journal for Parasitology 32:979–989.

Regina V, Felicia K. 2012. Effects of garlic mustard (*Alliaria petiolata*) removal on the abundance of entomopathogenic fungi.

Richardson D, Pyšek P, Rejmanek M, Barbour M, Panetta F, West C. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Richardson EA, Taylor CE, Jabot B, Martin E, Keiser CN. 2022. The effects of habitat type and pathogen infection on tick host-seeking behaviour. Parasitology 149:59–64.

Rochlin I, Toledo A. 2020. Emerging tick-borne pathogens of public health importance: a mini-review. Journal of Medical Microbiology 69:781.

Sambado S, Ryan SJ. 2024. Ecological and socioeconomic factors associated with globally reported tick-borne viruses. bioRxiv:2024.2010. 2011.617937.

Sauer JR, Hair JA. 1971. Water balance in the lone star tick (Acarina: Ixodidae): the effects of relative humidity and temperature on weight changes and total water content. Journal of Medical Entomology 8:479–485.

Schappach BL, Krell RK, Hornbostel VL, Connally NP. 2020. Exotic *Haemaphysalis longicornis* (Acari: Ixodidae) in the United States: Biology, ecology, and strategies for management. Journal of Integrated Pest Management 11:21.

Sonenshine DE. 2018. Range expansion of tick disease vectors in North America: implications for spread of tick-borne disease. International Journal of Environmental Research and Public Health 15:478.

Springer YP, Eisen L, Beati L, James AM, Eisen RJ. 2014. Spatial distribution of counties in the continental United States with records of occurrence of *Amblyomma americanum* (Ixodida: Ixodidae). Journal of Medical Entomology 51:342–351.

Stafford III KC. 1994. Survival of immature *Ixodes scapularis* (Acari: Ixodidae) at different relative humidities. Journal of Medical Entomology 31:310–314.

Stewart PS, Hill RA, Stephens PA, Whittingham MJ, Dawson W. 2021. Impacts of invasive plants on animal behaviour. Ecology Letters 24:891–907.

Swei A, Ostfeld RS, Lane RS, Briggs CJ. 2011. Effects of an invasive forest pathogen on abundance of ticks and their vertebrate hosts in a California Lyme disease focus. Oecologia 166:91–100.

Trumbore S, Brando P, Hartmann H. 2015. Forest health and global change. Science 349:814–818.

Tsao JI, Hamer SA, Han S, Sidge JL, Hickling GJ. 2021. The contribution of wildlife hosts to the rise of ticks and tick-borne diseases in North America. Journal of Medical Entomology 58:1565–1587.

Van Gestel M, Matthysen E, Heylen D, Verheyen K. 2022. Survival in the understorey: testing direct and indirect effects of microclimatological changes on *Ixodes ricinus*. Ticks and tick-borne diseases 13:102035.

Van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13:235–245.

VanAcker MC, Hofmeester TR, Zhang-Sun J, Goethert HK, Maria AD-W. 2024. Urban greenspace connectivity drive shifts in host assemblages and tick-borne pathogen infection. bioRxiv:2024.2011. 2012.623035.

Vial L, Stachurski F, Leblond A, Huber K, Vourc'h G, René-Martellet M, Desjardins I, Balança G, Grosbois V, Pradier S. 2016. Strong evidence for the presence of the tick *Hyalomma marginatum* Koch, 1844 in southern continental France. Ticks and tick-borne diseases 7:1162–1167.

Warren RJ, II, Wright JP, Bradford MA. 2011. The putative niche requirements and landscape dynamics of *Microstegium vimineum*: an invasive Asian grass. Biological Invasions 13:471–483.

Wei C-Y, Wang J-K, Shih H-C, Wang H-C, Kuo C-C. 2020. Invasive plants facilitated by socioeconomic change harbor vectors of scrub typhus and spotted fever. PLoS neglected tropical diseases 14:e0007519.

Williams SC, Ward JS. 2010. Effects of Japanese barberry (Ranunculales: Berberidaceae) removal and resulting microclimatic changes on *Ixodes scapularis* (Acari: Ixodidae) abundances in Connecticut, USA. Environmental Entomology 39:1911–1921.

Williams SC, Ward JS, Worthley TE, Stafford III KC. 2009. Managing Japanese barberry (Ranunculales: Berberidaceae) infestations reduces blacklegged tick (Acari: Ixodidae) abundance and infection prevalence with *Borrelia burgdorferi* (Spirochaetales: Spirochaetaceae). Environmental Entomology 38:977–984.

Yabsley MJ, Thompson AT. 2023. *Haemaphysalis longicornis* (Asian longhorned tick). Trends in Parasitology 39:305–306.