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The interface between invasive species and the increased incidence of tick-borne diseases, and the implications for federal land managers

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According to the Centers for Disease Control and Prevention (CDC), the incidence of tick-borne disease is on the rise in the United States. For example, there are more than 30,000 annually reported cases of Lyme disease in the US (Kuehn 2013), though this estimate may be an order of magnitude too low (Nelson et al 2015), due to a combined lack of definitive or incorrect disease diagnosis and under reporting. The region in which ticks and tick-borne diseases occur is expanding significantly every year.

There continues to be a steady range expansion of various tick and tick-borne pathogens, concurrent with expanding ranges and populations of wildlife that serve as hosts for various disease-causing pathogens. Several other factors also contribute to increases in tick-borne disease, including habitat fragmentation, changes to land-use patterns, growth of white-tailed deer and other tick-host populations, climate change, etc. In combination, these factors impact populations of disease vectors, hosts, and pathogens and alter the compatibility of ecosystems and host populations in often unpredictable or complex ways. For example, habitat fragmentation due to human infrastructure development may alter the presence mammal host vectors and increase contact between humans exposure to tick-borne disease.

Although the scientific literature has relatively few publications on the subject, the expanding distribution of ticks and their associated disease-causing pathogens are increasingly shown to be facilitated by the presence of certain invasive plant species, particularly plant understory and transition-zone species. Invasive species are "with regard to a particular ecosystem, a non-native organism whose introduction causes, or is likely to cause, economic or environmental harm, or harm to human, animal, or plant health. It is US policy to prevent the introduction, establishment, and spread of invasive species, as well as to eradicate and control populations of invasive species that are already established" (Executive Order 13751). Invasive species have been found to contribute to the spread and survival of ticks, hosts, and various disease-causing pathogens. For those species that have been investigated, several invasive plant species such as Japanese honeysuckle and barberry have been definitively shown to harbor and enhance tick, host, and pathogen populations by enhancing microhabitat and survival. Additionally, non-native tick species such as Asian longhorn tick have been introduced and potentially new invasive tick-borne pathogens or hosts can, and likely will, be introduced in the future.

The issue of increased incidence and range expansion of ticks and tick-borne diseases is of particular concern to federal land management agencies. For example, tick-borne diseases are an issue for the Department of Defense (DoD), adversely affecting military readiness by impacting military land users, such as active duty members, civil servants, contractors, foreign nationals, military dependents, recreational users and others with access to military lands. Tick-borne diseases also impact military working dogs and horses as well as pets and livestock present on DoD installations. For public land managers with responsibilities for parks, wildlife refuges, or other public access lands, ticks and tick-borne diseases originating on public lands can have serious adverse consequences to employees, other public-land users, and wildlife.

It is incumbent on federal agencies, and especially federal land managers, to understand the dynamic of ticks and tick-borne diseases, including life-cycle details of problematic ticks, hosts, and pathogens of concern. Additionally, land managers should pay close attention to local infection rates of land users, hosts (including pets), and tick species of concern. Important considerations for land managers include an awareness of reputable, timely, and relevant information from federal, state, and local sources concerning regional/local disease incidence, results of surveillance/monitoring data on regional tick distributions, and an awareness of specific diseases carried by region-specific tick populations.

Further, prudent attention to peer-reviewed scientific literature and other reputable sources related to the mitigation of invasive species impacts (e.g., CDC, university cooperative extensions, state or local public health institutions) will be valuable in reducing tick populations and tick-borne disease incidence. Once armed with relevant information, land managers must strive to acquire the resources and skills needed to conduct site-specific monitoring to determine tick, host, and pathogen densities and diversity. Having the most up-to-date and relevant data, land managers will be better able to make informed decisions, prioritize scarce resources and undertake vegetation or other habitat management activities that can effectively and safely reduce the threat of tick-borne diseases.

FINDINGS AND RECOMMENDATIONS

The challenge of managing multiple factors that contribute to the occurrence, distribution, and severity of ticks and tick-borne diseases are far more complex than what can be addressed in a single document. When certain invasive species are introduced to an already complex natural cycle of ticks, hosts, habitat, and tick-borne pathogens, it is impossible to effectively consider the relationship as a single topic. The only way to effectively approach management actions and mitigate tick-borne disease risk is to prioritize and determine which of the complex land management actions and vector/host/pathogen life-cycle attributes to target. Land management actions must consider which mitigation efforts are cost effective and environmentally acceptable.

For federal land managers, one step in the tick management process is to determine priority strategies to achieve important land management goals for a particular parcel of federal property and to determine the primary users/constituents of that land. Then, it is more feasible to identify and assess the greatest tick-related risks to those constituents and activities. Once the most likely and debilitating disease risks are identified, the role of invasive species management in the overall response to that disease risk can be evaluated, programmed, and mitigated.

For example, at US military installations and training facilities, where access is often limited, clearly the presence and welfare of uniformed personnel, civil servants, contractors, foreign nationals and military families is a higher priority than the health of the general public. For these sorts of land management examples, specific mission and recreational activities are more predictable and consistent. Likewise, for managers of National Parks, the priority will typically be members of the general public who visit the parks, and Park Service personnel who live and work within park boundaries. For land managers, the health and welfare of native wildlife, potentially including threatened or endangered species, is likely to be a priority, along with the protection of field staff, hunters, and other recreational users. On National Forest and Bureau of Land Management lands, in addition to the wildlife, resources, and recreational users, many regions allow grazing of privately owned livestock. The range of jurisdictions on the land and the range of priorities and concerns can complicate a holistic approach to resources management issues and the consideration of tick-borne diseases that may be circulated back and forth between domestic animals, wildlife, and people.

It is generally acknowledged that the incidence of tick-borne disease is on the increase in many parts of the United States, especially within specific regions. While Lyme disease is only one of a plethora of tick-borne diseases being tracked and studied across the United States, it is the most frequently reported. Lyme disease is spreading rapidly across the twelve states of the Northeast, Mid-Atlantic, and North Central regions (where 95% of the cases are currently found) and is expected to soon emerge as a major threat in new regions. Lyme disease provides a very useful case study for the broader study of tick-borne diseases, because it has been very thoroughly studied, vividly illustrates the complexity of the life-cycle of the tick vectors spreading this disease, and highlights the challenges of trying to manage or control the outbreak. Consequently, Lyme disease has been used in the appendices and references attached to this document as the primary example of tick-borne pathogens, to illustrate the disease cycle, the role that Ixodid ticks play at various life stages in the acquisition and spread of the disease, and the role that intermediate host species (primarily white-footed mice and white-tailed deer) play in providing a reservoir for the disease and assistance for the ticks to complete their life-cycles.

In the process of compiling this document and the attachments, it was found that multiple federal agencies and programs are focused on one aspect or another of tick-borne diseases, many with robust studies underway. While many of the scientists and researchers within the agencies are acquainted with one another on a professional basis, it quickly became clear that there is no central clearinghouse within the federal government, or even an effective communication network through which the primary stakeholders can readily access current and comprehensive information about various tick-borne disease issues on either a topical or regional basis. This already flawed situation is worsened when the role of invasive species (plants, tick, hosts, and pathogens) is added to the mix. While the National Invasive Species Council (NISC) exists as a result of Executive Order 13751, the principals within each of the member agencies have not met since 2008 to discuss how the coordination of efforts or sharing of information and resources related to invasive species could advance the agencies' respective and collective mission, whether that be the protection of human health, agriculture, natural resources, or national security and defense. As a result, federal land managers do not have a single source for information about which invasive species may exist on their respective land units, what role, if any, those invasive species have in the risk of tick-borne disease, or what control or eradication measures can be considered for invasive species that could mitigate the risk of tick-borne disease on a given land unit or regional division of an agency charged with any form of land management activities.

There are various federal agency experts monitoring tick-borne disease issues in certain regions, but not in others. Some researchers monitor ticks for their role in human disease, while others monitor for disease implications in livestock and domestic animals. Even though these studies may be looking at the same ticks, this information does not exist in a single database. The majority of tick-borne diseases are zoonotic; that is, they are able to be spread back and forth between humans and animals. So, information on wildlife or livestock disease could provide insight to human health initiatives and vice versa. There is little comprehensive study being given to the issue of tick-borne diseases affecting wildlife, beyond the role that various wildlife species play in the life-cycle of ticks, or the transmission and spread of various diseases.

Unfortunately, for federal land managers, this will make the job of making land-management decisions that can mitigate the risk of tick-borne diseases more complex and daunting. Nevertheless, taking the time to identify and tap into regional expertise, databases, and disease studies could help tremendously, especially when there is a targeted constituency, land-use mission or activity on which land management activities are focused, or regionally emergent diseases that may be present on, or approaching, a given land management unit. Further, for certain land units, managers may actually have an opportunity to collaborate with regional researchers to try various control strategies for the management of vectors, habitats, hosts, and pathogens that may not be appropriate or possible on a broader landscape.

As a result of the review of the attached studies and findings, the Invasive Species Advisory Committee makes the following recommendations to NISC for ways to assist the federal government, across all agencies, to mitigate the risk of tick-borne diseases, which are amplified, exacerbated, or complicated through the presence of invasive species.

Recommendation 1 – Within NISC member agencies and bureaus, ensure that the scope of Invasive Species Programs and activities embraces the One Health Concept and is sufficiently broad to facilitate an integrated response to issues related to the role of invasive species in human health, animal health, and/or environmental health. It is important to break the mindset that invasive species management is carried out on a species-by-species basis, often in a policy vacuum. Rather, the issue of invasive species must be viewed in the context of broader management activities and goals, with assurance that the impact of controlling or eradicating invasive species be evaluated in the context of full ecosystem health. Where necessary, formal communication and information sharing networks within a single agency need to be created and mandated to ensure that information sharing is carried out in a timely manner to facilitate cooperation among programs responsible for human safety and health, facilities and land management, and the specific management of invasive species (which could have implications for the former).

Recommendation 2 – NISC agencies with active programs related to the mitigation of risk associated with tick-borne diseases that affect humans or animals, most notably the Department of Health and Human Services, CDC, and the Department of Agriculture (USDA), should create and fund a formal information-sharing network or task force that gathers and compiles available information related to invasive diseases, plants, vectors or pathogens of interest to a broader suite of agencies, and proactively share this information with all NISC agencies, targeting human and animal health professionals and environmental and landscape managers. The purpose of this task force would be to create more comprehensive data resources on which other agencies of the federal government, or state and local entities, can predicate land or resource management decisions that could affect the risk of tick-borne diseases on either a regional or local basis. Communication can be in the form of a regular electronic digest or a website that assembles the points of access to all relevant federal information related to resource management studies, recommendations, or activities which could be of use to federal personnel and all federal partners or collaborators.

Recommendation 3 – Land and facility managers of all NISC agencies should identify and establish communication with regional experts and personnel within CDC, USDA, or other agencies, who may have information relevant to land-management decisions related to the issue of tick-borne disease. This can be prioritized within the context of the respective land manager's mandate or land management priority, whether human heath, animal health, environmental health, or other land-use mission. This communication should be such that it facilitates a regular and timely flow of information, recommendations, expertise, or advice on how best to identify and implement regionally relevant invasive species management and related disease risk mitigation strategies. For example, in certain parts of the country, invasive species of plant, such as Japanese honeysuckle and Japanese barberry are known to create artificially lush habitat for high-risk, disease-vector ticks, while also providing abundant vegetation for deer and other host species that exacerbate the spread of disease. In other parts of the country, tick-borne disease risk may be minimal. Understanding which invasive species have the greatest impact on the density of vectors or the likelihood of questing ticks to come in contact with wild or domestic host species, could enable managers to prioritize invasive species management activities, especially when resources and personnel are limited.

Background Information and Additional Resources

CONTENTS

ACKNOWLEDGMENTS

The following background information and additional resources have been compiled to support the content and findings of the preceding ISAC white paper, which responds to a request to the National Invasive Species Council (NISC) Secretariat by the Department of Defense in November 2018. Adopted unanimously by the full ISAC on May 2, 2019, the preceding white paper was initially developed by a task team comprised of the following ISAC members: Ed Clark, Wildlife Center of Virginia (chair); Janis McFarland, Syngenta Crop Protection, LLC; Blaine Parker, Columbia River Inter-Tribal Fish Commission; and Slade Franklin, Wyoming Department of Agriculture. The team engaged with the following federal employees to obtain background information and awareness of federal programs: Doug Burkett and Eric Hofmann, US Department of Defense; Camille Hopkins, US Geological Survey; Danielle Butke, Nation Park Service; Charles (Ben) Beard, Center for Disease Control; and Beto Perez de Leon, Andrew Li, Denise Bonilla, Angela James, and Morgan Wehjte, US Department of Agriculture. Further assistance in background information and developing the paper were provided by Drs. Ernesto Dominguez and Peach Van Wick of the Wildlife Center of Virginia. The NISC Secretariat is grateful for the responsiveness of the ISAC to develop this White paper, the background information provided by federal representatives, the leadership provide by Ed Clark in chairing the task team, and the extraordinary contributions of Dr. Dominguez in developing and refining the paper.

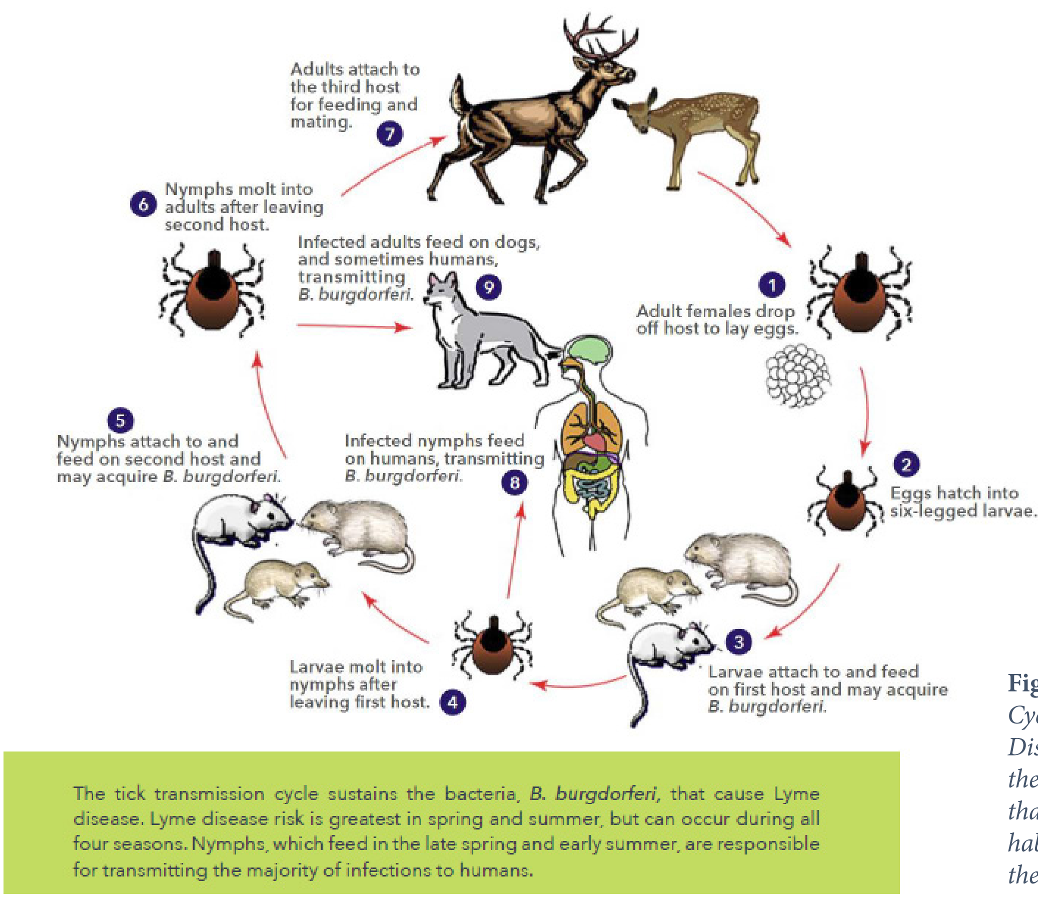


Figure 1 *Ixodes scapularis Tick Life Cycle and the Transmission of Lyme Disease (Borrelia burgdorferi) from the CDC (2018) and noting here that these cycles occur within a habitat comprised and impacted by their vegetation communities.*

THE DYNAMICS OF TICK-BORNE DISEASE

Throughout the 20th and 21st centuries, the number of infectious diseases in humans has been increasing as approximately 335 human infectious diseases have emerged since 1940 (Jones et al., 2008). Approximately 60 percent of those diseases are zoonotic, of which 72 percent are transmitted from wildlife and the remainder are transmitted from domestic animals. Furthermore, approximately 30 percent of emerging infectious diseases are vector-borne, which include tick-borne diseases (TBDs, see Table 1). Currently, there is incomplete and inadequate knowledge about key factors pertaining to persistence of reservoir, transmission, and host responses. More research is needed to better understand these diseases and to improve strategies to protect human health. (for more information see: https://www.ncbi.nlm.nih.gov/books/NBK57013/)

In some parts of the world ticks are the most dangerous animals followed by mosquitoes as ectoparasites and vectors of infectious agents, causing morbidity and mortality in domestic animals including wildlife and humans. The majority of tick-borne diseases are zoonotic (e.g. Lyme Disease (Borrelia burgdorferi, Figure 1). Here it is useful to note that each of the animals shown in Figure 1 live and are impacted by the vegetation communities that constitute the environment. As discussed below, invasive species can influence this zoonotic cycle.

> "Transboundary zoonotic tick-borne diseases can maintain a dynamic focus and have pathogens circulating in geographic regions encircling multiple geopolitical boundaries. Global change is intensifying transboundary problems, including the spatial variation of the risk and incidence of zoonotic tick-borne diseases. The complexity of these challenges can be greater in areas where rivers delineate international boundaries and encompass transitions between ecozones. The Rio Grande serves as a natural border between the US State of Texas and the Mexican States of Chihuahua, Coahuila, Nuevo León, and Tamaulipas. Not only do millions of people live in this transboundary region, but also a substantial amount of goods and people pass through it every day. Moreover, it occurs over a region that functions as a corridor for animal migrations, and thus links the Neotropic and Nearctic biogeographic zones, with the latter being a known foci of zoonotic diseases. However, the pathogenic landscape of important zoonotic diseases in the south Texas-Mexico transboundary region remains to be fully understood. An international perspective on the interplay between disease systems, ecosystem processes, land use, and human behaviors is applied here to analyze landscape and spatial features of Lyme Borreliosis and human Babesiosis. Surveillance systems following the One Health approach with a regional perspective will help identifying opportunities to mitigate the health burden of those diseases on human and animal populations. It is proposed that the Mexico-US border along the Rio Grande region be viewed as a continuum landscape where zoonotic tick-borne pathogens circulate regardless of national borders" (Esteve-Gassent et al. 2014).

The global importance of ticks and tick-borne diseases in veterinary medicine and public health keeps growing. Some

TICK-BORNE FAD	NATURAL/POTENTIAL U.S. VECTORS	GEOGRAPHIC DISTRIBUTIONS	COMMODITY
1. Equine piroplasmosis[1]	*Dermacentor variabilis; Dermacentor albipictus;* *Anocentor nitens;* *Amblyomma mixtum;* *Boophilus microplus*	Multiple States Texas	Equine
2. Bovine babesiosis[2]	*Rhipicephalus Boophilus microplus;* *Rhipicephalus Boophilus annulatus*	Texas only, both species	Cattle
3. African swine fever[3]	*Ornithodoros coriaceus*; *O. turicata*; *O. parkeri*	Multiple States	Swine
4. Heartwater - Cowdriosis[4]	*Amblyomma maculatum;* *A.mixtum; A. dissimile*	Southern states	Cattle

Table 1 *Invasive pathogens considered tick-borne diseases*

1 https://www.aphis.usda.gov/animal_health/animal_diseases/piroplasmosis/downloads/ep_literature_review_september_2010.pdf
2 https://pdfs.semanticscholar.org/7340/4c91761c117207e5ad205a5a5546ddb06286.pdf
3 https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5808196/pdf/fvets-05-00011.pdf
4 https://avmajournals.avma.org/doi/pdf/10.2460/javma.237.5.520

ticks are invasive and transmit pathogens causing transboundary diseases of high consequence for populations of domestic animals and humans. Integrated management pursues the optimized use of compatible methods to manage pests in a way that is safe, economically viable, and environmentally sustainable. The area-wide approach augments and expands the benefits of integrated pest management strategies. Issues challenging the implementation, adoption, and viability of area-wide tick management programs include funding and socio-political concerns, the availability of support systems related to extension and veterinary services, and stakeholder involvement. Management strategies need to adapt and integrate novel technologies to decrease significantly the use of pesticide and address the complex problem of ticks and tick-borne diseases effectively. Applying the "One Health" concept, the strategy to optimize health outcomes for humans, animals, and the environment, facilitates research on the interplay between climate, habitat, and hosts driving tick population dynamics. It enhances our understanding of the epidemiology of tick-borne diseases and advances their management.

FACTORS AFFECTING OCCURRENCE AND DENSITY OF TICKS

Wildlife Factors

Large increases in white-tailed deer (*Odocoileus virginianus*) populations in the 20th century may have facilitated the expansion of ticks and Lyme disease (Léger et al. 2013). High deer densities are common in many parts of the Midwest and mid-Atlantic regions due to extirpation of predators, decreased hunting pressure, and human-driven habitat fragmentation, leading to more edge areas with high-quality forage (Côte et al. 2004). Deer are also the primary host for adult-stage *I. scapularis* ticks and thus are a key blood meal for egg mass production; several studies have reported a positive relationship between deer density and tick density (Raizman et al. 2013; Kilpatrick et al. 2014; Werden et al. 2014; Kugeler et al. 2015). As selective herbivores, deer have indirect effects on ticks by altering tick habitat (Fisichelli et al. 2013) and other tick hosts (e.g., small mammals and songbirds; Habeck and Schultz 2015), but few studies have evaluated how these effects may influence pathogen systems. Intense deer browse pressure, due in part to overabundant populations, can alter and fragment understory vegetation structure and plant community composition (Mudrak et al. 2009; Fisichelli et al. 2012), causing simplified forest understories with abundant non-native and unpalatable plant species and dramatic reductions in understory-dependent mammal and bird species (Rooney et al. 2004 Fisichelli and Miller 2014). Dominance by less-palatable or browse-tolerant non-native and invasive shrubs is positively related to *I. scapularis* and pathogen abundance (Lubelczyk et al. 2004, Elias et al. 2006, Williams and Ward 2010).

Based on the observed differences in host competence for *B. burgdorferi* infection, previous models have suggested that biodiversity, i.e., a diverse animal community including non-competent hosts, can 'dilute' *B. burgdorferi* infections in a system (Ostfeld and Keesing 2000). Additionally, host superinfection, and transmission competence to feeding ticks, is dependent upon *B. burgdorferi* diversity within the host (here *Peromyscus leucopus*), which is dependent upon the number of ticks feeding on the host (Rogovskyy and Bankhead 2014). This suggests that more ticks a host feeds, the more effective it is at transmitting *B. burgdorferi*. Supporting this hypothesis, larger, older, male mice are more likely to be infected with *B. burgdorferi* and also carry higher tick loads regardless of questing tick aggregation in the environment (Ostfeld et al. 1996; Brunner and Ostfeld 2008; Devevey and Brisson 2012). Additionally, the proportion of adult, larger, male mice is inversely related to forest patch size and consequently bird and mammalian diversity (Nupp and Swihart 1996). In this way, forest patch size, which is driven largely by human-driven landscape change, may drive host infection prevalence and thus tick infection prevalence. Predation is also linked to tick-borne disease risk, which predator richness and density linked to lower risk of Lyme disease, and is also inversely related to forest patch size (Hofmeester et al 2017).

Habitat Factors

For many tick-borne diseases, a certain number of host relationships and seasonal dynamics of ticks are required to maintain a robust enzootic cycle. There must be established relationships between environmental conditions and tick-host associations,

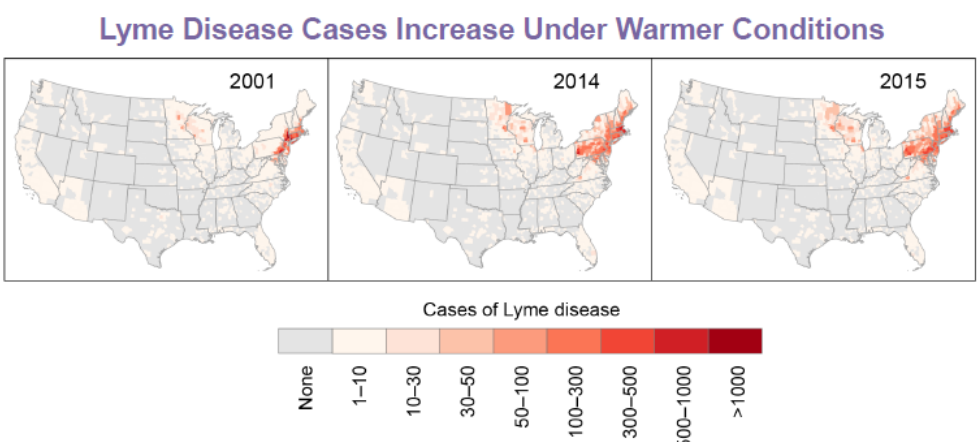


Figure 2 *Reported cases of Lyme disease in 2001, 2014, and 2015 are shown by county for the contiguous United States. Both the distribution and total number of cases have increased, particularily in the Midwest and the Northeast. From the U.S. 4th National Climate Assessment (USGCRP, 2018) using sources from CDC and ERT, Inc.*

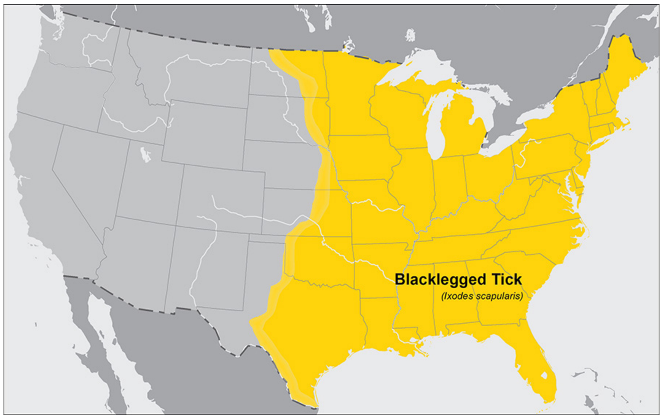


Figure 3 *General distribution of Blacklegged tick (*Ixodes scapularis*) (from* CDC*, with the following note: This map shows the estimated distribution of Ixodes scapularis tick populations, commonly known as blacklegged or deer ticks. However, tick abundance within this area varies locally. The map does not represent the risk of contracting any specific tick-borne illness.*

as both vertebrate host populations and tick questing behavior are influenced by abiotic factors (e.g., distributional limits, abundance, and seasonal dynamics) (Sonenshine and Clifford 1973). A tick's geographical distribution, life history, hosts, and its ability to transmit diseases are determined by biochemical and physiological aspects of the tick that determine its reaction to temperature, humidity, and other meteorological elements (e.g., the number of offspring produced per reproductive cycle). In addition to climatic factors, the spatial structure of the landscape and its connectivity and vegetation types also have an effect on tick populations and their distributions (Estrada-Pena et al. 2008).

Ticks are intermittent parasites, spending part of their lives off their hosts in habitats where they are influenced by abiotic factors. Temperature and rainfall are the main factors affecting the ecology and population dynamics of tick species, and these operate at critical levels on selection of tick populations (Estrada-Pena et al. 2009). For example, the distribution of *Ixodes ricinus* in Britain was associated with several environmental factors, such as substrata composed of less permeable soil types and less permeable superficial/bedrock geology, which would support moist microhabitats. Their distribution was also associated with calcareous/neutral grassland and heathland habitats, particularly those grazed by livestock (Medlock et al. 2008). McEnroe (1977) reported that there were relative differences in the distribution of the American dog tick from region to region, likely due to moisture and temperature differences. Campbell (1979) reported shifts in tick distribution and abundance related to vegetative types and attributed environmental determinants to tick survival.

Tick abundance is also limited by abiotic factors that influence the ability to actively quest for a host. Questing ticks are influenced by a variety of abiotic factors such as increasing or decreasing day length or fluctuations in temperature. Additionally, temperatures can change the questing behavior in ticks; for example, decreasing temperature associated with increasing altitude will negatively affect the number of questing numbers of nymphs and adults (Randolph 2004). Therefore, the opportunity to acquire a pathogen from a reservoir host can be positively or negatively impacted by abiotic factors. It has been observed with *I. ricinus* nymphs that drier conditions impacted the questing height, with more nymphal ticks questing lower and thus having increased exposure to rodents. In contrast, in wetter conditions, an increased number of larvae attached to rodents and fewer nymphs. These climatic factors influenced the questing behavior and thus the potential for a pathogen to be transmitted by nymphs or larvae feeding on rodents. The risk of infection to hosts depends on the number of infected questing ticks. In addition, the larger the number of hosts in an area the greater the probability of ticks attaching and progressing through their life cycle and transmitting a pathogen (Kitron and Kazmieerczak 1997; Randolph 2001).

Ecological information on tick species within in the United States is vital for developing and implementing a systematic approach to tick control. The assessment of the developmental times of the free-living tick stages on vegetation will be helpful in determining the major tick species' seasonal activities. With the additional analysis of environmental temperature, rainfall, and tick abundance, this information will aid in the prediction of peak abundance of ticks and the timing of appropriate tick control on a seasonal basis. Through the integration of field, laboratory, and modeling studies, we can gather new insights into the mechanisms of evolutionary ecology regarding the diverse spectrum of tickborne pathogens, tick species, and their vertebrate hosts.

Impacts from Climate Change

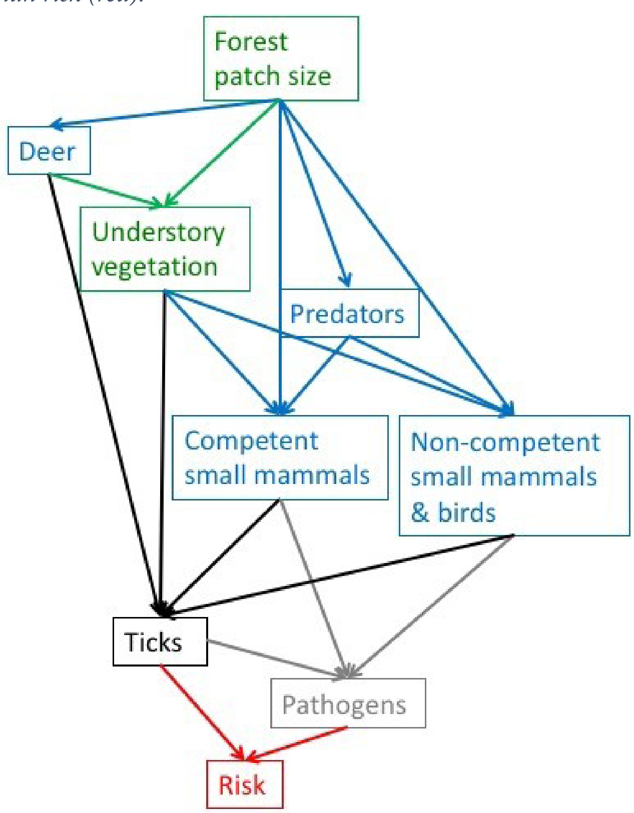
It is important to consider any management challenge in light of additional stress to the system. Both vector-borne disease and invasive species challenges are likely to be further complicated by climate dynamics: especially continued warming trends, extended droughts, and extreme events. Climate change can contribute to the spread of mosquitoes and ticks. A warmer climate enhances the suitability of habitats that were formerly too cold to support mosquito and tick populations, thus allowing these vectors and the diseases they transmit to invade new areas (Figure 2). Climate change is aiding the spread of invasive species (Burgiel and Hall 2014). Climate projections show that habitat for certain species will increase (e.g., *Berberis thunbergii* [Japanese barberry] in the Northeast; Merow et al 2017). Climate change can favor nonnative invading species over native ones (Sorte et al. 2013, Wolkovich and Cleland 2014). Extreme weather events can influence the invasion process, from initial introduction through establishment and spread, and potentially put native species at a competitive disadvantage (Diez et al. 2012). Because vector borne diseases and invasive species are compounded by climate change, a holistic approach to managing invasive species and ticks (and other vectors) could help a) avoid surprises as either (or both) become worse and b) ensure proper resources are in place to manage landscapes that are resilient to climate dynamics.

Taken together, the various factors affecting tick distribution result in the distribution of the various tick across the U.S. The current estimate for the distributions for blacklegged tick is show in Figure 4. Additional tick distribution maps are available at https://www.cdc.gov/ticks/geographic_distribution.html.

MATRICES OF TIES BETWEEN HABITAT, HUMAN ACTIVITIES, INVASIVE PLANTS, AND TICKS

Understanding complex tick-borne pathogen systems and responding to the urgent human health threat requires coordinated multidisciplinary research and management efforts across broad geographic areas and over long time periods (Rohr et al. 2010; Léger et al. 2013; Estrada-Pena et al. 2014; Ostfeld and Brunner 2015; Kilpatrick et al. 2017). Ticks, such as *Ixodes scapularis*, are part of complex disease systems that include multiple pathogens, life-stage-specific hosts, forest habitat characteristics, interactions across trophic levels, and climatic drivers (Figure 4). Ticks acquire pathogens during blood meals of competent hosts or less-commonly by transovarian spread. The likelihood of a pathogen transmission depends upon host community composition. Host communities, in turn, are influenced by habitat, predation, and resource availability.

Figure 4 *A simplified, general tick-borne-pathogen system conceptual model showing key direct and indirect influences among system components, including habitat and vegetation (green), host (blue), vector (black), pathogens (gray), and human risk (red).*



Human activities can therefore influence tick-borne disease risks on the landscape through several mechanisms. Human development results in increased forest fragmentation and decreased forest patch size, which in turn dramatically influences community composition in these remnant forests. Human activities have also influenced predator and community composition, resulting in complete removal of apex predators (i.e., red wolves, mountain lions) and significant impacts to mesopredators in eastern forests, which in turn affects population densities of the primary blood meal hosts of ticks in eastern forests, white-tailed deer and *Peromyscus* species. Human activity has also resulted in the introduction of invasive plant species that have been shown to dramatically influence tick density and infection prevalence (Lubelczyk et al. 2004; Elias et al. 2006; Williams and Ward 2010).

Invasive plants can serve a significant role and likely enhance tick, host, and tick-borne pathogen survival and distribution. Exotic plants often invade areas of high human activity, such as along trails, roads, and forest edges, and in disturbed riparian areas. These same habitat types are also favored by ticks, tick hosts, and the pathogens they carry. This convergence suggests that habitat modifications caused by exotic plant invasions may mediate disease vector habitat quality, indirectly affecting human disease risk at the local spatial scale. For those few species that have been evaluated, some invasive plant species are more important tick refugia than others. Forest understories are subject to invasion by exotic vegetation such as honeysuckle (Miller and Gorchov 2004) and multiflora rose (Adalsteinsson et al. 2016). These species form dense groves which provide suitable microclimate conditions for *I. scapularis* (Lubelczyk et al. 2004, Christopher and Cameron 2012) and abundant fruit and cover for wildlife.

Elias et al. 2006 found twice as many adult ticks (*Ix. scapularus*) and nearly twice as many nymphs in plots dominated by exotic-invasives than in plots dominated by native shrubs. Both adult and nymphal counts were lowest in open understory with coniferous litter. Adults were positively associated with increasing litter depth, medium soil moisture, and increasing abundance of white-footed deer mice (*Peromyscus leucopus*) and deer pellet group counts. Nymphs were positively associated with increasing litter depth, moderately wet soil, and mice. We concluded that deer browse-resistant exotic-invasive understory vegetation presented an elevated risk of human exposure to the vector tick of Lyme disease.

Racelis et al. 2012 found *Arundo donax* infestations present environmental conditions that facilitate the survival and persistence of cattle ticks, as well or better than native habitats and open grasslands representing an alarming complication for cattle fever tick management in the United States.

Allan et al. 2010 demonstrated that a widespread invasive shrub in North America, Amur honeysuckle (*Lonicera maackii*), increases human risk of exposure to ehrlichiosis, an emerging infectious disease caused by bacterial pathogens transmitted by the lone star tick (*Amblyomma americanum*). Using observational surveys in natural areas across the St. Louis, Missouri region, they found that white-tailed deer (*Odocoileus virginianus*), a preeminent tick host and pathogen reservoir, more frequently used areas invaded by honeysuckle. This habitat preference translated into considerably greater numbers of ticks infected with pathogens in honeysuckle-invaded areas relative to adjacent honeysuckle-uninvaded areas. They confirmed this biotic mechanism using an experimental removal of honeysuckle, which caused a decrease in deer activity and infected tick numbers, as well as a proportional shift in the blood meals of ticks away from deer. They concluded that disease risk is likely to be reduced when honeysuckle is eradicated, and suggest that management of biological invasions may help ameliorate the burden of vector-borne diseases on human health.

Lubelczyk et al. 2004 also found Japanese barberry and honeysuckle to enhance tick abundance (*Ix scapularus*). The authors concluded that natural resource managers should be aware that landscape changes, including the invasion by exotic vegetation, might create favorable tick habitat and that the findings could prove helpful in assessing local risk of exposure to this vector tick.

The invasive Japanese barberry (*Berberis thunbergii*) has been proven to enhance tick, host and Lyme disease pathogen densities and that barberry control significantly reduces tick populations and infection prevalence. Williams et al. 2009 found that eastern forests with an overabundance of white-tailed deer (*Odocoileus virginianus*), Japanese barberry (*Berberis thunbergii*) has become the dominant understory shrub, which may provide a habitat favorable to blacklegged tick (*Ixodes scapularis*) and white-footed mouse (*Peromyscus leucopus*) survival. To determine mouse and larval tick abundances at three replicate sites over 2 years, mice were trapped in unmanipulated dense barberry infestations, areas where barberry was controlled, and areas where barberry was absent. Total mouse counts did not differ between treatments. Mean number of feeding larval ticks per mouse was highest on mice captured in dense barberry. Adult tick densities in dense barberry were higher than in both controlled barberry and no barberry areas. Ticks sampled from full barberry infestations and controlled barberry areas had similar infection prevalence with *B. burgdorferi* the first year. In areas where barberry was controlled, infection prevalence was reduced to equal that of no barberry areas the second year of the study. Results indicate that managing Japanese barberry will have a positive effect on public health by reducing the number of *B. burgdorferi* (Lyme disease) infected blacklegged ticks that can develop into motile life stages that commonly feed on humans.

Not all invasive species in the understory are proving to enhance tick populations. For example, Civitello et al. 2008 tested whether Japanese stiltgrass (*Microstegium vimineum*) altered microclimate conditions and enhanced tick survival. Microstegium is an exotic annual grass that is highly invasive throughout the eastern United States where the vector ticks *Amblyomma americanum* (Linnaeus) and *Dermacentor variabilis* (Say) occur. For these particular specie,s where ticks were introduced into experimentally invaded and native vegetation control plots, *D. variabilis* mortality rate increased 173% and *A. americanum* mortality rate increased 70% in the invaded plots relative to those in control plots. Microstegium invasion also resulted in a 13.8% increase in temperature and an 18.8% decrease in humidity, which are known to increase tick mortality. The authors predicted that areas invaded by Microstegium would have lower densities of host-seeking ticks and therefore reduced human disease risk. These results emphasize the role of invasive species in mediating disease vector populations, the unpredictable consequences of biological invasions, and the need for integrative management strategies that can simultaneous address exotic plant invasions and vector-borne disease. For Japanese stiltgrass (*Microstegium vimineum*), tick numbers were lower than for native vegetation.

Morlando et al. 2012 concluded that although habitat restoration to native species is expensive, a cost benefit analysis shows that restoration such as removal of invasive trees reduces the Lyme disease risk by ~98%. Cost-of-illness studies show that the restoration would be financially justifiable if it averted 75 cases of Lyme disease per year. Given the local Lyme disease rate and the visitation rate to federal and military lands, habitat restoration can plausibly be justified solely on the benefit of cases averted.

Surprisingly, fire management using prescribed burns has been found to have an unintended consequence of increasing tick densities in areas recently burned. Allan et al. 2009 found that the increasingly widespread use of prescribed burns to manage oak (*Quercus spp.*)-hickory (*Carya spp.*) forests in the Missouri Ozarks, USA, has considerable potential to alter the abundance of *Amblyomma americanum* (L.) (Acari: Ixodidae), the lone star tick, an important vector of several emerging pathogens. In particular, responses of important tick hosts, primarily white-tailed deer (*Odocoileus virginianus*), to fire management and the resultant changes in the distribution and abundance of *A. americanum* are largely unknown. Using several large burn units (61–242 ha) within the Ozark ecosystem, they measured the effect of the time elapsed since sites were burned on the density of white-tailed deer (*Odocoileus virginianus*) and the larval life stage of *A. americanum*. Larval tick densities were highest in areas that were 2 yr postburn and were >6 times higher than tick densities in control units. Deer densities were highest in sites that were burned in the same year as this study and decreased significantly with time since burn. These results suggest that intensive use of postburn sites by white-tailed deer may increase the abundance of *A. americanum* to levels greater than occurs in sites that remain unburned. Thus, fire management, although beneficial in many aspects of ecosystem management, may bear the unintended cost of locally increasing abundance of *A. americanum.*

FEDERAL RESOURCES AND PROGRAMS RELATED TO TICKS AND VECTOR-BORNE DISEASE

The following summary information and links provide a sample of federal programs and information related to ticks and vector-borne diseases. It is not intended to be an exhaustive list but rather a guide for further information. It also demonstrates that multiple federal agencies and federally funded programs are focused on one aspect or another of tick-borne diseases, many with robust programs and documentation. However, there is currently no central clearinghouse within the federal government through which the primary stakeholders can readily access current and comprehensive information about various tick-borne disease issues on either a topical or regional basis.

Free tick identification and testing services for Department of Defense (DoD) affiliated personnel, including Active Duty Service Members, Families, Retirees, Civilians, and Contractors.

- Army Public Health Center: DoD Human Tick Test Kit Program, operated by the Tick-Borne Disease Laboratory
- https://phc.amedd.army.mil/topics/envirohealth/epm/Pages/HumanTickTestKitProgram.aspx
- Data Portal, to download or view tick and pathogen data by installation or state: https://carepoint.health.mil/sites/ENTO (Government only)
- Data also available through VectorMap, from the Walter Reed Biosystematics Unit based at the Smithsonian Institution: http://vectormap.si.edu/

Documents and Online Resources for Ticks and Tick-Borne Diseases

Further resources related to tick-borne disease in humans, domestic animal and wildlife can be found at:

Institute of Medicine (US). Committee on Lyme Disease and Other Tick-Borne Diseases: the State of the Science, 2011. *Critical Needs and Gaps in Understanding Prevention, Amelioration, and Resolution of Lyme and Other Tick-borne Diseases: The Short-term and Long-term Outcomes: Workshop Report*. National Academies Press.

- https://www.ncbi.nlm.nih.gov/books/NBK57009/

For more information on tick-disease vectors, surveillance, and prevention see:

Report of the Disease Vectors, Surveillance, and Prevention Subcommittee to the Tick-Borne Disease Working Group

- https://www.hhs.gov/ash/advisory-committees/tickbornedisease/reports/disease-vectors-2018-5-9/index.html

An overview of Tick-borne disease by the CDC

- https://www.cdc.gov/ticks/tickbornediseases/overview.html

USDA's APHIS National Veterinary Services Laboratories

- https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/lab-info-services

USDA's APHIS National Animal Health Laboratory Network

- https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/sa_lab_information_services/sa_nahln/ct_national_animal_health_laboratory_network

Online Resources for Monitoring Ticks and Tick-Borne Diseases

Army Public Health Center: Vector-Borne Disease Report

- https://phc.amedd.army.mil/news/Pages/PeriodicPublications.aspx

Tick Trapper App

- https://ticktracker.com

The Tick App / University of Wisconsin

- https://thetickapp.org

Tick Insiders / Purdue University

- https://tickinsiders.org/tick-encounter-disease-risk-map

CDC / Tick-Borne Diseases Home Page

- https://www.cdc.gov/ticks

The Tick App for Texas and the Southern Region /

Texas A&M University

- https://tickapp.tamu.edu

USGS Disease Maps

- https://diseasemaps.usgs.gov

Resources Related to Mitigation Strategies of Tick-Borne Diseases

Tick Bites/Prevention

- https://www.cdc.gov/ticks/tickbornediseases/tick-bites-prevention.html

Preventing Ticks in the Yard

- https://www.cdc.gov/lyme/prev/in_the_yard.html

Tick Management Handbook

- https://portal.ct.gov/-/media/CAES/DOCUMENTS/Publications/Bulletins/b1010pdf.pdf?la=en

Armed Forces Pest Management Board Technical Guide No. 26 Tick-Borne Diseases: Vector Surveillance and Control

- https://www.acq.osd.mil/eie/afpmb/docs/techguides/tg26.pdf

American Veterinary Medical Association (AVMA) disease precautions for hunters

- https://www.avma.org/public/Health/Pages/Disease-Precautions-for-Hunters.aspx

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ANNOTATED BIBLIOGRAPHY FOR LITERATURE ON TICKS, VECTOR-BORNE DISEASES, AND INVASIVE SPECIES

Search terms used: tick*, tick habitat*, invasive plant*, climate change
Databases: PubMed, CAB Abstracts
Dates: 3/21/2019 through 4/9/2019

1. **Scale-dependent effects of nonnative plant invasion on host-seeking tick abundance**.
Adalsteinsson SA, D'Amico V, Shriver WG, Brisson D, Buler JJ
Ecosphere **7**(3): e01317. 2016.

Abstract: Nonnative, invasive shrubs can affect human disease risk through direct and indirect effects on vector populations. Multiflora rose (Rosa multiflora) is a common invader within eastern deciduous forests where tick-borne disease (e.g. Lyme disease) rates are high. We tested whether R. multiflora invasion affects blacklegged tick (Ixodes scapularis) abundance, and at what scale. We sampled host-seeking ticks at two spatial scales: fine-scale, within R. multiflora-invaded forest fragments; and patch scale, among R. multiflora-invaded and R. multiflora-free forest fragments. At a fine scale, we trapped 2.3 times more ticks under R. multiflora compared to paired traps 25 m away from R. multiflora. At the patch scale, we trapped 3.2 times as many ticks in R. multiflora-free forests compared to R. multiflora-invaded forests. Thus, ticks are concentrated beneath R. multiflora within invaded forests, but uninvaded forests support significantly more ticks. Among all covariates tested, leaf litter volume was the best predictor of tick abundance; at the patch scale, R. multiflora-invaded forests had less leaf litter than uninvaded forests. We suggest that leaf litter availability at the patch-scale plays a greater role in constraining tick abundance than the fine-scale, positive effect of invasive shrubs.

2. **Multiflora rose invasion amplifies prevalence of Lyme disease pathogen, but not necessarily Lyme disease risk**.
Adalsteinsson SA, Shriver WG, Hojgaard A, Bowman JL, Brisson D, D'Amico V, Buler JJ
Parasit Vectors **11**(1): 54. 2018.

Abstract: BACKGROUND: Forests in urban landscapes differ from their rural counterparts in ways that may alter vector-borne disease dynamics. In urban forest fragments, tick-borne pathogen prevalence is not well characterized; mitigating disease risk in densely-populated urban landscapes requires understanding ecological factors that affect pathogen prevalence. We trapped blacklegged tick (Ixodes scapularis) nymphs in urban forest fragments on the East Coast of the United States and used multiplex real-time PCR assays to quantify the prevalence of four zoonotic, tick-borne pathogens. We used Bayesian logistic regression and WAIC model selection to understand how vegetation, habitat, and landscape features of urban forests relate to the prevalence of B. burgdorferi (the causative agent of Lyme disease) among blacklegged ticks. RESULTS: In the 258 nymphs tested, we detected Borrelia burgdorferi (11.2% of ticks), Borrelia miyamotoi (0.8%) and Anaplasma phagocytophilum (1.9%), but we did not find Babesia microti (0%). Ticks collected from forests invaded by non-native multiflora rose (Rosa multiflora) had greater B. burgdorferi infection rates (mean = 15.9%) than ticks collected from uninvaded forests (mean = 7.9%). Overall, B. burgdorferi prevalence among ticks was positively related to habitat features (e.g. coarse woody debris and total understory cover) favorable for competent reservoir host species. CONCLUSIONS: Understory structure provided by non-native, invasive shrubs appears to aggregate ticks and reservoir hosts, increasing opportunities for pathogen transmission. However, when we consider pathogen prevalence among nymphs in context with relative abundance of questing nymphs, invasive plants do not necessarily increase disease risk. Although pathogen prevalence is greater among ticks in invaded forests, the probability of encountering an infected tick remains greater in uninvaded forests characterized by thick litter layers, sparse understories, and relatively greater questing tick abundance in urban landscapes.

3. **Influence of prescribed burns on the abundance of Amblyomma americanum (Acari: Ixodidae) in the Missouri Ozarks**.
Allan BF
J Med Entomol **46**(5): 1030-1036. 2009.

Abstract: The increasingly widespread use of prescribed burns to manage oak (Quercus spp.)-hickory (Carya spp.) forests in the Missouri Ozarks, USA, has considerable potential to alter the abundance of Amblyomma americanum (L.) (Acari: Ixodidae), the lone star tick, an important vector of several emerging pathogens. In particular, responses of important tick hosts, primarily white-tailed deer (Odocoileus virginianus), to fire management and the resultant changes in the distribution and abundance of A. americanum are largely unknown. Using several large burn units (61-242 ha) within the Ozark ecosystem, I measured the effect of the time elapsed since sites were burned on the density of white-tailed deer and the larval life stage of A. americanum. Larval tick densities were highest in areas that were 2 yr postburn and were > 6 times higher than tick densities in control units. Deer densities were highest in sites that were burned in the same year as this study and decreased significantly with time since burn. These results suggest that intensive use of postburn sites by white-tailed deer may increase the abundance of A. americanum to levels greater than occurs in sites that remain unburned. Thus, fire management, although beneficial in many aspects of ecosystem management, may bear the unintended cost of locally increasing abundance of A. americanum.

4. **Invasive honeysuckle eradication reduces tick-borne disease risk by altering host dynamics**.
Allan BF, Dutra HP, Goessling LS, Barnett K, Chase JM, Marquis RJ, Pang G, Storch GA, Thach RE, Orrock JL
Proc Natl Acad Sci USA **107**(43): 18523-18527. 2010.

Abstract: Despite the ubiquity of invasive organisms and their often deleterious effects on native flora and fauna, the consequences of biological invasions for human health and the ecological mechanisms through which they occur are rarely considered. Here we demonstrate that a widespread invasive shrub in North America, Amur honeysuckle (Lonicera maackii), increases human risk of exposure to ehrlichiosis, an emerging infectious disease caused by bacterial pathogens transmitted by the lone star tick (Amblyomma americanum). Using large-scale observational surveys in natural areas across the St. Louis, Missouri region, we found that white-tailed deer (Odocoileus virginianus), a preeminent tick host and pathogen reservoir, more frequently used areas invaded by honeysuckle. This habitat preference translated into considerably greater numbers of ticks infected with pathogens in honeysuckle-invaded areas relative to adjacent honeysuckle-uninvaded areas. We confirmed this biotic mechanism using an experimental removal of honeysuckle, which caused a decrease in deer activity and infected tick numbers, as well as a proportional shift in the blood meals of ticks away from deer. We conclude that disease risk is likely to be reduced when honeysuckle is eradicated, and suggest that management of biological invasions may help ameliorate the burden of vector-borne diseases on human health.

5. **Socioeconomics drive woody invasive plant richness in new England, USA through forest fragmentation**.
Allen JM, Leininger TJ, Hurd JD, Jr., Civco DL, Gelfand AE, Silander JA, Jr.
Landscape ecology **28**(9): 1671-1686. 2013.

Abstract: Woody invasive plants are an increasing component of the New England flora. Their success and geographic spread are mediated in part by landscape characteristics. We tested whether woody invasive plant richness was higher in landscapes with many forest edges relative to other forest types and explained land use/land cover and forest fragmentation patterns using socioeconomic and physical variables. Our models demonstrated that woody invasive plant richness was higher in landscapes with more edge forest relative to patch, perforated, and especially core forest types. Using spatially-explicit, hierarchical Bayesian, compositional data models we showed that infrastructure and physical factors, including road length and elevation range, and time-lagged socioeconomic factors, primarily population, help to explain development and forest fragmentation patterns. Our social-ecological approach identified landscape patterns driven by human development and linked them to increased woody plant invasions. Identifying these landscape patterns will aid ongoing efforts to use current distribution patterns to better predict where invasive species may occur in unsampled regions under current and future conditions.

6. **Invasive species: "back-seat drivers" of ecosystem change?**
Bauer JT
Biol Invasions **14**(7): 1295-1304. 2012.

Abstract: Invasive species are often assumed to be the cause (drivers) of declines in native species and alterations of native ecosystems. However, an alternative model suggests that many invasive plants are better described as passengers of altered disturbance regimes or other changes in

ecosystem properties. Some species do seem to be easily categorized as passengers or drivers, but others may be better described as -back-seat drivers-. Back-seat drivers require or benefit from disruptions of ecosystem processes or properties that lead to declines of native species but also contribute to changes in ecosystem properties and further declines of native species. Among these possibilities, drivers are a direct cause of the decline of native species through the introduction of novel traits or functions to an ecosystem, whereas back-seat drivers interact with ecosystem change to cause native species declines. Passengers are better considered as a symptom of an underlying problem, rather than the cause of native species declines. Driver, back-seat driver and passenger models suggest different associations between invasive species, ecosystem change and native species declines, and these models provide a framework for predicting and understanding the response of native species to invasive species management.

7. **Epidemiology and impact of coinfections acquired from Ixodes ticks**.
Belongia EA
Vector Borne Zoonotic Dis **2**(4): 265-273. 2002.

Abstract: Ixodes scapularis and other ticks in the Ixodes ricinus complex may transmit multiple pathogens, but research on coinfections has been limited. Coinfections occur with varying frequency in ticks, but single infections are more common than dual infections. The proportion of I. scapularis or I. ricinus ticks coinfected with both Borrelia burgdorferi sensu lato and Anaplasma phagocytophila is generally low, ranging from < 1% to 6% in six geographic areas. A higher prevalence of tick coinfection (26%) has been reported in Westchester County, New York. Genetic variants of the human disease-causing strain of A. phagocytophila are present in some tick populations, and they may affect the risk of coinfection or clinical illness. The proportion of Ixodes ticks coinfected with B. burgdorferi and Babesia microti has ranged from 2% in New Jersey to 19% on Nantucket Island, Massachusetts. In humans, cross-sectional seroprevalence studies have found markers of dual infection in 9-26% of patients with a tick-borne infection, but such studies often fail to distinguish simultaneous coinfection from sequential infections. Several studies have prospectively assessed the occurrence of acute coinfection. Among patients with a confirmed tick-borne infection, coinfection rates as high as 39% have been reported. The most commonly recognized coinfection in most of the eastern United States is Lyme borreliosis (LB) and babesiosis, accounting for approximately 80% of coinfections. LB and human granulocytic ehrlichiosis coinfections are less common, occurring in 3-15% of patients with a tick-borne infection in Connecticut or Wisconsin. Studies of clinical outcomes suggest that patients with acute Babesia coinfection have more severe symptoms and a longer duration of illness than patients with LB alone, but the risk of spirochete dissemination is similar. Coinfections can modify the immune response and alter the severity of arthritis in animal models. Future coinfection research should focus on long-term clinical outcomes, the role of genetic variants, immunologic effects, and the potential role of Bartonella species as tick-borne pathogens.

8. **Adverse moisture events predict seasonal abundance of Lyme disease vector ticks (Ixodes scapularis)**.
Berger KA, Ginsberg HS, Dugas KD, Hamel LH, Mather TN
Parasit Vectors **7**: 181. 2014.

Abstract: BACKGROUND: Lyme borreliosis (LB) is the most commonly reported vector-borne disease in north temperate regions worldwide, affecting an estimated 300,000 people annually in the United States alone. The incidence of LB is correlated with human exposure to its vector, the blacklegged tick (Ixodes scapularis). To date, attempts to model tick encounter risk based on environmental parameters have been equivocal. Previous studies have not considered (1) the differences between relative humidity (RH) in leaf litter and at weather stations, (2) the RH threshold that affects nymphal blacklegged tick survival, and (3) the time required below the threshold to induce mortality. We clarify the association between environmental moisture and tick survival by presenting a significant relationship between the total number of tick adverse moisture events (TAMEs - calculated as microclimatic periods below a RH threshold) and tick abundance each year. METHODS: We used a 14-year continuous statewide tick surveillance database and corresponding weather data from Rhode Island (RI), USA, to assess the effects of TAMEs on nymphal populations of I. scapularis. These TAMEs were defined as extended periods of time (>8 h below 82% RH in leaf litter). We fit a sigmoid curve comparing weather station data to those collected by loggers placed in tick habitats to estimate RH experienced by nymphal ticks, and compiled the number of historical TAMEs during the 14-year record. RESULTS: The total number of TAMEs in June of each year was negatively related to total seasonal nymphal tick densities, suggesting that sub-threshold humidity episodes >8 h in duration naturally lowered nymphal blacklegged tick abundance. Furthermore, TAMEs were positively related to the ratio of tick abundance early in the season when compared to late season, suggesting that lower than average tick abundance for a given year resulted from tick mortality and not from other factors. CONCLUSIONS: Our results clarify the mechanism by which environmental moisture affects blacklegged tick populations, and offers the possibility to more accurately predict tick abundance and human LB incidence. We describe a method to forecast LB risk in endemic regions and identify the predictive role of microclimatic moisture conditions on tick encounter risk.

9. **Does high biodiversity reduce the risk of Lyme disease invasion?**
Bouchard C, Beauchamp G, Leighton PA, Lindsay R, Belanger D, Ogden NH
Parasit Vectors **6**: 195. 2013.

Abstract: BACKGROUND: It has been suggested that increasing biodiversity, specifically host diversity, reduces pathogen and parasite transmission amongst wildlife (causing a "dilution effect"), whereby transmission amongst efficient reservoir hosts, (e.g. Peromyscus spp. mice for the agent of Lyme disease Borrelia burgdorferi) is reduced by the presence of other less efficient host species. If so, then increasing biodiversity should inhibit pathogen and parasite invasion. METHODS: We investigated this hypothesis by studying invasion of B. burgdorferi and its tick vector Ixodes scapularis in 71 field sites in southeastern Canada. Indices of trapped rodent host diversity, and of biodiversity of the wider community, were investigated as variables explaining the numbers of I. scapularis collected and B. burgdorferi infection in these ticks. A wide range of alternative environmental explanatory variables were also considered. RESULTS: The observation of low I. scapularis abundance and low B. burgdorferi infection prevalence in sites where I. scapularis were detected was consistent with early-stage invasion of the vector. There were significant associations between the abundance of ticks and season, year of study and ambient temperature. Abundance of host-seeking larvae was significantly associated with deer density, and abundance of host-seeking larvae and nymphs were positively associated with litter layer depth. Larval host infestations were lower where the relative proportion of non-Peromyscus spp. was high. Infestations of hosts with nymphs were lower when host species richness was higher, but overall nymphal abundance increased with species richness because Peromyscus spp. mouse abundance and host species richness were positively correlated. Nymphal infestations of hosts were lower where tree species richness was higher. B. burgdorferi infection prevalence in ticks varied significantly with an index of rates of migratory bird-borne vector and pathogen invasion. CONCLUSIONS: I. scapularis abundance and B. burgdorferi prevalence varied with explanatory variables in patterns consistent with the known biology of these species in general, and in the study region in particular. The evidence for a negative effect of host biodiversity on I. scapularis invasion was mixed. However, some evidence suggests that community biodiversity beyond just host diversity may have direct or indirect inhibitory effects on parasite invasion that warrant further study.

10. **Harvested white-tailed deer as sentinel hosts for early establishing Ixodes scapularis populations and risk from vector-borne zoonoses in southeastern Canada**.
Bouchard C, Leighton PA, Beauchamp G, Nguon S, Trudel L, Milord F, Lindsay LR, Belanger D, Ogden NH
J Med Entomol **50**(2): 384-393. 2013.

Abstract: Due to recent establishment of the blacklegged tick, Ixodes scapularis Say, in southeastern Canada, tick-borne zoonoses (Lyme disease, human granulocytotropic anaplasmosis, and babesiosis) are of growing concern for public health. Using white-tailed deer (Odocoileus virginianus) culled in southwestern Quebec during 2007-2008, we investigated whether hunter-killed deer could act as sentinels for early establishing tick populations and for tick-borne pathogens. Accounting for environmental characteristics of culling sites, and age and sex of deer, we investigated whether their tick infestation levels could identify locations of known tick populations detected in active surveillance, presumed tick populations detected by passive surveillance, or both. We also used spatial cluster analyses to identify spatial patterns of tick infestation and occurrence of tick-borne zoonoses infection in ticks collected from the deer. Adult ticks were found on 15% of the 583 deer examined. Adult male deer had the greatest number (approximately 90%) of adult ticks. Overall, 3, 15, and 0% of the ticks collected were polymerase chain reaction (PCR)-positive for Borrelia burgdorferi, Anaplasma phagocytophilum, and Babesia microti, respectively. Our statistical analyses suggest that sex and age of deer, temperature, precipitation, and an index of tick dispersion by migratory birds were significantly associated with tick infestation levels. Cluster analysis identified significant clusters of deer carrying ticks PCR-positive for A. phagocytophilum, and for deer carrying two or more I. scapularis. Our study suggests that hunter-killed deer may be effective as sentinels for emerging areas of tick-borne anaplasmosis. They may have limited use as sentinels for early emerging I. scapularis tick populations and emerging Lyme disease risk.

11. **Molting success of Ixodes scapularis varies among individual blood meal hosts and species**.
Brunner JL, Cheney L, Keesing F, Killilea M, Logiudice K, Previtali A, Ostfeld RS
J Med Entomol **48**(4): 860-866. 2011.

Abstract: The blacklegged tick (Ixodes scapularis) is an important vector of emerging human pathogens. It has three blood-feeding stages, as follows: larva, nymph, and adult. Owing to inefficient transovarial transmission, at least for the Lyme disease agent (Borrelia burgdorferi), larval ticks rarely hatch infected, but they can acquire infection during their larval blood meal. Nymphal ticks are primarily responsible for transmitting pathogens to hosts, including humans. The transition from uninfected host-seeking larva to infectious host-seeking nymph is therefore a key aspect of human risk of infection. It can be divided into a series of steps, as follows: finding a host, taking a blood meal, becoming infected, molting, and overwintering. The chance of succeeding in each of these steps may depend on the species identity of the blood meal host. We used a Bayesian method to estimate the molting success of larval I. scapularis collected from four commonly parasitized species of birds and eight commonly parasitized small and mid-sized mammals found in the forests of Dutchess County, New York. We show that molting success varies substantially

among host species; white-footed mice, veeries, and gray catbirds support particularly high molting success, whereas ticks feeding on short-tailed shrews, robins, and wood thrushes were less successful. We also show that larval molting success varies substantially between individual blood meal hosts, and that this intraspecific variability is much higher in some species than in others. The causes of both inter- and intraspecific variation in molting success remain to be determined.

12. **Effects of deer density on tick infestation of rodents and the hazard of tick-borne encephalitis. I: empirical assessment**.
Cagnacci F, Bolzoni L, Rosa R, Carpi G, Hauffe HC, Valent M, Tagliapietra V, Kazimirova M, Koci J, Stanko M, Lukan M, Henttonen H, Rizzoli A
Int J Parasitol **42**(4): 365-372. 2012.

Abstract: Tick borne encephalitis (TBE) is endemic to eastern and central Europe with broad temporal and spatial variation in infection risk. Although many studies have focused on understanding the environmental and socio-economic factors affecting exposure of humans to TBE, comparatively little research has been devoted to assessing the underlying ecological mechanisms of TBE occurrence in enzootic cycles, and therefore TBE hazard. The aim of this study was to evaluate the effect of the main ungulate tick hosts on the pattern of tick infestation in rodents and TBE occurrence in rodents and questing adult ticks. In this empirical study, we considered three areas where endemic human TBE occurs and three control sites having no reported human TBE cases. In these six sites located in Italy and Slovakia, we assessed deer density using the pellet group count-plot sampling technique, collected questing ticks, live-trapped rodents (primarily Apodemus flavicollis and Myodes glareolus) and counted ticks feeding on rodents. Both rodents and questing ticks were screened for TBE infection. TBE infection in ticks and rodents was positively associated with the number of co-feeding ticks on rodents and negatively correlated with deer density. We hypothesise that the negative relationship between deer density and TBE occurrence on a local scale (defined by the minimum overlapping area of host species) could be attributed to deer (incompetent hosts) diverting questing ticks from rodents (competent hosts), know as the 'dilution effect hypothesis'. We observed that, after an initial increase, the number of ticks feeding on rodents reached a peak for an intermediate value of estimated deer density and then decreased. Therefore, while at a regional scale, tick host availability has already been shown to be directly correlated with TBE distribution, our results suggest that the interactions between deer, rodents and ticks are much more complex on a local scale, supporting the possibility of a dilution effect for TBE.

13. **Exotic grass invasion reduces survival of Amblyomma americanum and Dermacentor variabilis ticks (Acari: Ixodidae)**.
Civitello DJ, Flory SL, Clay K
J Med Entomol **45**(5): 867-872. 2008.

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

14. **Northward range expansion of Ixodes scapularis evident over a short timescale in Ontario, Canada**.
Clow KM, Leighton PA, Ogden NH, Lindsay LR, Michel P, Pearl DL, Jardine CM
PLoS One **12**(12): e0189393. 2017.

Abstract: The invasion of the blacklegged tick, Ixodes scapularis into Ontario, Canada poses a significant risk to public health because it is a vector for numerous pathogens, including Borrelia burgdorferi sensu stricto, the causative agent of Lyme disease. Baseline field sampling in 2014 and 2015 detected I. scapularis and B. burgdorferi at sites across southern, eastern and central Ontario, including a hot spot in eastern Ontario. A "speed of spread" model for I. scapularis developed by Leighton and colleagues (2012) estimated that the tick's range was expanding northward at 46 km/year. In 2016, we revisited a subset of sites sampled in 2014 and 2015 to understand the changing nature of risk, and assess whether the rate of tick invasion is consistent with the speed of spread estimate. Ticks were collected via tick dragging at 17 out of 36 sites, 5 of which were new sites for I. scapularis. Samples were positive for B. burgdorferi at 8 sites. No other I. scapularis-borne pathogens were detected. Centrographic statistics revealed an increase in the dispersion of I. scapularis positive sites in eastern Ontario.

Field data for each site were then compared to the model's predicted year of establishment for each census subdivision. Our findings illustrate that the range expansion of I. scapularis and the emergence of B. burgdorferi is ongoing, and provide short timescale evidence of the processes associated with I. scapularis spread. The range front appears to be moving at a rate of ~46 km/year, with colonization of the tick behind this range front occurring at a slower and heterogeneous rate. Assessment of site-level ecological factors did not provide any insight into the underlying processes that may be influencing the colonization of I. scapularis in specific areas. Ongoing field sampling is needed to monitor this dynamic process. This study highlights the current geographic risk associated with Lyme disease, which can be used to target public health interventions to the areas of greatest risk.

15. **Invasive plant alters ability to predict disease vector distribution**.
Conley AK, Watling JI, Orrock JL
Ecol Appl **21**(2): 329-334. 2011.

Abstract: Risk models for vector-borne diseases rely on accurate quantification of the relationship between vector abundance and habitat, but this relationship can be obscured if habitats are modified by invasive species in ways that alter vector behavior but are undetectable in remotely sensed data. At a forest in eastern Missouri we assessed whether the presence of an invasive shrub, Amur honeysuckle, Lonicera maackii, affects oviposition by treehole mosquitoes, Aedes triseriatus, a primary vector of La Crosse virus in the United States. Oviposition significantly decreased with increasing density of L. maackii. Moreover, our results indicate that L. maackii may hinder the efficacy of models that use remotely sensed data to predict vector abundance: there was a strong relationship between landscape composition around plots and oviposition, but only in plots not invaded by L. maackii. Overlooking potentially important but cryptic effects of invasive plants on habitat selection by vectors may undermine accurate forecasting of disease risk.

16. **Climate change, biodiversity, ticks and tick-borne diseases: The butterfly effect**.
Dantas-Torres F
Int J Parasitol Parasites Wildl **4**(3): 452-461. 2015.

Abstract: We have killed wild animals for obtaining food and decimated forests for many reasons. Nowadays, we are burning fossil fuels as never before and even exploring petroleum in deep waters. The impact of these activities on our planet is now visible to the naked eye and the debate on climate change is warming up in scientific meetings and becoming a priority on the agenda of both scientists and policy decision makers. On the occasion of the Impact of Environmental Changes on Infectious Diseases (IECID) meeting, held in the 2015 in Sitges, Spain, I was invited to give a keynote talk on climate change, biodiversity, ticks and tick-borne diseases. The aim of the present article is to logically extend my rationale presented on the occasion of the IECID meeting. This article is not intended to be an exhaustive review, but an essay on climate change, biodiversity, ticks and tick-borne diseases. It may be anticipated that warmer winters and extended autumn and spring seasons will continue to drive the expansion of the distribution of some tick species (e.g., Ixodes ricinus) to northern latitudes and to higher altitudes. Nonetheless, further studies are advocated to improve our understanding of the complex interactions between landscape, climate, host communities (biodiversity), tick demography, pathogen diversity, human demography, human behaviour, economics, and politics, also considering all ecological processes (e.g., trophic cascades) and other possible interacting effects (e.g., mutual effects of increased greenhouse gas emissions and increased deforestation rates). The multitude of variables and interacting factors involved, and their complexity and dynamism, make tick-borne transmission systems beyond (current) human comprehension. That is, perhaps, the main reason for our inability to precisely predict new epidemics of vector-borne diseases in general.

17. **Seasonal and annual abundance of Amblyomma americanum (Acari: Ixodidae) in central Georgia**.
Davidson WR, Siefken DA, Creekmore LH
J Med Entomol **31**(1): 67-71. 1994.

Abstract: Seasonal and annual changes in the abundance of Amblyomma americanum (L.) larvae, nymphs, and adults were monitored over a 5-yr period in the Piedmont physiographic region of Georgia. Tick abundance was monitored with cloth drags (all life stages) and CO_2-baited cloth panels (nymphs and adults) monthly during March through September from 1987 through 1991. Larvae appeared in substantial numbers in July and were most numerous in August and September. Small numbers of unfed larvae apparently overwintered each year based on their presence during March, April, or May. Nymphs were most numerous from April through June and declined to much lower numbers by August and September. Adults were most numerous from March through May and virtually disappeared by August. These seasonal patterns were similar to those reported for A. americanum at other southeastern locations. Each life stage exhibited similar trends of annual abundance with an increase in 1988 followed by a relatively steady decline to levels equivalent to or below initial 1987 values by 1991. Major environmental variables that potentially could have influenced annual abundance were identified from Haile & Mount's (1987) computerized model of A. americanum population dynamics. Habitat type, host density, and day length were constants and rationally could be excluded as causes of annual variations in abundance; weather and host-finding rate were presumed to have been primarily responsible for these annual differences.

18. **Spatiotemporal patterns of host-seeking Ixodes scapularis nymphs (Acari: Ixodidae) in the United States**.

Diuk-Wasser MA, Gatewood AG, Cortinas MR, Yaremych-Hamer S, Tsao J, Kitron U, Hickling G, Brownstein JS, Walker E, Piesman J, Fish D
J Med Entomol **43**(2): 166-176. 2006.

Abstract: The risk of Lyme disease for humans in the eastern United States is dependent on the density of host-seeking Ixodes scapularis Say nymphal stage ticks infected with Borrelia burgdorferi. Although many local and regional studies have estimated Lyme disease risk using these parameters, this is the first large-scale study using a standardized methodology. Density of host-seeking I. scapularis nymphs was measured by drag sampling of closed canopy deciduous forest habitats in 95 locations spaced among 2 degrees quadrants covering the entire United States east of the 100th meridian. Sampling was done in five standardized transects at each site and repeated three to six times during the summer of 2004. The total number of adults and nymphs of the seven tick species collected was 17,972, with 1,405 nymphal I. scapularis collected in 31 of the 95 sites. Peak global spatial autocorrelation values were found at the smallest lag distance (300 km) and decreased significantly after 1,000 km. Local auto-correlation statistics identified two significant high-density clusters around endemic areas in the northeast and upper Midwest and a low-density cluster in sites south of the 39th parallel, where only 21 nymphs were collected. Peak nymphal host-seeking density occurred earlier in the southern than in the most northern sites. Spatiotemporal density patterns will be combined with Borrelia prevalence data as part of a 4-yr survey to generate a nationwide spatial risk model for I. scapularis-borne Borrelia, which will improve targeting of disease prevention efforts.

19. **Relatively low prevalence of Babesia microti and Anaplasma phagocytophilum in Ixodes scapularis ticks collected in the Lehigh Valley region of eastern Pennsylvania**.
Edwards MJ, Barbalato LA, Makkapati A, Pham KD, Bugbee LM
Ticks Tick Borne Dis **6**(6): 812-819. 2015.

Abstract: Several human pathogens are transmitted by the blacklegged tick, Ixodes scapularis. These include the spirochetes that cause Lyme disease (Borrelia burgdorferi) which is endemic to the Lehigh Valley region of eastern Pennsylvania. Emerging and currently rare tick-borne diseases have been of increasing concern in this region, including tick-borne relapsing fever (caused by Borrelia miyamotoi), human granulocytic anaplasmosis (caused by Anaplasma phagocytophilum), and human babesiosis (caused by Babesia microti). Real-time PCR assays and in some instances, conventional PCR followed by DNA sequencing, were used to screen 423 DNA samples that were prepared from questing adult and nymph stage I. scapularis ticks for infection with four tick-borne human pathogens. B. burgdorferi was detected in 23.2% of the sampled ticks, while B. miyamotoi, B. microti and a human variant of A. phagocytophilum were detected in less than 0.5% of the ticks. Our results are consistent with those expected in a region where Lyme disease is prevalent and human cases of tick-borne relapsing fever, babesiosis and human granulocytic anaplasmosis are not currently widespread. It is expected that this study will serve as a baseline for future studies of tick-borne pathogens in an area that is in close proximity to regions of high endemicity for Lyme disease, human granulocytic anaplasmosis and human babesiosis.

20. **Linkages of Weather and Climate With Ixodes scapularis and Ixodes pacificus (Acari: Ixodidae), Enzootic Transmission of Borrelia burgdorferi, and Lyme Disease in North America**.
Eisen RJ, Eisen L, Ogden NH, Beard CB
J Med Entomol **53**(2): 250-261. 2016.

Abstract: Lyme disease has increased both in incidence and geographic extent in the United States and Canada over the past two decades. One of the underlying causes is changes during the same time period in the distribution and abundance of the primary vectors: Ixodes scapularis Say and Ixodes pacificus Cooley and Kohls in eastern and western North America, respectively. Aside from short periods of time when they are feeding on hosts, these ticks exist in the environment where temperature and relative humidity directly affect their development, survival, and host-seeking behavior. Other important factors that strongly influence tick abundance as well as the proportion of ticks infected with the Lyme disease spirochete, Borrelia burgdorferi, include the abundance of hosts for the ticks and the capacity of tick hosts to serve as B. burgdorferi reservoirs. Here, we explore the linkages between climate variation and: 1) duration of the seasonal period and the timing of peak activity; 2) geographic tick distributions and local abundance; 3) enzootic B. burgdorferi transmission cycles; and 4) Lyme disease cases. We conclude that meteorological variables are most influential in determining host-seeking phenology and development, but, while remaining important cofactors, additional variables become critical when exploring geographic distribution and local abundance of ticks, enzootic transmission of B. burgdorferi, and Lyme disease case occurrence. Finally, we review climate change-driven projections for future impact on vector ticks and Lyme disease and discuss knowledge gaps and research needs.

21. **Deer browse resistant exotic-invasive understory: an indicator of elevated human risk of exposure to Ixodes scapularis (Acari: Ixodidae) in southern coastal Maine woodlands**.
Elias SP, Lubelczyk CB, Rand PW, Lacombe EH, Holman MS, Smith RP, Jr.
J Med Entomol **43**(6): 1142-1152. 2006.

Abstract: We evaluated the relationships between forest understory structure and the abundance of questing adult and nymphal blacklegged ticks, Ixodes scapularis Say (Acari:

Ixodidae), in three Maine towns endemic for Lyme disease, 2001-2003. In fragmented New England woodlands, over-abundant white-tailed deer, Odocoileus virginianus Zimmerman, overbrowse palatable species, allowing browse-resistant exotic-invasive species to replace native forest understory structures. We predicted there would be more ticks in plots dominated by exotic-invasive shrubs (such as Japanese barberry, Berberis thunbergii DC) than in plots dominated by native shrubs, ferns, or open understory. We assessed canopy composition and closure, tree basal area, litter composition, percentage of coverage and stem density of understory species, litter depth, soil moisture, and abundance of small mammals and white-tailed deer pellet groups. We used generalized linear mixed model analysis of covariance to determine the effect of understory structure on tick counts, controlling for continuous habitat and host covariates and adjusting for random spatial effects. There were twice as many adults and nearly twice as many nymphs in plots dominated by exotic-invasives than in plots dominated by native shrubs. Both adult and nymphal counts were lowest in open understory with coniferous litter. Adults were positively associated with increasing litter depth, medium soil moisture, and increasing abundance of white-footed deer mice, Peromyscus leucopus Rafinesque, and deer pellet group counts. Nymphs were positively associated with increasing litter depth, moderately wet soil, and mice. We concluded that deer browse-resistant exotic-invasive understory vegetation presented an elevated risk of human exposure to the vector tick of Lyme disease.

22. **The Influence of Prescribed Fire, Habitat, and Weather on Amblyomma americanum (Ixodida: Ixodidae) in West-Central Illinois, USA**.
Gilliam ME, Rechkemmer WT, McCravy KW, Jenkins SE
Insects **9**(2): E36. 2018.

Abstract: The distribution of Amblyomma americanum (L.) is changing and reports of tick-borne disease transmitted by A. americanum are increasing in the USA. We used flagging to collect ticks, surveyed vegetation and collected weather data in 2015 and 2016. A. americanum dominated collections in both years (97%). Ticks did not differ among burn treatments; however, tick abundance differed between years among total, adult, and larval ticks. Habitat variables showed a weak negative correlation to total ticks in respect to: Shannon diversity index, percent bare ground, perennial cover, and coarse woody debris. Nymphal ticks showed a weak negative correlation to percent bare ground and fewer adults were collected in areas with more leaf litter and coarse woody debris. Conversely, we found larvae more often in areas with more total cover, biennials, vines, shrubs, and leaf litter, suggesting habitat is important for this life stage. We compared weather variables to tick presence and found, in 2015, temperature, precipitation, humidity, and sample period influenced tick collection and were life stage specific. In 2016, temperature, precipitation, humidity, wind, and sample period influenced tick collection and were also life stage specific. These results indicate that spring burns in an oak woodland do not reduce ticks; other variables such as habitat and weather are more influential on tick abundance or presence at different life stages.

23. **The phenology of ticks and the effects of long-term prescribed burning on tick population dynamics in southwestern Georgia and northwestern Florida**.
Gleim ER, Conner LM, Berghaus RD, Levin ML, Zemtsova GE, Yabsley MJ
PLoS One **9**(11): e112174. 2014.

Abstract: Some tick populations have increased dramatically in the past several decades leading to an increase in the incidence and emergence of tick-borne diseases. Management strategies that can effectively reduce tick populations while better understanding regional tick phenology is needed. One promising management strategy is prescribed burning. However, the efficacy of prescribed burning as a mechanism for tick control is unclear because past studies have provided conflicting data, likely due to a failure of some studies to simulate operational management scenarios and/or account for other predictors of tick abundance. Therefore, our study was conducted to increase knowledge of tick population dynamics relative to long-term prescribed fire management. Furthermore, we targeted a region, southwestern Georgia and northwestern Florida (USA), in which little is known regarding tick dynamics so that basic phenology could be determined. Twenty-one plots with varying burn regimes (burned surrounded by burned [BB], burned surrounded by unburned [BUB], unburned surrounded by burned [UBB], and unburned surrounded by unburned [UBUB]) were sampled monthly for two years while simultaneously collecting data on variables that can affect tick abundance (e.g., host abundance, vegetation structure, and micro- and macro-climatic conditions). In total, 47,185 ticks were collected, of which, 99% were Amblyomma americanum, 0.7% were Ixodes scapularis, and fewer numbers of Amblyomma maculatum, Ixodes brunneus, and Dermacentor variabilis. Monthly seasonality trends were similar between 2010 and 2011. Long-term prescribed burning consistently and significantly reduced tick counts (overall and specifically for A. americanum and I. scapularis) regardless of the burn regimes and variables evaluated. Tick species composition varied according to burn regime with A. americanum dominating at UBUB, A. maculatum at BB, I. scapularis at UBB, and a more even composition at BUB. These data indicate that regular prescribed burning is an effective tool for reducing tick populations and ultimately may reduce risk of tick-borne disease.

24. **The effectiveness of permethrin-treated deer stations for control of the Lyme disease vector Ixodes scapularis on Cape Cod and the islands: a five-year experiment**.
Grear JS, Koethe R, Hoskins B, Hillger R, Dapsis L, Pongsiri M
Parasit Vectors **7**: 292. 2014.

Abstract: BACKGROUND: The use of animal host-targeted pesticide application to control blacklegged ticks,

which transmit the Lyme disease bacterium between wildlife hosts and humans, is receiving increased attention as an approach to Lyme disease risk management. Included among the attractive features of host-targeted approaches is the reduced need for broad-scale pesticide usage. In the eastern USA, one of the best-known of these approaches is the corn-baited "4-poster" deer feeding station, so named because of the four pesticide-treated rollers that surround the bait troughs. Wildlife visitors to these devices receive an automatic topical application of acaricide, which kills attached ticks before they can reproduce. We conducted a 5-year controlled experiment to estimate the effects of 4-poster stations on tick populations in southeastern Massachusetts, where the incidence of Lyme disease is among the highest in the USA. METHODS: We deployed a total of forty-two 4-posters among seven treatment sites and sampled for nymph and adult ticks at these sites and at seven untreated control sites during each year of the study. Study sites were distributed among Cape Cod, Martha's Vineyard, and Nantucket. The density of 4-poster deployment was lower than in previous 4-poster studies and resembled or possibly exceeded the levels of effort considered by county experts to be feasible for Lyme disease risk managers. RESULTS: Relative to controls, blacklegged tick abundance at treated sites was reduced by approximately 8.4%, which is considerably less than in previous 4-poster studies. CONCLUSIONS: In addition to the longer duration and greater replication in our study compared to others, possible but still incomplete explanations for the smaller impact we observed include the lower density of 4-poster deployment as well as landscape and mammalian community characteristics that may complicate the ecological relationship between white-tailed deer and blacklegged tick populations.

25. **Predicting the risk of Lyme disease: habitat suitability for Ixodes scapularis in the north central United States**.
Guerra M, Walker E, Jones C, Paskewitz S, Cortinas MR, Stancil A, Beck L, Bobo M, Kitron U
Emerg Infect Dis **8**(3): 289-297. 2002.

Abstract: The distribution and abundance of Ixodes scapularis were studied in Wisconsin, northern Illinois, and portions of the Upper Peninsula of Michigan by inspecting small mammals for ticks and by collecting questing ticks at 138 locations in state parks and natural areas. Environmental data were gathered at a local level (i.e., micro and meso levels), and a geographic information system (GIS) was used with several digitized coverages of environmental data to create a habitat profile for each site and a grid map for Wisconsin and Illinois. Results showed that the presence and abundance of I. scapularis varied, even when the host population was adequate. Tick presence was positively associated with deciduous, dry to mesic forests and alfisol-type soils of sandy or loam-sand textures overlying sedimentary rock. Tick absence was associated with grasslands, conifer forests, wet to wet/mesic forests, acidic soils of low fertility and a clay soil texture, and Precambrian bedrock. We performed a discriminant analysis to determine environmental differences between positive and negative tick sites and derived a regression equation to examine the probability of I. scapularis presence per grid. Both analyses indicated that soil order and land cover were the dominant contributors to tick presence. We then constructed a risk map indicating suitable habitats within areas where I. scapularis is already established. The risk map also shows areas of high probability the tick will become established if introduced. Thus, this risk analysis has both explanatory power and predictive capability.

26. **Ecological factors characterizing the prevalence of bacterial tick-borne pathogens in Ixodes ricinus ticks in pastures and woodlands**.
Halos L, Bord S, Cotte V, Gasqui P, Abrial D, Barnouin J, Boulouis HJ, Vayssier-Taussat M, Vourc'h G
Appl Environ Microbiol **76**(13): 4413-4420. 2010.

Abstract: Ecological changes are recognized as an important driver behind the emergence of infectious diseases. The prevalence of infection in ticks depends upon ecological factors that are rarely taken into account simultaneously. Our objective was to investigate the influences of forest fragmentation, vegetation, adult tick hosts, and habitat on the infection prevalence of three tick-borne bacteria, Borrelia burgdorferi sensu lato, Anaplasma phagocytophilum, and Rickettsia sp. of the spotted fever group, in questing Ixodes ricinus ticks, taking into account tick characteristics. Samples of questing nymphs and adults were taken from 61 pastures and neighboring woodlands in central France. The ticks were tested by PCR of pools of nymphs and individual adults. The individual infection prevalence was modeled using multivariate regression. The highest infection prevalences were found in adult females collected in woodland sites for B. burgdorferi sensu lato and A. phagocytophilum (16.1% and 10.7%, respectively) and in pasture sites for Rickettsia sp. (8.7%). The infection prevalence in nymphs was lower than 6%. B. burgdorferi sensu lato was more prevalent in woodlands than in pastures. Forest fragmentation favored B. burgdorferi sensu lato and A. phagocytophilum prevalence in woodlands, and in pastures, the B. burgdorferi sensu lato prevalence was favored by shrubby vegetation. Both results are probably because large amounts of edges or shrubs increase the abundance of small vertebrates as reservoir hosts. The Rickettsia sp. prevalence was maximal on pasture with medium forest fragmentation. Female ticks were more infected by B. burgdorferi sensu lato than males and nymphs in woodland sites, which suggests an interaction between the ticks and the bacteria. This study confirms the complexity of the tick-borne pathogen ecology. The findings support the importance of small vertebrates as reservoir hosts and make a case for further studies in Europe on the link between the composition of the reservoir host community and the infection prevalence in ticks.

27. **Increased diversity of zoonotic pathogens and Borrelia burgdorferi strains in established versus incipient Ixodes scapularis populations across the Midwestern United States**.
Hamer SA, Hickling GJ, Walker ED, Tsao JI
Infect Genet Evol **27**: 531-542. 2014.

Abstract: The center of origin theory predicts that genetic diversity will be greatest near a specie's geographic origin because of the length of time for evolution. By corollary, diversity will decrease with distance from the origin; furthermore, invasion and colonization are frequently associated with founder effects that reduce genetic variation in incipient populations. The blacklegged tick, Ixodes scapularis, harbors a suite of zoonotic pathogens, and the geographic range of the tick is expanding in the upper Midwestern United States. Therefore, we posited that diversity of I. scapularis-borne pathogens across its Midwestern range should correlate with the rate of the range expansion of this tick as well as subsequent disease emergence. Analysis of 1565 adult I. scapularis ticks from 13 sites across five Midwestern states revealed that tick infection prevalence with multiple microbial agents (Borrelia burgdorferi, Borrelia miyamotoi, Babesia odocoilei, Babesia microti, and Anaplasma phagocytophilum), coinfections, and molecular genetic diversity of B. burgdorferi all were positively correlated with the duration of establishment of tick populations, and therefore generally support the center of origin - pathogen diversity hypothesis. The observed differences across the gradient of establishment, however, were not strong and were nuanced by the high frequency of coinfections in tick populations at both established and recently-invaded tick populations. These results suggest that the invasion of ticks and their associated pathogens likely involve multiple means of pathogen introduction, rather than the conventionally presented scenario whereby infected, invading ticks are solely responsible for introducing pathogens to naive host populations.

28. **Relationship between invasive plant species and forest fauna in eastern North America**.
Hayes SJ, Holzmueller EJ
Forests **3**(3): 840-852. 2012.

Abstract: Invasive plant species have long been known to cause extensive damage, both economically and ecologically, to native ecosystems. They have historically been introduced by the public, both intentional and not, for a variety of reasons. Many of the woody shrubs, such as Lonicera maackii and Rosa multiflora were introduced for wildlife cover, forage, and ornamental value. These invasives have quickly out-competed native flora, in many cases drastically impacting and changing the environment they inhabit. In this review, chosen species characteristics have been described, their pathway to invasion explained, and their impacts to native wildlife highlighted. Based on a review of the scientific literature, we determined that not all effects by invasive plants are negative. Many positive impacts can be seen throughout the literature, such as native frogs utilizing Microstegium vimineum for cover and nesting habitat. However, some important invasive plant species were not included in this review due to a lack of literature on the subject of the effects on fauna. While much is known about their economic impact and the impact on native plant species, additional work needs to be done in the field of wildlife research to determine current impacts and future implications of non-native, invasive plants on native fauna.

29. **Effects of tick control by acaricide self-treatment of white-tailed deer on host-seeking tick infection prevalence and entomologic risk for Ixodes scapularis-borne pathogens**.
Hoen AG, Rollend LG, Papero MA, Carroll JF, Daniels TJ, Mather TN, Schulze TL, Stafford KC, 3rd, Fish D
Vector Borne Zoonotic Dis **9**(4): 431-438. 2009.

Abstract: We evaluated the effects of tick control by acaricide self-treatment of white-tailed deer on the infection prevalence and entomologic risk for three Ixodes scapularis-borne bacteria in host-seeking ticks. Ticks were collected from vegetation in areas treated with the "4-Poster" device and from control areas over a 6-year period in five geographically diverse study locations in the Northeastern United States and tested for infection with two known agents of human disease, Borrelia burgdorferi and Anaplasma phagocytophilum, and for a novel relapsing fever-group spirochete related to Borrelia miyamotoi. Overall, 38.2% of adults and 12.5% of nymphs were infected with B. burgdorferi; 8.5% of adults and 4.2% of nymphs were infected with A. phagocytophilum; and 1.9% of adults and 0.8% of nymphs were infected with B. miyamotoi. In most cases, treatment with the 4-Poster device was not associated with changes in the prevalence of infection with any of these three microorganisms among nymphal or adult ticks. However, the density of nymphs infected with B. burgdorferi, and consequently the entomologic risk for Lyme disease, was reduced overall by 68% in treated areas compared to control areas among the five study sites at the end of the study. The frequency of bacterial coinfections in ticks was generally equal to the product of the proportion of ticks infected with a single bacterium, indicating that enzootic maintenance of these pathogens is independent. We conclude that controlling ticks on deer by self-application of acaricide results in an overall decrease in the human risk for exposure to these three bacterial agents, which is due solely to a reduction in tick density.

30. **Prevalence Rates of Borrelia burgdorferi (Spirochaetales: Spirochaetaceae), Anaplasma phagocytophilum (Rickettsiales: Anaplasmataceae), and Babesia microti (Piroplasmida: Babesiidae) in Host-Seeking Ixodes scapularis (Acari: Ixodidae) from Pennsylvania**.

Hutchinson ML, Strohecker MD, Simmons TW, Kyle AD, Helwig MW
J Med Entomol **52**(4): 693-698. 2015.

Abstract: The etiological agents responsible for Lyme disease (Borrelia burgdorferi), human granulocytic anaplasmosis (Anaplasma phagocytophilum), and babesiosis (Babesia microti) are primarily transmitted by the blacklegged tick, Ixodes scapularis Say. Despite Pennsylvania having in recent years reported the highest number of Lyme disease cases in the United States, relatively little is known regarding the geographic distribution of the vector and its pathogens in the state. Previous attempts at climate-based predictive modeling of I. scapularis occurrence have not coincided with the high human incidence rates in parts of the state. To elucidate the distribution and pathogen infection rates of I. scapularis, we collected and tested 1,855 adult ticks statewide from 2012 to 2014. The presence of I. scapularis and B. burgdorferi was confirmed from all 67 Pennsylvania counties. Analyses were performed on 1,363 ticks collected in the fall of 2013 to avoid temporal bias across years. Infection rates were highest for B. burgdorferi (47.4%), followed by Ba. microti (3.5%) and A. phagocytophilum (3.3%). Coinfections included B. burgdorferi+Ba. microti (2.0%), B. burgdorferi+A. phagocytophilum (1.5%) and one tick positive for A. phagocytophilum+Ba. microti. Infection rates for B. burgdorferi were lower in the western region of the state. Our findings substantiate that Lyme disease risk is high throughout Pennsylvania.

31. **Habitat Suitability Model for the Distribution of Ixodes scapularis (Acari: Ixodidae) in Minnesota**.
Johnson TL, Bjork JK, Neitzel DF, Dorr FM, Schiffman EK, Eisen RJ
J Med Entomol **53**(3): 598-606. 2016.

Abstract: Ixodes scapularis Say, the black-legged tick, is the primary vector in the eastern United States of several pathogens causing human diseases including Lyme disease, anaplasmosis, and babesiosis. Over the past two decades, I. scapularis-borne diseases have increased in incidence as well as geographic distribution. Lyme disease exists in two major foci in the United States, one encompassing northeastern states and the other in the Upper Midwest. Minnesota represents a state with an appreciable increase in counties reporting I. scapularis-borne illnesses, suggesting geographic expansion of vector populations in recent years. Recent tick distribution records support this assumption. Here, we used those records to create a fine resolution, subcounty-level distribution model for I. scapularis using variable response curves in addition to tests of variable importance. The model identified 19% of Minnesota as potentially suitable for establishment of the tick and indicated with high accuracy (AUC = 0.863) that the distribution is driven by land cover type, summer precipitation, maximum summer temperatures, and annual temperature variation. We provide updated records of established populations near the northwestern species range limit and present a model that increases our understanding of the potential distribution of I. scapularis in Minnesota.

32. **Effects of reduced deer density on the abundance of Ixodes scapularis (Acari: Ixodidae) and Lyme disease incidence in a northern New Jersey endemic area**.
Jordan RA, Schulze TL, Jahn MB
J Med Entomol **44**(5): 752-757. 2007.

Abstract: We monitored the abundance of Ixodes scapularis Say (Acari: Ixodidae) and the Lyme disease incidence rate after the incremental removal of white-tailed deer, Odocoileus virginianus Zimmermann, within a suburban residential area to determine whether there was a measurable decrease in the abundance of ticks due to deer removal and whether the reduction in ticks resulted in a reduction in the incidence rate within the human population. After three seasons, the estimated deer population was reduced by 46.7%, from the 2002 postfawning estimate of 2,899 deer (45.6 deer per km2) to a 2005 estimate of 1,540 deer (24.3 deer per km2). There was no apparent effect of the deer culling program on numbers of questing I. scapularis subadults in the culling areas, and the overall numbers of host-seeking ticks in the culling areas seemed to increase in the second year of the program. The Lyme disease incidence rate generated by both passive and active surveillance systems showed no clear trend among years, and it did not seem to vary with declining deer density. Given the resources required to mount and maintain a community-based program of sufficient magnitude to effectively reduce vector tick density in ecologically open situations where there are few impediments to deer movement, it may be that deer reduction, although serving other community goals, is unlikely to be a primary means of tick control by itself. However, in concert with other tick control interventions, such programs may provide one aspect of a successful community effort to reduce the abundance of vector ticks.

33. **Hosts as ecological traps for the vector of Lyme disease**.
Keesing F, Brunner J, Duerr S, Killilea M, Logiudice K, Schmidt K, Vuong H, Ostfeld RS
Proc Biol Sci **276**(1675): 3911-3919. 2009.

Abstract: Vectors of infectious diseases are generally thought to be regulated by abiotic conditions such as climate or the availability of specific hosts or habitats. In this study we tested whether blacklegged ticks, the vectors of Lyme disease, granulocytic anaplasmosis and babesiosis can be regulated by the species of vertebrate hosts on which they obligately feed. By subjecting field-caught hosts to parasitism by larval blacklegged ticks, we found that some host species (e.g. opossums, squirrels) that are abundantly parasitized in nature kill 83-96% of the ticks that attempt to attach and feed, while other species are more permissive of tick feeding. Given natural tick burdens we document on these hosts, we show that some hosts can kill thousands of ticks per hectare. These results indicate that the abundance of tick vectors can be regulated by the identity of the hosts

upon which these vectors feed. By simulating the removal of hosts from intact communities using empirical models, we show that the loss of biodiversity may exacerbate disease risk by increasing both vector numbers and vector infection rates with a zoonotic pathogen.

34. **Geographical and environmental factors driving the increase in the Lyme disease vector Ixodes scapularis**.
Khatchikian CE, Prusinski M, Stone M, Backenson PB, Wang IN, Levy MZ, Brisson D
Ecosphere **3**(10): art85. 2012.

Abstract: The population densities of many organisms have changed dramatically in recent history. Increases in the population density of medically relevant organisms are of particular importance to public health as they are often correlated with the emergence of infectious diseases in human populations. Our aim is to delineate increases in density of a common disease vector in North America, the blacklegged tick, and to identify the environmental factors correlated with these population dynamics. Empirical data that capture the growth of a population are often necessary to identify environmental factors associated with these dynamics. We analyzed temporally- and spatially-structured field collected data in a geographical information systems framework to describe the population growth of blacklegged ticks (Ixodes scapularis) and to identify environmental and climatic factors correlated with these dynamics. The density of the ticks increased throughout the study's temporal and spatial ranges. Tick density increases were positively correlated with mild temperatures, low precipitation, low forest cover, and high urbanization. Importantly, models that accounted for these environmental factors accurately forecast future tick densities across the region. Tick density increased annually along the south-to-north gradient. These trends parallel the increases in human incidences of diseases commonly vectored by I. scapularis. For example, I. scapularis densities are correlated with human Lyme disease incidence, albeit in a non-linear manner that disappears at low tick densities, potentially indicating that a threshold tick density is needed to support epidemiologically-relevant levels of the Lyme disease bacterium. Our results demonstrate a connection between the biogeography of this species and public health.

35. **The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community**.
Kilpatrick HJ, LaBonte AM, Stafford KC
J Med Entomol **51**(4): 777-784. 2014.

Abstract: White-tailed deer (Odocoileus virginianus Zimmerman), serve as the primary host for the adult blacklegged tick (Ixodes scapularis Say), the vector for Lyme disease, human babesiosis, and human granulocytic anaplasmosis. Our objective was to evaluate the degree of association between deer density, tick abundance, and human cases of Lyme disease in one Connecticut community over a 13-yr period. We surveyed 90-98% of all permanent residents in the community six times from 1995 to 2008 to document resident's exposure to tick-related disease and frequency and abundance of deer observations. After hunts were initiated, number and frequency of deer observations in the community were greatly reduced as were resident-reported cases of Lyme disease. Number of resident-reported cases of Lyme disease per 100 households was strongly correlated to deer density in the community. Reducing deer density to 5.1 deer per square kilometer resulted in a 76% reduction in tick abundance, 70% reduction in the entomological risk index, and 80% reduction in resident-reported cases of Lyme disease in the community from before to after a hunt was initiated.

36. **Prevalence of Borrelia burgdorferi and Anaplasma phagocytophilum in Ixodes scapularis (Acari: Ixodidae) nymphs collected in managed red pine forests in Wisconsin**.
Lee X, Coyle DR, Johnson DK, Murphy MW, McGeehin MA, Murphy RJ, Raffa KF, Paskewitz SM
J Med Entomol **51**(3): 694-701. 2014.

Abstract: Changes in the structure of managed red pine forests in Wisconsin caused by interacting root- and stem-colonizing insects are associated with increased abundance of the blacklegged tick, Ixodes scapularis Say, in comparison with nonimpacted stands. However, the frequency and variability of the occurrence of tick-borne pathogens in this coniferous forest type across Wisconsin is unknown. Red pine forests were surveyed from 2009 to 2013 to determine the prevalence of Borrelia burgdorferi and Anaplasma phagocytophilum in questing I. scapularis nymphs. Polymerase chain reaction analysis revealed geographical differences in the nymphal infection prevalence (NIP) of these pathogens in red pine forests. In the Kettle Moraine State Forest (KMSF) in southeastern Wisconsin, NIP of B. burgdorferi across all years was 35% (range of 14.5-53.0%). At the Black River State Forest (BRSF) in western Wisconsin, NIP of B. burgdorferi across all years was 26% (range of 10.9-35.5%). Differences in NIP of B. burgdorferi between KMSF and BRSF were statistically significant for 2010 and 2011 and for all years combined ($P < 0.05$). NIP of A. phagocytophilum (human agent) averaged 9% (range of 4.6-15.8%) at kmsf and 3% (range of 0-6.4%) at BRSF, and was significantly different between the sites for all years combined ($P < 0.05$). Differences in coinfection of B. burgdorferi and A. phagocytophilum were not statistically significant between KMSF and BRSF, with an average of 3.4% (range of 1.7-10.5%) and 2.5% (range of 0-5.5%), respectively. In 2013, the density of infected nymphs in KMSF and BRSF was 14 and 30 per 1000m2, respectively, among the highest ever recorded for the state. Differences in the density of nymphs and NIP among sites were neither correlated with environmental factors nor time since tick colonization. These results document significant unexplained variation in tick-borne pathogens between coniferous forests in Wisconsin that warrants further study.

37. **Changing distributions of ticks: causes and consequences**.
Leger E, Vourc'h G, Vial L, Chevillon C, McCoy KD
Exp Appl Acarol **59**(1-2): 219-244. 2013.

Abstract: Today, we are witnessing changes in the spatial distribution and abundance of many species, including ticks and their associated pathogens. Evidence that these changes are primarily due to climate change, habitat modifications, and the globalisation of human activities are accumulating. Changes in the distribution of ticks and their invasion into new regions can have numerous consequences including modifications in their ecological characteristics and those of endemic species, impacts on the dynamics of local host populations and the emergence of human and livestock disease. Here, we review the principal causes for distributional shifts in tick populations and their consequences in terms of the ecological attributes of the species in question (i.e. phenotypic and genetic responses), pathogen transmission and disease epidemiology. We also describe different methodological approaches currently used to assess and predict such changes and their consequences. We finish with a discussion of new research avenues to develop in order to improve our understanding of these host-vector-pathogen interactions in the context of a changing world.

38. **Invasive plants as catalysts for the spread of human parasites**.
Mack RN, Smith MC
NeoBiota **9**: 13-29. 2011.

Abstract: To a degree not widely recognized, some naturalized and invasive plants increase the risks to human health by enhancing the proliferation of vectors of virulent human parasites. These potential risks are restricted by neither ecosystem nor geography. The dense, floating mats of the tropical South American invasive macrophyte Eichhornia crassipes (water hyacinth) creates habitat for larvae of the dipteran vectors of Plasmodium spp., the causative agents of malaria, and other parasites. In Africa, the South American shrub Lantana camara (lantana) provides suitable habitat in otherwise treeless areas for dipteran vectors (Glossina spp.) of protozoans (Trypanosoma spp.) that cause trypanosomiasis. In the eastern United States, proliferation of the invasive Berberis thunbergii provides questing sites for the blacklegged ticks that carry the spirochete Borrelia burgdorferi, the causative agent of Lyme disease. Unanticipated health consequences will likely continue to emerge from new plant introductions. Hantaviruses are rodent-borne parasites that cause lethal hemorrhagic fevers in humans. Populations of rodent Hantavirus vectors in South America increase rapidly in response to fruit availability among masting, native bamboos. In the United States the omnivorous deer mouse Peromyscus maniculatus also carries Hantavirus (Sin Nombre Virus). The on-going escape of Asian frost-tolerant bamboos from cultivation raises the possibility of their becoming invaders - several have already become naturalized - and in turn providing a temporary food source for populations of infected native rodents. Proposed introductions of floating aquatic vascular species, species with masting reproduction and species that could occupy an unfilled niche in a new range deserve careful evaluation as catalysts of unintended species interactions, especially of human parasites.

39. **Positive effects of an invasive shrub on aggregation and abundance of a native small rodent**.
Malo AF, Godsall B, Prebble C, Grange Z, McCandless S, Taylor A, Coulson T
Behav Ecol **24**(3): 759-767. 2013.

Abstract: Invasive plants can have dramatic effects on natural ecosystems. It is unclear, though, whether these will have a positive or negative effect on animal species' behavior and population parameters within ecosystems where invasive plants occur. Here, we use a 2-year time series of mouse trapping data to test the effects of an evergreen invasive shrub, Rhododendron ponticum, on population distribution and abundance in a population of wood mice (Apodemus sylvaticus) in southern England. Given the importance of aerial predators on rodent survival and the shield that the thick cover of Rhododendron branches and leaves provides, we predicted that Rhododendron would have a positive effect on mouse aggregation and abundance. The results confirmed both predictions: proximity to Rhododendron positively influenced mouse abundance, whereas a significant interaction between protective microhabitat features (logs) and Rhododendron suggest that reductions in predation risk drive the proximity results. In addition, as mouse densities increased, competition increased. During spring, when mouse territoriality was greatest, we found primarily large adults in the Rhododendron habitat, with subadult and juvenile mice more likely to be found away from Rhododendron patches. The effects of Rhododendron-driven increases in mouse density on lower (seed predation and dispersal) and upper trophic level (weasel populations) are also discussed. Questing tick's density and invertebrate biomass were also lower under Rhododendron. Our research shows that an invasive plant species can increase the abundance of a native mammal and that this could potentially lead to increases/decreases in other species populations within the community.

40. **Which forest bird species are the main hosts of the tick, Ixodes ricinus, the vector of Borrelia burgdorferi sensu lato, during the breeding season?**
Marsot M, Henry PY, Vourc'h G, Gasqui P, Ferquel E, Laignel J, Grysan M, Chapuis JL
Int J Parasitol **42**(8): 781-788. 2012.

Abstract: Wild birds are important hosts for vector-borne pathogens, especially those borne by ticks. However, few studies have been conducted on the role of different bird species within a community as hosts of vector-borne pathogens. This study addressed individual and species factors that could explain the burden of Ixodes ricinus on forest birds during the reproductive periods of both vectors and

hosts. The goal was to identify which bird species contribute the most to the tick population at the community level. Birds were mist-netted on four plots in 2008 and on seven plots in 2009 in two forests (Senart and Notre Dame, near Paris, France). The dependence of the tick load per bird upon environmental conditions (questing nymph density, year and plot) and on host species traits (species, age, sex, body size, vertical space use, level of innate and acquired immunity) was analysed. Finally, the relative contribution of each bird species to the local dynamics of ticks was estimated, while accounting for their respective abundance. Tick burden differed markedly between bird species and varied according to questing nymph density. Bird species with a high body mass, those that forage low in the vegetation, and those that had a high innate immune response and a high spleen mass were more likely to have a high tick burden. Four species (the Common Blackbird, Turdus merula, the European Robin, Erithacus rubecula, the Song Thrush, Turdus philomelos, and the Winter Wren, Troglodytes troglodytes) hosted more than 90% of the ticks in the local bird community. These species, and particularly T. merula which was host to a high proportion of the nymphs, are likely to contribute significantly to the circulation of pathogens for which they are competent, such as the agent of Lyme borreliosis.

41. **Driving forces for changes in geographical distribution of Ixodes ricinus ticks in Europe**.
Medlock JM, Hansford KM, Bormane A, Derdakova M, Estrada-Pena A, George JC, Golovljova I, Jaenson TG, Jensen JK, Jensen PM, Kazimirova M, Oteo JA, Papa A, Pfister K, Plantard O, Randolph SE, Rizzoli A, Santos-Silva MM, Sprong H, Vial L, Hendrickx G, Zeller H, Van Bortel W
Parasit Vectors **6**: 1. 2013.

Abstract: Many factors are involved in determining the latitudinal and altitudinal spread of the important tick vector Ixodes ricinus (Acari: Ixodidae) in Europe, as well as in changes in the distribution within its prior endemic zones. This paper builds on published literature and unpublished expert opinion from the VBORNET network with the aim of reviewing the evidence for these changes in Europe and discusses the many climatic, ecological, landscape and anthropogenic drivers. These can be divided into those directly related to climatic change, contributing to an expansion in the tick's geographic range at extremes of altitude in central Europe, and at extremes of latitude in Scandinavia; those related to changes in the distribution of tick hosts, particularly roe deer and other cervids; other ecological changes such as habitat connectivity and changes in land management; and finally, anthropogenically induced changes. These factors are strongly interlinked and often not well quantified. Although a change in climate plays an important role in certain geographic regions, for much of Europe it is non-climatic factors that are becoming increasingly important. How we manage habitats on a landscape scale, and the changes in the distribution and abundance of tick hosts are important considerations during our assessment and management of the public health risks associated with ticks and tick-borne disease issues in 21(st) century Europe. Better understanding and mapping of the spread of I. ricinus (and changes in its abundance) is, however, essential to assess the risk of the spread of infections transmitted by this vector species. Enhanced tick surveillance with harmonized approaches for comparison of data enabling the follow-up of trends at EU level will improve the messages on risk related to tick-borne diseases to policy makers, other stake holders and to the general public.

42. **Highly variable acquisition rates of Ixodes scapularis (Acari: Ixodidae) by birds on an Atlantic barrier island**.
Mitra SS, Buckley PA, Buckley FG, Ginsberg HS
J Med Entomol **47**(6): 1019-1027. 2010.

Abstract: Acquisition of ticks by bird hosts is a central process in the transmission cycles of many tick-borne zoonoses, but tick recruitment by birds has received little direct study. We documented acquisition of Ixodes scapularis Say on birds at Fire Island, NY, by removing ticks from mist-netted birds, and recording the number of ticks on birds recaptured within 4 d of release. Eight bird species acquired at least 0.8 ticks bird(-1) day(-1) during the seasonal peak for at least one age class of I. scapularis. Gray Catbirds, Eastern Towhees, Common Yellowthroats, and Northern Waterthrushes collectively accounted for 83% of all tick acquisitions; and six individuals apportioned among Black-billed Cuckoo, Gray Catbird, Eastern Towhee, and Common Yellowthroat were simultaneously infested with both larvae and nymphs. Bird species with the highest acquisition rates were generally ground foragers, whereas birds that did not acquire ticks in our samples generally foraged above the ground. Tick acquisition by birds did not differ between deciduous and coniferous forests. Among the 15 bird species with the highest recruitment rates, acquisition of nymphs was not correlated with acquisition of larvae. Tick acquisition rates by individual bird species were not correlated with the reservoir competence of those species for Lyme borreliae. However, birds with high tick acquisition rates can contribute large numbers of infected ticks, and thus help maintain the enzootic cycle, even if their levels of reservoir competence are relatively low.

43. **Population and Evolutionary Genomics of Amblyomma americanum, an Expanding Arthropod Disease Vector**.
Monzon JD, Atkinson EG, Henn BM, Benach JL
Genome Biol Evol **8**(5): 1351-1360. 2016.

Abstract: The lone star tick, Amblyomma americanum, is an important disease vector and the most frequent tick found attached to humans in the eastern United States. The lone star tick has recently experienced a rapid range expansion into the Northeast and Midwest, but despite this emerging infectious threat to wildlife, livestock, and human health, little is known about the genetic causes and consequences of the geographic expansion. In the first population genomic analysis of any tick species, we characterize the genetic diversity and population structure of A. americanum across its current geographic range, which has recently expanded. Using a high-throughput genotyping-by-sequencing approach, we discovered more than 8,000 single nucleotide polymorphisms in 90 ticks from five locations. Surprisingly, newly established populations in New York (NY) and Oklahoma (OK) are as diverse as historic range populations in North and South Carolina. However, substantial population structure occurs among regions, such that new populations in NY and OK are genetically distinct from historic range populations and from one another. Ticks from a laboratory colony are genetically distinct from wild populations, underscoring the need to account for natural variation when conducting transmission or immunological studies, many of which utilize laboratory-reared ticks. An FST-outlier analysis comparing a recently established population to a long-standing population detected numerous outlier sites, compatible with positive and balancing selection, highlighting the potential for adaptation during the range expansion. This study provides a framework for applying high-throughput DNA sequencing technologies for future investigations of ticks, which are common vectors of diseases.

44. **Comparative population genetics of two invading ticks: Evidence of the ecological mechanisms underlying tick range expansions**.
Nadolny R, Gaff H, Carlsson J, Gauthier D
Infect Genet Evol **35**: 153-162. 2015.

Abstract: Two species of ixodid tick, Ixodes affinis Neumann and Amblyomma maculatum Koch, are simultaneously expanding their ranges throughout the mid-Atlantic region of the US. Although we have some understanding of the ecology and life history of these species, the ecological mechanisms governing where and how new populations establish and persist are unclear. To assess population connectivity and ancestry, we sequenced a fragment of the 16S mitochondrial rRNA gene from a representative sample of individuals of both species from populations throughout the eastern US. We found that despite overlapping host preferences throughout ontogeny, each species exhibited very different genetic and geographic patterns of population establishment and connectivity. I. affinis was of two distinct mitochondrial clades, with a clear geographic break separating northern and southern populations. Both I. affinis populations showed evidence of recent expansion, although the southern population was more genetically diverse, indicating a longer history of establishment. A. maculatum exhibited diverse haplotypes that showed no significant relationship with geographic patterns and little apparent connectivity between sites. Heteroplasmy was also observed in the 16S mitochondrial rRNA gene in 3.5% of A. maculatum individuals. Genetic evidence suggests that these species rely on different key life stages to successfully disperse into novel environments, and that host vagility, habitat stability and habitat connectivity all play critical roles in the establishment of new tick populations.

45. **Population-based passive tick surveillance and detection of expanding foci of blacklegged ticks Ixodes scapularis and the Lyme disease agent Borrelia burgdorferi in Ontario, Canada**.
Nelder MP, Russell C, Lindsay LR, Dhar B, Patel SN, Johnson S, Moore S, Kristjanson E, Li Y, Ralevski F
PLoS One **9**(8): e105358. 2014.

Abstract: We identified ticks submitted by the public from 2008 through 2012 in Ontario, Canada, and tested blacklegged ticks Ixodes scapularis for Borrelia burgdorferi and Anaplasma phagocytophilum. Among the 18 species of ticks identified, I. scapularis, Dermacentor variabilis, Ixodes cookei and Amblyomma americanum represented 98.1% of the 14,369 ticks submitted. Rates of blacklegged tick submission per 100,000 population were highest in Ontario's Eastern region; D. variabilis in Central West and Eastern regions; I. cookei in Eastern and South West regions; and A. americanum had a scattered distribution. Rates of blacklegged tick submission per 100,000 population were highest from children (0-9 years old) and older adults (55-74 years old). In two health units in the Eastern region (i.e., Leeds, Grenville & Lanark District and Kingston-Frontenac and Lennox & Addington), the rate of submission for engorged and B. burgdorferi-positive blacklegged ticks was 47x higher than the rest of Ontario. Rate of spread for blacklegged ticks was relatively faster and across a larger geographic area along the northern shore of Lake Ontario/St. Lawrence River, compared with slower spread from isolated populations along the northern shore of Lake Erie. The infection prevalence of B. burgdorferi in blacklegged ticks increased in Ontario over the study period from 8.4% in 2008 to 19.1% in 2012. The prevalence of B. burgdorferi-positive blacklegged ticks increased yearly during the surveillance period and, while increases were not uniform across all regions, increases were greatest in the Central West region, followed by Eastern and South West regions. The overall infection prevalence of A. phagocytophilum in blacklegged ticks was 0.3%. This study provides essential information on ticks of medical importance in Ontario, and identifies demographic and geographic areas for focused public education on the prevention of tick bites and tick-borne diseases.

46. **Lack of spatial autocorrelation in fine-scale distributions of Ixodes scapularis (Acari: Ixodidae)**.
Pardanani N, Mather TN
J Med Entomol **41**(5): 861-864. 2004.

Abstract: Spatial patterns of Ixodes scapularis Say, the vector of the Lyme disease agent, have been examined at various geographic scales, demonstrating that distributions of these ticks are spatially autocorrelated at both national and state scales. We tested the hypothesis that distributions of nymphal I scapularis ticks at the fine scale of an endemic community also are spatially autocorrelated. Nymphal tick densities were determined by collecting ticks from 51 and 47 wooded residential properties in a southern Rhode Is-

land town in 2002 and 2003, respectively. The average tick density at residences during 2002 was 51.17 (+/- 46.04) nymphs per hour, with a range of 3-297 and median of 40.82. In 2003, the average tick density was 44.48 (+/- 38.31) nymphs per hour, with a range of 3-153 and median of 36. Semivariance analysis revealed no spatial autocorrelation in tick densities between residences, likely due to the high variability of tick distributions at this scale. Further analysis of drag-sampling data at individual residences by using Lloyd's patchiness index (m*/m) demonstrated a patchy distribution of nymphs. High variability of nymphal I. scapularis densities may greatly affect predicting spatial patterns of ticks at a fine scale.

47. **The ecology of tick-borne diseases**.
Pfaffle M, Littwin N, Muders SV, Petney TN
Int J Parasitol **43**(12-13): 1059-1077. 2013.

Abstract: Zoonotic diseases are major causes of infection related morbidity and mortality worldwide. Of the various arthropods capable of transmitting pathogens that cause such diseases to humans, ticks, which are vectors of more kinds of pathogens than any other group of invertebrate, have become an increasing focus of attention. This is particularly the case in the temperate northern hemisphere where they are a significant vector of human disease. Here, we provide an overview of the complex ecological systems defining the various epidemiological cycles of tick-borne diseases. We highlight the abiotic and biotic factors influencing the establishment and persistence of tick populations and their associated pathogens. Furthermore, we emphasize the dynamic nature of such systems, especially when they are under the influence of both small and large-scale anthropogenic changes to the environment. Although a great deal of work has been done on ticks and the diseases which they transmit, the very dynamism of the system means that new factors are continually arising which shift the epidemiological pattern within specific areas. We therefore consider that more detailed, long-term (i.e. at least 10 years), multidisciplinary studies need to be carried out to define why and how these pattern shifts take place and to determine their public health significance.

48. **Facilitative ecological interactions between invasive species: Arundo donax stands as favorable habitat for cattle ticks (Acari: Ixodidae) along the U.S.-Mexico border**.
Racelis AE, Davey RB, Goolsby JA, Perez de Leon AA, Varner K, Duhaime R
J Med Entomol **49**(2): 410-417. 2012.

Abstract: The cattle tick, Rhipicephalus (Boophilus) spp. is a key vector of protozoa that cause bovine babesiosis. Largely eradicated from most of the United States, the cattle tick continues to infest south Texas, and recent outbreaks in this area may signal a resurgence of cattle tick populations despite current management efforts. An improved understanding of the dynamic ecology of cattle fever ticks along the U.S.-Mexico border is required to devise strategies for sustainable eradication efforts. Management areas of the cattle tick overlap considerably with dense, wide infestations of the non-native, invasive grass known as giant reed (Arundo donax L.). Here we show that stands of giant reed are associated with abiotic and biotic conditions that are favorable to tick survival, especially when compared with other nearby habitats (open pastures of buffelgrass (Pennisetum ciliare) and closed canopy native forests). Overhead canopies in giant reed stands and native riparian forests reduce daily high temperature, which was the best abiotic predictor of oviposition by engorged females. In sites where temperatures were extreme, specifically open grasslands, fewer females laid eggs and the resulting egg masses were smaller. Pitfall trap collections of ground dwelling arthropods suggest a low potential for natural suppression of tick populations in giant reed stands. The finding that A. donax infestations present environmental conditions that facilitate the survival and persistence of cattle ticks, as well or better than native riparian habitats and open grasslands, represents an alarming complication for cattle fever tick management in the United States.

49. **Deer density and the abundance of Ixodes scapularis (Acari: Ixodidae)**.
Rand PW, Lubelczyk C, Lavigne GR, Elias S, Holman MS, Lacombe EH, Smith RP, Jr.
J Med Entomol **40**(2): 179-184. 2003.

Abstract: The abundance of Ixodes scapularis Say (Ixodes dammini Spielman, Clifford, Piesman & Corwin), the vector tick of the Lyme disease spirochete and other human pathogens, is related to the presence of its primary reproductive stage host, white-tailed deer (Odocoileus virginianus Zimmerman). However, this relationship has not been quantified in terms that would guide wildlife management in areas in which the public is, or is likely to become, exposed to infected ticks. In this study, deer density and tick abundance were measured in an emergent area for Lyme disease at three spatial scales using estimation methods appropriate for each. Simple linear regression was used to relate (1) the number of ticks found on deer at tagging stations in southern Maine to harvest-derived estimates of the density of deer within the towns in which they were killed, (2) tick densities estimated from fall flagging counts to deer densities estimated from pellet group counts made within multiple transects distributed through 5.2-km2 study sites, and (3) tick counts to pellet group counts within the individual transects. At the broadest scale, ticks on deer decreased with elevation and distance from the coast and increased with deer density, although deer and tick presence were only weakly related. Among the 5.2-km2 study sites and within individual transects, tick abundance related more strongly to deer pellet group counts. Few ticks were collected at deer densities <7/km2.

50. **To what extent has climate change contributed to the recent epidemiology of tick-borne diseases?**
Randolph SE
Vet Parasitol **167**(2-4): 92-94. 2010.

Abstract: There is no doubt that all vector-borne diseases are very sensitive to climatic conditions. Many such diseases have shown marked increases in both distribution and incidence during the past few decades, just as human-induced climate change is thought to have exceeded random fluctuations. This coincidence has led to the general perception that climate change has driven disease emergence, but climate change is the inevitable backdrop for all recent events, without implying causality. Coincidence and causality can be disentangled using tick-borne encephalitis (TBE) as a test case, based on the excellent long-term data for this medically significant European disease system. Detailed analysis of climate records since 1970 has revealed abrupt temperature increases just prior to the dramatic upsurge in TBE incidence in many parts of central and eastern Europe. Furthermore, the seasonal patterns of this temperature change are such as might have favoured the transmission of TBE virus between co-feeding ticks. Nevertheless, the pattern of climate change is too uniform to explain the marked heterogeneity in the timing and degree of TBE upsurge, for example in different counties within each of the Baltic countries. Recent decreases as well as increases in TBE incidence must also be taken into account. Instead of a single cause, a network of interacting factors, acting synergistically but with differential force in space and time, would generate this epidemiological heterogeneity. From analysis of past and present events, it appears that human behavioural factors have played a more significant role than purely biological enzootic factors, although there is an explicit causal linkage from one to the other. This includes a range of abiotic and biotic environmental factors, together with human behaviour determined by socio-economic conditions. Many of the abrupt changes followed from the shift from planned to market economies with the fall of Soviet rule. Comparisons between eight countries have indeed revealed a remarkable correlation between poverty indicators and the relative degree of upsurge in TBE from 1993. Against this background of longer-term shifts in TBE incidence, sudden spikes in incidence appear to be due to exceptional weather conditions affecting people's behaviour, which have a differential impact depending on socio-economic factors. This new perspective may also help explain the epidemiology of Crimean-Congo haemorrhagic fever around the eastern Mediterranean region, including the current exceptional epidemic in Turkey.

51. **Seasonal variation in nymphal blacklegged tick abundance in southern New England forests**.
Rodgers SE, Miller NJ, Mather TN
J Med Entomol **44**(5): 898-900. 2007.

Abstract: In the northeastern United States, risk of human exposure to tick transmitted disease is primarily a function of the abundance of the blacklegged tick, Ixodes scapularis Say. We assessed seasonal variability in the abundance of nymphal stage I. scapularis over 13 yr, collected from several forested areas throughout Rhode Island. Specifically, we examined intraseasonal differences by using two temporally distinct tick collections made during the peak nymphal tick season. Intraseasonal factors significantly impacted tick abundance, with the June tick rate (mean = 40.42, SD = 14.79) significantly more abundant than the July tick rate (mean = 27.64, SD = 15.47). The greater variability in July (coefficient of variation: June, 36.61%; July, 55.95%) lead us to conclude June tick rates are relatively stable from year to year, whereas July tick rates contribute more to intraseasonal and yearly variation.

52. **The role of deer as vehicles to move ticks, Ixodes ricinus, between contrasting habitats**.
Ruiz-Fons F, Gilbert L
Int J Parasitol **40**(9): 1013-1020. 2010.

Abstract: In Europe the most important hosts maintaining Ixodes ricinus tick populations are deer. Therefore, excluding deer by fencing or culling are potential tick management tools. Here we test the hypothesis that deer act as vehicles for moving ticks between two distinct habitats: forest and open heather moorland. We utilised an ideal "natural experiment" whereby forests were either fenced or unfenced to prevent or allow deer to move between habitats. We aimed to test the hypothesis that deer cause a net movement of ticks from high tick density areas, i.e. forests, to low tick density areas, i.e. open moorland. We recorded I. ricinus and host abundance in 10 unfenced and seven fenced forests and their respective surrounding heather moorland. We found that fenced forests had fewer deer and fewer I. ricinus nymphs than unfenced forests. However, we found no evidence that fencing forests reduced I. ricinus abundance on adjacent heather moorland. Thus there was insufficient evidence for our hypothesis that deer cause a net movement of ticks from forest onto adjacent moorland. However, we found that deer abundance generally correlates with I. ricinus abundance. We conclude that fencing can be used as a tool to reduce ticks and disease risk in forests, but that fencing forests is unlikely to reduce ticks or disease risk on adjacent moorland. Instead, reducing deer numbers could be a potential tool to reduce tick abundance with implications for disease mitigation.

53. **Ixodes scapularis and Borrelia burgdorferi among diverse habitats within a natural area in east-central Illinois**.
Rydzewski J, Mateus-Pinilla N, Warner RE, Hamer S, Weng HY
Vector Borne Zoonotic Dis **11**(10): 1351-1358. 2011.

Abstract: The distributions of the tick vector, Ixodes scapularis, and of the etiologic agent of Lyme disease, Borrelia burgdorferi (Bb), have continued expanding in Illinois over the past 20 years, but the extent of their spread is not well known. The role of multiple habitats in the establishment

and maintenance of I. scapularis and Bb at local scales is not well understood, and the use of integrated approaches to evaluate local scale dynamics is rare. We evaluated habitat diversity and temporal changes of I. scapularis occurrence and Bb infection within a natural area in Piatt County, Illinois, where I. scapularis were first detected in 2002. Small mammals were trapped and attached ticks were collected in young forest, prairie, mature forest, and flood plain sites from 2005 to 2009. Small mammal abundance, and the prevalence (% mammals infested), mean intensity (I. scapularis per infested mammal), and relative density (I. scapularis per mammal trapped) of I. scapularis were computed for each habitat type and compared. Immature I. scapularis were tested for Bb infection using polymerase chain reaction techniques. Out of 2446 trapped small mammals, 388 were infested with I. scapularis. The prairie had the highest diversity of small mammal hosts. Prevalence, mean intensity, and relative density of I. scapularis and prevalence of Bb infection were highest for the prairie and young forest sites; in the former, all infection was associated with the prairie vole, Microtus ochrogaster. The minimum Bb infection prevalence of on-host I. scapularis collected in the natural area was 14% (n=56). Unlike previous studies solely focused on forested areas and Peromyscus leucopus, our study is the first to provide evidence of I. scapularis collected from prairie habitat and other reservoir hosts, particularly M. ochrogaster.

54. **Tick community composition in Midwestern US habitats in relation to sampling method and environmental conditions**.
Rynkiewicz EC, Clay K
Exp Appl Acarol **64**(1): 109-119. 2014.

Abstract: The ranges of many tick species are changing due to climate change and human alteration of the landscape. Understanding tick responses to environmental conditions and how sampling method influences measurement of tick communities will improve our assessment of human disease risk. We compared tick sampling by three collection methods (dragging, CO_2 trapping and rodent surveys) in adjacent forested and grassland habitats in the lower Midwest, USA, and analyzed the relationship between tick abundance and microclimate conditions. The study areas were within the overlapping ranges of three tick species, which may provide conditions for pathogen exchange and spread into new vectors. Dermacentor variabilis (American dog tick) was found using all methods, Amblyomma americanum (lonestar tick) was found by dragging and CO_2 trapping and Ixodes scapularis (blacklegged deer tick) was found only on rodents. Proportion of each species differed significantly among sampling methods. More ticks were found in forests compared to open habitats. Further, more ticks were collected by dragging and from rodents in hotter, drier conditions. Our results demonstrate that multiple sampling methodologies better measure the tick community and that microclimate conditions strongly influence the abundance and activity of individual tick species.

55. **Fire and Parasites: An Under-Recognized Form of Anthropogenic Land Use Change and Mechanism of Disease Exposure**.
Scasta JD
Ecohealth **12**(3): 398-403. 2015.

Abstract: Anthropogenic land use changes have altered ecosystems and exacerbated the spread of infectious diseases. Recent reviews, however, have revealed that fire suppression in fire-prone natural areas has not been recognized as a form of anthropogenic land use change. Furthermore, fire suppression has been an under-recognized mechanism altering the risk and transmission of infectious disease pathogens and host-parasite dynamics. However, as settlement patterns changed, especially due to colonial expansion in North America, Africa, and Australia, fire suppression became a major form of land use change which has led to broad-scale ecosystem changes. Because parasites of humans and animals can vector viral, bacterial, prion, fungal, or protozoan pathogens, concomitant changes associated with anthropogenic-induced changes to fire frequencies and intensities are of concern. I provide reference to 24 studies that indicate that restoring fire in natural areas has the potential to reduce ectoparasites without wings such as ticks, chiggers, fleas, and lice; ectoparasites with wings such as mosquitos, horn flies, face flies, and stable flies; and endoparasites affecting livestock and wildlife. This suggests that fire ecology and parasitology be considered as a priority area for future research that has implications for both humans and animals.

56. **Influence of meso- and microscale habitat structure on focal distribution of sympatric Ixodes scapularis and Amblyomma americanum (Acari: Ixodidae)**.
Schulze TL, Jordan RA
J Med Entomol **42**(3): 285-294. 2005.

Abstract: We compared the distribution of sympatric Ixodes scapularis Say and Amblyomma americanum (L.) within several suitable forested habitats at different spatial scales and characterized differences in microhabitat features accounting for the observed distribution of questing ticks. We used automatic data loggers placed in the shrub and litter layers to contrast mesoclimate and microclimate conditions experienced by questing ticks. Larger numbers of I. scapularis were collected at sites where the forest canopy was more fragmented and where the canopy contained more hardwood species than pitch pine, Pinus rigida Mill. Dominance of pine in the canopy affected the character of the shrub layer vegetation and composition of the litter layer, which concomitantly affected the microclimate conditions experienced by questing ticks. Pitch pine-dominated habitats were drier and hotter than those under a broad-leaved canopy, and questing ticks experienced increased saturation deficit in the later spring and summer in pine forest sites. The shrub layer vegetation seemed to have a moderating effect on the microclimate experienced by questing ticks and subtle differences in vegetation structure resulted in sub-

stantially different conditions as encountered by questing ticks over the space of a few meters. In contrast to questing I. scapularis, all three stages of questing A. americanum exhibited poor relationships with microclimate variables recorded in the litter and shrub layers. Further research is required to determine which environmental conditions and which habitats are most likely to support this species.

57. **Long-Term Effects of White-Tailed Deer Exclusion on the Invasion of Exotic Plants: A Case Study in a Mid-Atlantic Temperate Forest**.
Shen X, Bourg NA, McShea WJ, Turner BL
PLoS One **11**(3): e0151825. 2016.

Abstract: Exotic plant invasions and chronic high levels of herbivory are two of the major biotic stressors impacting temperate forest ecosystems in eastern North America, and the two problems are often linked. We used a 4-ha deer exclosure maintained since 1991 to examine the influence of a generalist herbivore, white-tailed deer (Odocoileus virginianus), on the abundance of four exotic invasive (Rosa multiflora, Berberis thunbergii, Rubus phoenicolasius and Microstegium vimineum) and one native (Cynoglossum virginianum) plant species, within a 25.6-ha mature temperate forest dynamics plot in Virginia, USA. We identified significant predictors of the abundance of each focal species using generalized linear models incorporating 10 environmental and landscape variables. After controlling for those predictors, we applied our models to a 4-ha deer exclusion site and a 4-ha reference site, both embedded within the larger plot, to test the role of deer on the abundance of the focal species. Slope, edge effects and soil pH were the most frequent predictors of the abundance of the focal species on the larger plot. The abundance of C. virginianum, known to be deer-dispersed, was significantly lower in the exclosure. Similar patterns were detected for B. thunbergii, R. phoenicolasius and M. vimineum, whereas R. multiflora was more abundant within the exclosure. Our results indicate that chronic high deer density facilitates increased abundances of several exotic invasive plant species, with the notable exception of R. multiflora. We infer that the invasion of many exotic plant species that are browse-tolerant to white-tailed deer could be limited by reducing deer populations.

58. **Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels**.
Simao MCM, Flory SL, Rudgers JA
Oikos **119**(10): 1553-1562. 2010.

Abstract: Plant invasions are known to have negative impacts on native plant communities, yet their influence on higher trophic levels has not been well documented. Past studies investigating the effects of invasive plants on herbivores and carnivores have been largely observational in nature and thus lack the ability to tease apart whether differences are a cause or consequence of the invasion. In addition, understanding how plant traits and plant species compositions change in invaded habitats may increase our ability to predict when and where invasive plants will have effects that cascade to animals. To assess effects on arthropods, we experimentally introduced a non-native plant (Microstegium vimineum, Japanese stiltgrass) in a community re-assembly experiment. We also investigated possible mechanisms through which the invader could affect associated arthropods, including changes in native plant species richness, above-ground plant biomass, light availability and vegetation height. In experimentally invaded plots, arthropod abundance was reduced by 39%, and species richness declined by 19%. Carnivores experienced greater reductions in abundance than herbivores (61% vs 31% reduction). Arthropod composition significantly diverged between experimentally invaded and control plots, and particular species belonging to the abundant families Aphididae (aphids), Formicidae (ants) and Phalacridae (shining flower beetles) contributed the most to compositional differences. Among the mechanisms we investigated, only the reduction in native plant species richness caused by invasion was strongly correlated with total arthropod abundance and richness. In sum, our results demonstrate negative impacts of M. vimineum invasion on higher trophic levels and suggest that these effects occur, in part, indirectly through invader-mediated reductions in the richness of the native plant community. The particularly strong response of carnivores suggests that plant invasion could reduce top-down control of herbivorous species for native plants.

59. **Range Expansion of Tick Disease Vectors in North America: Implications for Spread of Tick-Borne Disease**.
Sonenshine DE
Int J Environ Res Public Health **15**(3): E478. 2018.

Abstract: Ticks are the major vectors of most disease-causing agents to humans, companion animals and wildlife. Moreover, ticks transmit a greater variety of pathogenic agents than any other blood-feeding arthropod. Ticks have been expanding their geographic ranges in recent decades largely due to climate change. Furthermore, tick populations in many areas of their past and even newly established localities have increased in abundance. These dynamic changes present new and increasing severe public health threats to humans, livestock and companion animals in areas where they were previously unknown or were considered to be of minor importance. Here in this review, the geographic status of four representative tick species are discussed in relation to these public health concerns, namely, the American dog tick, Dermacentor variabilis, the lone star tick, Amblyomma americanum, the Gulf Coast Tick, Amblyomma maculatum and the black-legged tick, Ixodes scapularis. Both biotic and abiotic factors that may influence future range expansion and successful colony formation in new habitats are discussed.

60. **Modeling the Present and Future Geographic Distribution of the Lone Star Tick, Amblyomma americanum (Ixodida: Ixodidae), in the Continental United States**.
Springer YP, Jarnevich CS, Barnett DT, Monaghan AJ, Eisen RJ
Am J Trop Med Hyg **93**(4): 875-890. 2015.

Abstract: The Lone star tick (Amblyomma americanum L.) is the primary vector for pathogens of significant public health importance in North America, yet relatively little is known about its current and potential future distribution. Building on a published summary of tick collection records, we used an ensemble modeling approach to predict the present-day and future distribution of climatically suitable habitat for establishment of the Lone star tick within the continental United States. Of the nine climatic predictor variables included in our five present-day models, average vapor pressure in July was by far the most important determinant of suitable habitat. The present-day ensemble model predicted an essentially contiguous distribution of suitable habitat extending to the Atlantic coast east of the 100th western meridian and south of the 40th northern parallel, but excluding a high elevation region associated with the Appalachian Mountains. Future ensemble predictions for 2061-2080 forecasted a stable western range limit, northward expansion of suitable habitat into the Upper Midwest and western Pennsylvania, and range contraction along portions of the Gulf coast and the lower Mississippi river valley. These findings are informative for raising awareness of A. americanum-transmitted pathogens in areas where the Lone Star tick has recently or may become established.

61. **The effects of vegetation density and habitat disturbance on the spatial distribution of ixodid ticks (Acari: Ixodidae)**.
Stein KJ, Waterman M, Waldon JL
Geospat Health **2**(2): 241-252. 2008.

Abstract: Larval, nymphal, and adult Amblyomma americanum (L.), and adult Dermacentor variabilis (Say) ticks were collected using timed dragging techniques, in an attempt to examine how different habitat variables affect models that describe the distribution of ticks in Virginia, USA. Tick count data were modeled using two approaches: (i) habitat and edge, and (ii) habitat, edge, vegetation density and levels of disturbance. Nymphs and adults tended to follow a forest edge distribution when analysed by habitat and edge. Using all variables, we detected a positive relationship with forest edges and negative associations with high-density vegetation. When larvae were modeled by habitat and edge, we failed to detect associations with the edges of habitats. When all variables were included in the larval analysis, disturbed meadow edges emerged as important in the first year, and the categories of disturbed and maturing habitat in the second year. Vegetation density and levels of disturbance were marginally important towards explaining the distribution of nymphs and adults; however, levels of disturbance were potentially more important to the distribution of larvae, than habitat types. Using the habitat and edge variables, and predicted mean encounter rates for all stages of A. americanum and adult D. variabilis, we successfully cross-validated our predictions of high, moderate and low tick densities in both years. The results for nymphs and adults were combined to develop a colour-coded threat assessment map. We estimated that the majority of ticks were located on approximately 20% of the landscape. The potential uses of geographical information system-based threat maps are discussed.

62. **Impacts of an introduced forest pathogen on the risk of Lyme disease in California**.
Swei A, Briggs CJ, Lane RS, Ostfeld RS
Vector Borne Zoonotic Dis **12**(8): 623-632. 2012.

Abstract: Global changes such as deforestation, climate change, and invasive species have the potential to greatly alter zoonotic disease systems through impacts on biodiversity. This study examined the impact of the invasive pathogen that causes sudden oak death (SOD) on the ecology of Lyme disease in California. The Lyme disease bacterium, Borrelia burgdorferi, is maintained in the far western United States by a suite of animal reservoirs including the dusky-footed woodrat (Neotoma fuscipes) and deer mouse (Peromyscus maniculatus), and is transmitted by the western black-legged tick (Ixodes pacificus). Other vertebrates, such as the western fence lizard (Sceloporus occidentalis), are important tick hosts but are not reservoirs of the pathogen. Previous work found that higher levels of SOD are correlated with greater abundance of P. maniculatus and S. occidentalis and lower N. fuscipes abundance. Here we model the contribution of these tick hosts to Lyme disease risk and also evaluate the potential impact of SOD on infection prevalence of the tick vector. By empirically parameterizing a static model with field and laboratory data on tick hosts, we predict that SOD reduces an important index of disease risk, nymphal infection prevalence, leading to a reduction in Lyme disease risk in certain coastal woodlands. Direct observational analysis of the impact of SOD on nymphal infection prevalence supports these model results. This study underscores the important direct and indirect impacts of invasive plant pathogens on biodiversity, the transmission cycles of zoonotic diseases, and ultimately human health.

63. **Effects of an invasive forest pathogen on abundance of ticks and their vertebrate hosts in a California Lyme disease focus**.
Swei A, Ostfeld RS, Lane RS, Briggs CJ
Oecologia **166**(1): 91-100. 2011.

Abstract: Invasive species, including pathogens, can have important effects on local ecosystems, including indirect consequences on native species. This study focuses on the effects of an invasive plant pathogen on a vertebrate community and Ixodes pacificus, the vector of the Lyme disease pathogen (Borrelia burgdorferi) in California. Phytoph-

thora ramorum, the causative agent of sudden oak death, is a non-native pathogen killing trees in California and Oregon. We conducted a multi-year study using a gradient of SOD-caused disturbance to assess the impact on the dusky-footed woodrat (Neotoma fuscipes) and the deer mouse (Peromyscus maniculatus), two reservoir hosts of B. burgdorferi, as well as the impact on the Columbian black-tailed deer (Odocoileus hemionus columbianus) and the western fence lizard (Sceloporus occidentalis), both of which are important hosts for I. pacificus but are not pathogen reservoirs. Abundances of P. maniculatus and S. occidentalis were positively correlated with greater SOD disturbance, whereas N. fuscipes abundance was negatively correlated. We did not find a change in space use by O. hemionus. Our data show that SOD has a positive impact on the density of nymphal ticks, which is expected to increase the risk of human exposure to Lyme disease all else being equal. A positive correlation between SOD disturbance and the density of nymphal ticks was expected given increased abundances of two important hosts: deer mice and western fence lizards. However, further research is needed to integrate the direct effects of SOD on ticks, for example via altered abiotic conditions with host-mediated indirect effects.

64. **Habitat and Vegetation Variables Are Not Enough When Predicting Tick Populations in the Southeastern United States**.
Trout Fryxell RT, Moore JE, Collins MD, Kwon Y, Jean-Philippe SR, Schaeffer SM, Odoi A, Kennedy M, Houston AE
PLoS One **10**(12): e0144092. 2015.

Abstract: Two tick-borne diseases with expanding case and vector distributions are ehrlichiosis (transmitted by Amblyomma americanum) and rickettiosis (transmitted by A. maculatum and Dermacentor variabilis). There is a critical need to identify the specific habitats where each of these species is likely to be encountered to classify and pinpoint risk areas. Consequently, an in-depth tick prevalence study was conducted on the dominant ticks in the southeast. Vegetation, soil, and remote sensing data were used to test the hypothesis that habitat and vegetation variables can predict tick abundances. No variables were significant predictors of A. americanum adult and nymph tick abundance, and no clustering was evident because this species was found throughout the study area. For A. maculatum adult tick abundance was predicted by NDVI and by the interaction between habitat type and plant diversity; two significant population clusters were identified in a heterogeneous area suitable for quail habitat. For D. variabilis no environmental variables were significant predictors of adult abundance; however, D. variabilis collections clustered in three significant areas best described as agriculture areas with defined edges. This study identified few landscape and vegetation variables associated with tick presence. While some variables were significantly associated with tick populations, the amount of explained variation was not useful for predicting reliably where ticks occur; consequently, additional research that includes multiple sampling seasons and locations throughout the southeast are warranted. This low amount of explained variation may also be due to the use of hosts for dispersal, and potentially to other abiotic and biotic variables. Host species play a large role in the establishment, maintenance, and dispersal of a tick species, as well as the maintenance of disease cycles, dispersal to new areas, and identification of risk areas.

65. **Invasive shrub alters native forest amphibian communities**.
Watling JI, Hickman CR, Orrock JL
Biol Conserv **144**(11): 2597-2601. 2011.

Abstract: Although invasive plants can have transformative effects on native plant communities, studies of the consequences of plant invasion for native fauna are generally restricted to primary consumers. Here we investigate whether an invasive shrub, Lonicera maackii, impacts native amphibians and evaluate evidence for the role of invasive plant-induced alteration of forest understory microclimate as a mechanism driving amphibian responses to L. maackii invasion. We sampled amphibian communities in forest plots with high or low density of L. maackii, and monitored microclimate (temperature and humidity at ground level) in the same forest plots. Amphibian species richness and evenness were lower in invaded plots. Invasion also resulted in shifts in amphibian species composition. Mean daily maximum temperature and mean daily temperature were lower in invaded plots, and counts of the Green frog Lithobates clamitans were marginally negatively related to mean daily temperature. Our work illustrates how an invasive ecosystem engineer may affect native organisms with which it shares no trophic connection, and suggests that changes in microclimate may be one mechanism by which alien plants affect communities where they invade.

66. **Geography, deer, and host biodiversity shape the pattern of Lyme disease emergence in the Thousand Islands Archipelago of Ontario, Canada**.
Werden L, Barker IK, Bowman J, Gonzales EK, Leighton PA, Lindsay LR, Jardine CM
PLoS One **9**(1): e85640. 2014.

Abstract: In the Thousand Islands region of eastern Ontario, Canada, Lyme disease is emerging as a serious health risk. The factors that influence Lyme disease risk, as measured by the number of blacklegged tick (Ixodes scapularis) vectors infected with Borrelia burgdorferi, are complex and vary across eastern North America. Despite study sites in the Thousand Islands being in close geographic proximity, host communities differed and both the abundance of ticks and the prevalence of B. burgdorferi infection in them varied among sites. Using this archipelago in a natural experiment, we examined the relative importance of various biotic and abiotic factors, including air temperature, vegetation, and host communities on Lyme disease

risk in this zone of recent invasion. Deer abundance and temperature at ground level were positively associated with tick abundance, whereas the number of ticks in the environment, the prevalence of B. burgdorferi infection, and the number of infected nymphs all decreased with increasing distance from the United States, the presumed source of this new endemic population of ticks. Higher species richness was associated with a lower number of infected nymphs. However, the relative abundance of Peromyscus leucopus was an important factor in modulating the effects of species richness such that high biodiversity did not always reduce the number of nymphs or the prevalence of B. burgdorferi infection. Our study is one of the first to consider the interaction between the relative abundance of small mammal hosts and species richness in the analysis of the effects of biodiversity on disease risk, providing validation for theoretical models showing both dilution and amplification effects. Insights into the B. burgdorferi transmission cycle in this zone of recent invasion will also help in devising management strategies as this important vector-borne disease expands its range in North America.

67. **Effects of Japanese barberry (Ranunculales: Berberidaceae) removal and resulting microclimatic changes on Ixodes scapularis (Acari: Ixodidae) abundances in Connecticut, USA**.
Williams SC, Ward JS
Environ Entomol **39**(6): 1911-1921. 2010.

Abstract: Japanese barberry (Berberis thunbergii de Candolle) is a thorny, perennial, exotic, invasive shrub that is well established throughout much of the eastern United States. It can form dense thickets that limit native herbaceous and woody regeneration, alter soil structure and function, and harbor increased blacklegged tick (Ixodes scapularis Say) populations. This study examined a potential causal mechanism for the link between Japanese barberry and blacklegged ticks to determine if eliminating Japanese barberry could reduce tick abundance and associated prevalence of Borrelia burgdorferi (Johnson, Schmid, Hyde, Steigerwalt, and Brenner). Japanese barberry was controlled at five study areas throughout Connecticut; adult ticks were sampled over three years. Each area had three habitat plots: areas where barberry was controlled, areas where barberry remained intact, and areas where barberry was minimal or absent. Sampled ticks were retained and tested for B. burgdorferi presence. At two study areas, temperature and relative humidity data loggers were deployed in each of the three habitat plots over two growing seasons. Intact barberry stands had 280 +/- 51 B. burgdorferi-infected adult ticks/ha, which was significantly higher than for controlled (121 +/- 17/ha) and no barberry (30 +/- 10/ha) areas. Microclimatic conditions where Japanese barberry was controlled were similar to areas without barberry. Japanese barberry infestations are favorable habitat for ticks, as they provide a buffered microclimate that limits desiccation-induced tick mortality. Control of Japanese barberry reduced the number of ticks infected with B. burgdorferi by nearly 60% by reverting microclimatic conditions to those more typical of native northeastern forests.

68. **Managing Japanese barberry (Ranunculales: Berberidaceae) infestations reduces blacklegged tick (Acari: Ixodidae) abundance and infection prevalence with Borrelia burgdorferi (Spirochaetales: Spirochaetaceae)**.
Williams SC, Ward JS, Worthley TE, Stafford KC, 3rd
Environ Entomol **38**(4): 977-984. 2009.

Abstract: In many Connecticut forests with an overabundance of white-tailed deer (Odocoileus virginianus Zimmermann), Japanese barberry (Berberis thunbergii DC) has become the dominant understory shrub, which may provide a habitat favorable to blacklegged tick (Ixodes scapularis Say) and white-footed mouse (Peromyscus leucopus Rafinesque) survival. To determine mouse and larval tick abundances at three replicate sites over 2 yr, mice were trapped in unmanipulated dense barberry infestations, areas where barberry was controlled, and areas where barberry was absent. The number of feeding larval ticks/mouse was recorded. Adult and nymphal ticks were sampled along 200-m draglines in each treatment, retained, and were tested for Borrelia burgdorferi (Johnson, Schmid, Hyde, Steigerwalt, and Brenner) presence. Total first-captured mouse counts did not differ between treatments. Mean number of feeding larval ticks per mouse was highest on mice captured in dense barberry. Adult tick densities in dense barberry were higher than in both controlled barberry and no barberry areas. Ticks sampled from full barberry infestations and controlled barberry areas had similar infection prevalence with B. burgdorferi the first year. In areas where barberry was controlled, infection prevalence was reduced to equal that of no barberry areas the second year of the study. Results indicate that managing Japanese barberry will have a positive effect on public health by reducing the number of B. burgdorferi-infected blacklegged ticks that can develop into motile life stages that commonly feed on humans.

69. **Relationship between habitat type, fire frequency, and Amblyomma americanum populations in east-central Alabama**.
Willis D, Carter R, Murdock C, Blair B
J Vector Ecol **37**(2): 373-381. 2012.

Abstract: Ticks were collected from 20 sites in the Calhoun, Cherokee, and Cleburne Counties in east-central Alabama areas to determine the relationship between plant physiognomy, environmental variables, and tick populations. Sites investigated included various burning regimes, wildland-urban-interface (WUI), a college campus, and an unmanaged area. Amblyomma americanum (L.) (Acari: Ixodidae) dominated the tick population while Ixodes scapularis Say was not encountered. There were complex differences in tick populations among site conditions. After prescribed burning, the tick population size was small but was larger in subsequent 2- and 5-year post-burn sites. An increase in Odocoileus virginianus foraging in recently burned sites is likely responsible for this phenomenon. WUI areas had the largest tick populations likely due to Odocoileus virginianus activity in an area that provides cover, forage, and a connection to a wildlife refuge. It is possible that the likelihood of humans coming in contact with ticks and tick-borne diseases is greater in WUI areas than in unbroken contiguous forest. A. americanum showed a positive correlation with percent cover of grass and leaf litter mass and a negative relationship with pine sapling density. Variables expected to be strongly correlated with A. americanum populations such as soil moisture, canopy closure, and tree density were found to have weak correlations.