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) transmission. 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. Finally, we discuss range expansion of ticks and pathogens, spatial and temporal research scales, and modeling approaches for predicting TBD risk amidst global change. We highlight how plant invasions and climate change can impact ticks, hosts, and pathogens, and we identify research needs to improve models of TBDs in a changing world.

Introductions of species to non-native ranges have resulted in widespread biological invasions, which are a key driver of global change (Trumbore et al. 2015, Paini et al. 2016). Accumulating evidence demonstrates that invasive species 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 disease transmission (Goss et al. 2020), including vector-borne diseases transmitted by ticks and other arthropods. 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., threatens human and animal health (Schappach et al. 2020, Yabsley and Thompson 2023), and is capable of using multiple native small and medium sized mammalian host species for blood meals (Ferreira et al. 2023).

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 risk. The knockon effects of plant invasions in landscapes on potential tick hosts, including those also impacted by invasive hosts (Cheeseman et al. 2018), 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 (see Figure 1).

Historically, effects of plant invasions have focused on measuring direct economic impacts or potential threats to biodiversity conservation and maintenance of ecosystem functions (Duncan et al. 2004, Holmes et al. 2009). However, invasions may also alter disease risk by changing habitat structure and microclimate (Civitello et al. 2008). Change in TBD risk is defined here as any change in probability of encountering an infected tick due to differences in tick density or pathogen infection prevalence (Barbour and Fish 1993). Environmental tick abundance is influenced by tick survival and availability of tick blood meal hosts (e.g., deer, rodents) for completion of the tick life cycle (Ostfeld et al. 2006). Microclimate, specifically temperature and humidity, is the primary determinant of off-host tick survival (Hiatt et al. 2024), which can be directly influenced by climate, but also by landscape characteristics (e.g., slope, aspect, elevation, tree cover) and disturbance (e.g., land use change, extreme weather) as well as the local-scale composition and traits of vegetation (Diuk-Wasser et al. 2021, Mathisson et al. 2021). Host abundance and activity are strongly affected by habitat structure, such as plant diversity and composition and relative abundance of plant species, especially when species vary in functional traits. Altogether, TBD risk is driven by complex species interactions involving ticks, hosts, plants, and their environment (Ostfeld et al. 2018, Morand and Lajaunie 2021), all of which can be altered by plant invasions through shifts in microclimate and host habitat structure across various environmental contexts (Fig. 1).

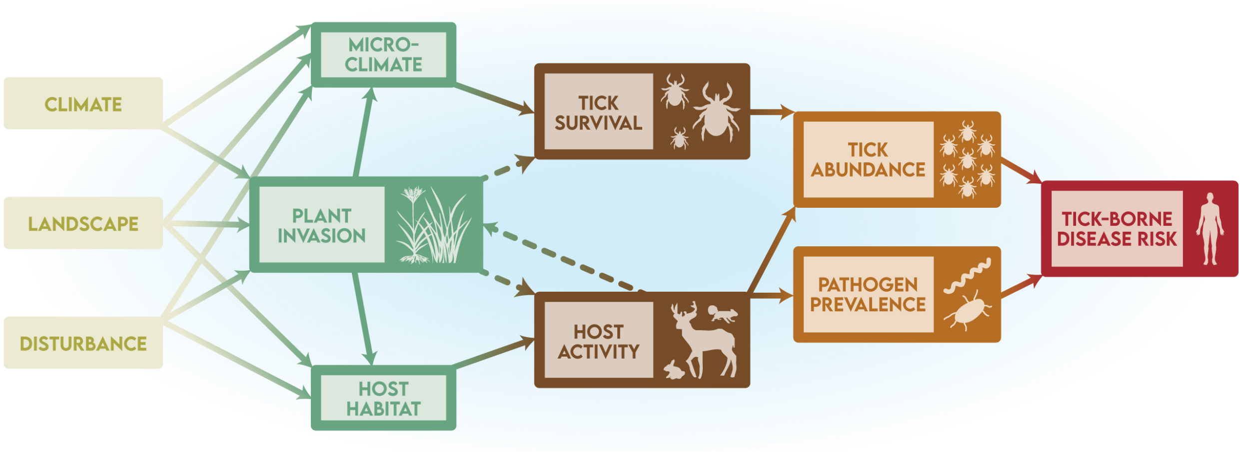


Figure 1. A One Health framework depicting the pathways by which plant invasions can be influenced by climate, landscape characteristics, and disturbance, which can then affect microclimate and host habitat, ticks and pathogens, and TBD risk. Plant invasions can affect microclimate and host habitat directly (solid lines), and each of these factors may directly or indirectly (dashed lines) alter 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 the pathogens they carry.

Documented effects of plant invasions on tick survival and host habitat structure

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]. Time between blood meals comprises over 90% of an Ixodid tick's life, and a primary cause of off-host tick mortality is desiccation (i.e., loss of water through the cuticle, (Needham and Teel 1991)). To maintain water balance, ticks must be in microclimates that are at or above their critical equilibrium humidity (e.g., 80-82% relative humidity for adult lone star ticks (*Amblyomma americanum*), (Hair et al. 1975, Knülle and Rudolph 1982); temperatures greater than 35ºC can also contribute to desiccation and mortality, (Sauer and Hair 1971). Field studies demonstrating higher tick abundances in areas invaded by barberry (*Berberis thunbergia*) and giant reed (*Arundo donax*) attribute greater tick abundances to favorable microclimates that reduce off-host tick desiccation, including lower temperatures and higher humidity (Williams and Ward 2010, Racelis et al. 2012). 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 enhances plant cover, reduces temperatures, and increases humidity, which was associated with greater longevity of lone star ticks (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 barberry and Amur honeysuckle, increased habitat use by white footed mice and/or white-tailed deer, 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, these studies fall 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 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 black-legged (*Ixodes scapularis*) larval ticks on white-footed mice (*Peromyscus leucopus*) and adult ticks questing in barberry (*Berberis thunbergii*), and Williams & Ward (2010) showed that barberry plots had more infected black-legged ticks than when barberry was managed or absent. Intact barberry plots had higher humidity and lower vapor pressure deficit, potentially increasing tick survival. Linske et al. (2018) found more black-legged ticks per mouse in barberry but no difference in tick or mouse abundance, suggesting barberry provides better tick habitat. 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 higher humidity and lower temperatures.

Berberis thunbergii

Arundo donax

Imperata cylindrica

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 temperature. Malo et al. (2013) found lower castor bean tick (*Ixodes ricinus*) abundance in *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 black-legged tick abundance in forest fragments invaded by multiflora rose (*Rosa multiflora*) due to reduced leaf litter which decreased tick survival.

Microstegium vimineum

<u>Plant invasions have no effect on tick survival</u>

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

Rhododendron ponticum

Mechanism 2: Changes in Host Activity/Abundance

<u>Plant invasions increase host activity/abundance</u>

Elias et al. (2006) found black-legged 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

Rosa multiflora

Lonicera maackii

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 black-legged ticks on white-footed mice. Noden et al. (2021) found more *Ehrlichia*- and *Rickettsia*-infected lone star ticks in eastern red cedar (*Juniperus virginiana*) invaded plots where they are more likely to encounter hosts. D'Antonio et al. (2023) found more black-legged ticks and white-footed mice in barberry-invaded plots, which provide protection from predators and greater opportunities for questing ticks.

Leucaena leucocephala

Rhamnus cathartica

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 were located out of tick questing range.

Plant invasions have no effect on host activity/abundance

Hiatt et al. (2024) found no relationship between cogongrass invasion and white-tailed deer activity on lone star tick 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.

Mechanism 3: Cascading Indirect Effects

Swei et al. (2011) found a positive correlation between western black-legged (*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

Alliaria petiolata

garlic mustard (*Alliaria petiolata*) removal promoted entomopathogenic soil fungi, potentially lowering black-legged tick survival.

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 (Civitello et al. 2008, Allan et al. 2010b, Williams and Ward 2010, Mack and Smith 2011, Racelis et al. 2012) 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 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.

Each arrow in Figure 1 represents a unique hypothesis explaining the 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.

A. Impacts of invasive plant functional traits on microclimates

We predict that invasive plants have measurable and unique effects on microclimate compared to native species, and that these effects can be predicted by invader functional traits. 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 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 (LMA), and leaf mass ratio (LMR). Invasive species frequently exhibit distinct and novel traits compared to native species in a community (van Kleunen et al. 2010, Mathakutha et al. 2019) such as exceptionally dense growth, taller stature, or greater leafiness, all of which might alter microclimate (Fig. 2). Community species composition, which can be altered by highly abundant, dense, and dominant invasive plant species can also significantly influence microclimate (Chapin, 2003). Moreover, invaders can have unique growth forms 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. (Warren et al. 2010) where there are no 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 density (Hiatt et al. 2024). Consequently, the unique functional traits and forms of plant invaders may exert a disproportionate 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 expect 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) compared to native plant dominated habitats. Conversely, if an invader has a unique growth form such as an open canopy and replaces a more densely growing native species, microclimate temperature or humidity extremes may increase.

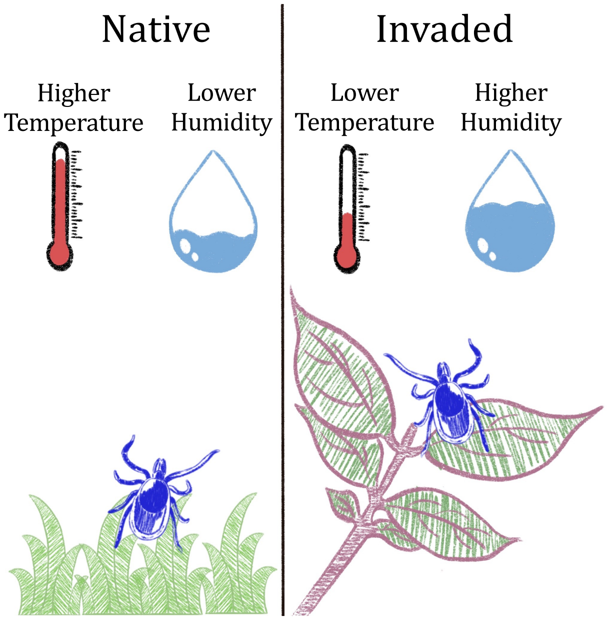


Figure 2. Example of how an invasive plant with a unique growth form and different functional traits may alter microclimate conditions. Here, the invader is a tall forb with a dense canopy that is replacing a shorter statured native grass species. As a result, the invaded area has a lower temperature and higher humidity than the native plant dominated area.

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 (Stafford 1994, Bertrand and Wilson 1996). 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). For example, high humidity and low temperature promotes optimal hydration status between questing bouts when ticks climb vegetation, which prompts water loss and physiological stress. 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 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 or high biomass 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. Tick life-history can be impacted by the microclimate conditions created by invasive plants; while we describe this as a potential 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 depending on other biotic factors such as blood meal host availability.

C. Invasive plant effects on host activity and pathogen prevalence

Invasive plants can alter host activity through changes in habitat suitability and food availability. The word ‘host’ is used generically here to capture the range of potential animal species available to provide blood meals to a tick in the context of plant invasions. Ticks can feed on a range of animals, both wild and domestic (including humans); these blood meals can also be routes of transmission of pathogens that will either survive or not within the tick and will either be possible to transmit to another host or may not be (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 risk.

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 and density (Fig. 3). Hosts may utilize invaded habitats for protection from predators (Orrock et al. 2010, Borden et al. 2022), 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 mechanisms for host use of invaded areas can promote host activity and potentially tick abundance. For example, black-legged tick abundance was positively correlated with white-tailed deer and white-footed mouse abundances in dense barberry invasions, which the authors attribute to the physical protection provided by 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). 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.

Greater host activity can impact pathogen prevalence 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 the Lyme disease causing *Borrelia burgdorferi* – infected black-legged nymphs in multiflora rose plots 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, which is the ultimate outcome of a far greater chain of events in this One Health system (Sambado and Ryan 2024). Whether humans living in areas with greater prevalence of non-native plant invasions experience higher rates of infection by TBDs is an urgent research priority.

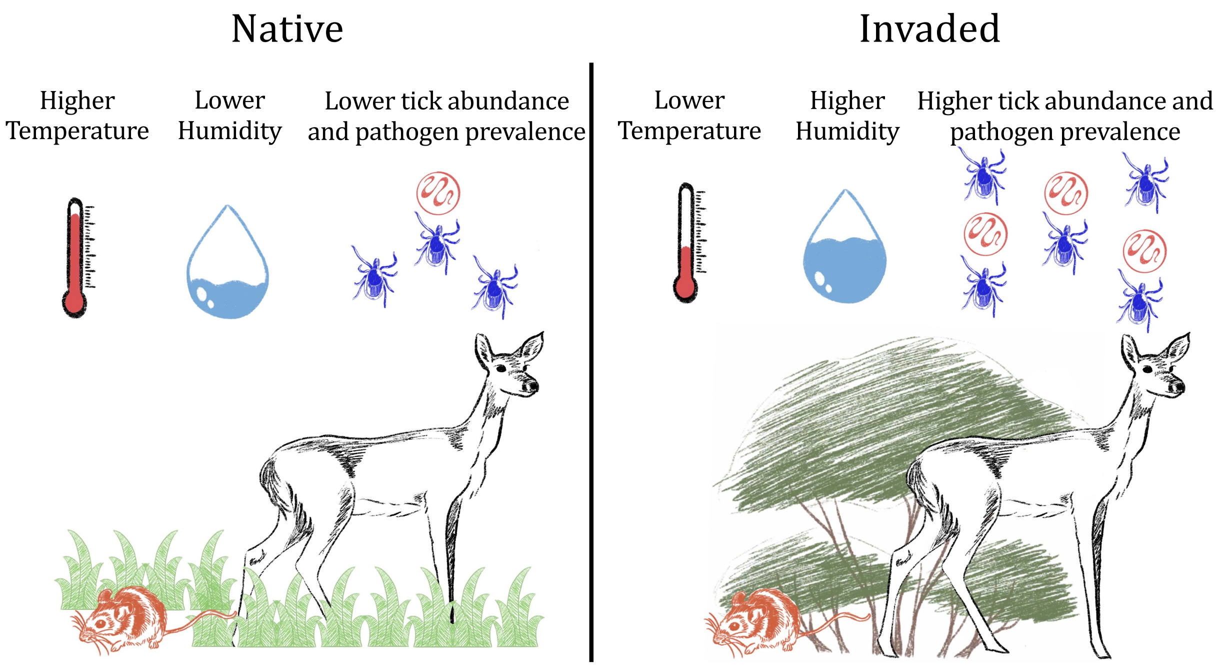


Figure 3. Invasive plants may enhance tick survival and provide better host habitat compared to native plant dominated areas. In this example, the invaded community has a cooler and wetter microclimate, and more food and shelter for hosts, which promotes tick survival and abundance and enhances pathogen prevalence compared to the uninvaded native plant dominated area.

Potential for 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). Expanding distributions 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). However, the role of non-native plant invasions in altering dispersal or habitat suitability for tick invasions has received scant attention. Parker et al. (2017) found avian migrants were less likely to be infested with multiple species of juvenile ticks in forest patches invaded by non-native shrubs, and hypothesized this pattern was due to birds foraging on berries from shrubs higher than the questing range of ticks. However, it was unknown whether these migrants arrived in these patches already infested by these tick species or if they acquired them locally. We predict that when invaded habitats serve to attract dispersing wildlife, plant invasions may increase geographic dispersal of ticks by enhancing wildlife host movements. Additionally, should invaded habitats offer more suitable microclimates for tick survival, plant invasions may increase tick establishment success during dispersal to new areas. Considering the ongoing geographic range expansion of numerous tick and tick-borne pathogen species, determining to what extent plant invasions alter dispersal and establishment probabilities is another urgent research priority.

Scales of measurement and models

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). Fewer studies have explored relationships across scales, for example, between local habitats and broad scale climatologies to compare functional impact of habitat features on seasonality (Randolph et al. 2002, Estrada-Peña et al. 2004, Ogden et al. 2008, MacDonald et al. 2020). To understand how microclimate, mediated by plant invasions, is described by larger scale climate measurements, models should explicitly incorporate multiple spatial scales: **(a)** micro, **(b)** meso, and **(c)** macro scales (Box 2). Adopting a variety of modeling approaches with appropriately scaled data inputs will allow for the exploration of potential trade-offs between modeling with large scale climate layers, versus localized climate and microclimate measures that capture sub-annual seasonal impacts on tick survival hypothesized to be influenced by invasive plants.

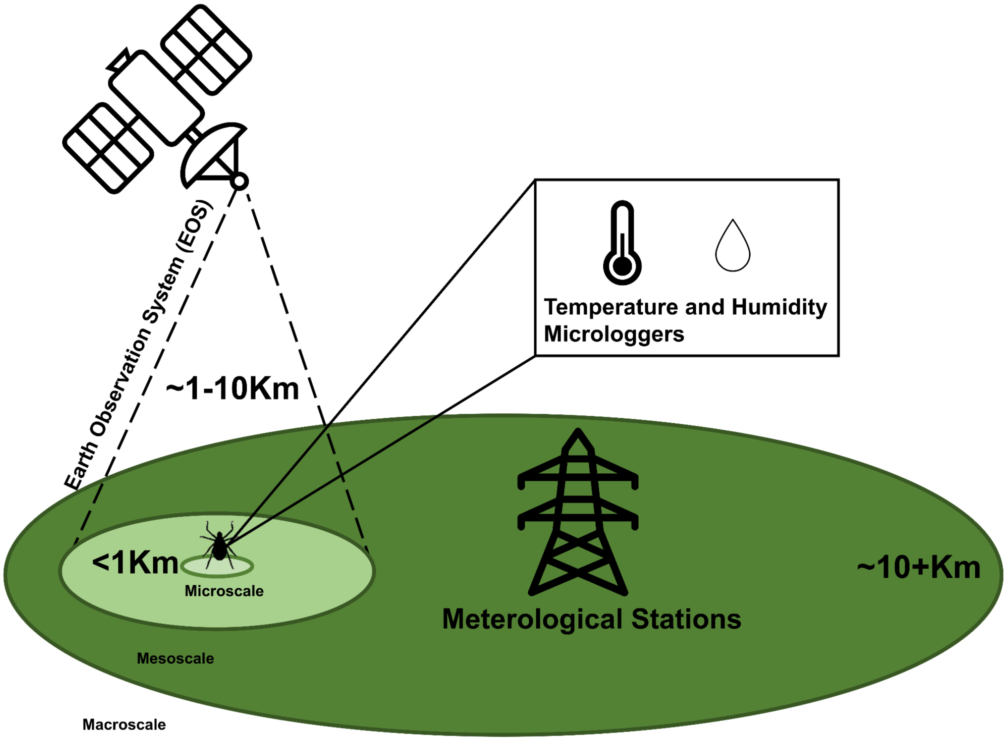
Box 2. Data collection across scales to quantify the ecological connections between ticks and their environment.

Scale, both spatial and temporal, is fundamental to the research question asked, determines how field data (on microclimate, plants, ticks, hosts) are collected, which environmental data products are appropriate (e.g., on-site climate measurements, Earth Observation Satellite (EOS) imagery, or gridded data such as interpolated surfaces or projected climate models), and how data must be prepared, aggregated, and modeled.

For understanding vector-borne diseases on the landscape, spatial scales generally range from the i) microscale (e.g., individual plants, sampling points for ticks), to the ii) mesoscale (e.g., sites or plots, described within a pixel of EOS data), and iii) macroscale (e.g., entire field sites, parks, or geographic regions). Microscale data have the advantage of capturing very fine scale relationships, for example, the immediate questing habitat of an off-host tick, when it is both sensitive to microclimate and most likely to be involved in human TBD transmission. Mesoscale may thus either aggregate microscale measured impacts or may instead reflect a different type of data measurements. For example, the mesoscale, describing the site or plot, may incorporate multiple temperature and humidity loggers to capture the variability of microscale climatologies, perhaps incorporating both 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., 1km^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. 2005, 2011), allows for rapid observation data acquisition that can be replicated across multiple mesoscale sites.

How microclimate scales to mesoscales (and what we describe as 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. Similarly, the scaling 'up' issue is also applicable to the macroscale, describing geographic regions, or entire preserved ecosystems. However, at the macroscale, 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, which is a proxy for disturbance history, leading to 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. 2022a, VanAcker et al. 2024), and see (Kache et al. 2022b) for a multiscale model for a mosquito-borne disease.

To date, few studies have explored relationships between local habitats and broad scale climatologies to compare the functional impact of habitat features on tick seasonality. Models that explicitly incorporate these multiscalar relationships will allow for exploration and comparisons of trade-offs in utility between large scale modeling approaches for TBD risk, and descriptions of fine scale, sub-annual dynamics of seasonality that are generated by plant invasions across the landscape. The figure below illustrates the proposed nesting of scales needed to capture climatological measurements combined with remotely sensed (EOS) data to describe and capture multiple scales of potential impacts of invasive plants in a landscape on larger landscape processes of TBD risk.



At present, models describing how ticks and TBDs exist on the landscape are mostly confined to rigorously captured data in specific locations, and models of ticks on those landscapes primarily assume stationarity of vegetation composition and phenology (for reviews, see (Lippi et al. 2021a, 2021c). When applied to larger landscapes using modeling approaches such as ecological niche modeling (ENM) or species distribution modeling (SDM), e.g. (Lippi et al. 2021b, Flenniken et al. 2022, Lippi et al. 2023b) retain similar assumptions, although projecting climate components of environmental variables at these larger scales is feasible, with the caveat of uncertainty inherent in extrapolating beyond the known environmental boundary conditions. Inherent in models based on niche assumptions is that the environment has shaped the presence of the occurrence in that place – which, when extended to a human case of a vector-borne disease, assumes that the case represents all the processes in the transmission chain in a location.

Thus, 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. 2021b, 2023a). 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, MLAs, 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 the most 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 product, NDVI. With sufficient fine-scale and high frequency data, a similar approach could capture year-on-year impacts of invasions to re-run and re-validate predictive models. To our knowledge, this does not yet exist for TBDs or even tick or host distributions, separately.

Future research directions and opportunities

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 transmission of diseases 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 identify and structure study systems involving multiple invasive plant and tick species and must focus more on underlying mechanisms to advance understanding of plant invasions on TBD risk under global change. We encourage the use of previous theory, existing data from field surveys, field and lab experiments, and Earth observation satellite (EOS) data; thereby leveraging existing infrastructure and extensive datasets to effectively address the questions highlighted here.

Evidence synthesized from studies to date suggest non-native plant invasions may alter TBD risk through both direct and indirect mechanistic pathways, and the direction and magnitude of these effects so far appear variable. However, the potential role of plant functional traits, growth form (e.g., grass vs shrub), phenology, or form of subsidy provided to wildlife hosts (e.g., shelter vs food), has been largely neglected in most studies. Focusing on invader functional traits may facilitate development of a generalizable and predictive approach that links traits to microclimate, host activity, and tick abundance, to advance understanding on how plant invasions may alter TBD risk (Fig. 1). Thus, future studies should attempt to quantify not only the mechanisms by which plant invasions alter the risk of TBD transmission, but also report key differences in the functional traits of native and invasive plant species within study sites.

To determine whether plant invasions consistently alter TBD risk, several other factors require further exploration. While some of the studies reviewed here suggested invader effects were due to changes in tick survival, and a few field-based survival studies have been performed comparing invaded to native plant dominated habitats, it remains largely unknown whether changes in tick survival or other parameters meaningfully impact disease transmission. 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 ticks but also changes in human disease incidence. 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. With sufficiently resolved geospatial data on human case reports, over sufficient periods of time, coupling tick surveillance records (which are still sparse, but improving, e.g. (Foster et al. 2023)) with vegetation surveys, remotely sensed classified imagery describing landcover change, particularly in the context of known plant invasions, we can start to identify and quantify these connections. Additionally, as many TBDs are expanding in geographic distribution, understanding what 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 also places limits on tick and pathogen invasions and reduces TBD risk, natural areas managers and users may benefit from a win-win solution to address both pressing environmental challenges.

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