Geospatial Health
Geospatial Health 2026; 21:1479
doi:10.4081/gh.2026.1479

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Synergistic drivers of Lyme disease emergence in North America: an eco-syndemic review

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Abstract

Lyme disease is a growing public health threat driven by interplay of climatic, ecological and social factors. This review adopts an eco-syndemic framework, viewing Lyme disease emergence as the confluence of multiple synergistic drivers rather than a single-cause phenomenon. We synthesize evidence that climate conditions, ecological circumstances and human behavioural patterns intersect to amplify Lyme disease risk. By integrating these seemingly separate domains, our review highlights novel insights; for example, habitat fragmentation and predator loss may magnify the effects of a warming climate on reservoir or host populations, and human activities in suburban green spaces may mediate infection cycles. This holistic perspective is a departure from reductionist explanations and emphasizes the importance of coupled human–environment systems in studies of disease emergence. We discuss how an eco-syndemic frame can improve surveillance and prevention emphasizing One Health approaches that unite environmental management with animal health and public health outreach. Understanding the interactive and non-linear dynamics of Lyme disease drivers is crucial for developing effective interventions and preparing for future tick-borne disease challenges. While selected comparative evidence from Europe is used where relevant, the review's primary empirical focus is North America.

Key words: Lyme disease, eco-syndemic, wildland-urban interface, one health.

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Abstract

Lyme disease is a growing public health threat driven by interplay of climatic, ecological and social factors. This review adopts an eco-syndemic framework, viewing Lyme disease emergence as the confluence of multiple synergistic drivers rather than a single-cause phenomenon. We synthesize evidence that climate conditions, ecological circumstances and human behavioural patterns intersect to amplify Lyme disease risk. By integrating these seemingly separate domains, our review highlights novel insights; for example, habitat fragmentation and predator loss may magnify the effects of a warming climate on reservoir or host populations, and human activities in suburban green spaces may mediate infection cycles. This holistic perspective is a departure from reductionist explanations and emphasizes the importance of coupled human-environment systems in studies of disease emergence. We discuss how an eco-syndemic frame can improve surveillance and prevention emphasizing One Health approaches that unite environmental management with animal health and public health outreach. Understanding the interactive and non-linear dynamics of Lyme disease drivers is crucial for developing effective interventions and preparing for future tick-borne disease challenges. While selected comparative evidence from Europe is used where relevant, the review's primary empirical focus is North America.

Introduction

Lyme disease has become the most common vector-borne disease in North America and parts of Europe, with tens of thousands of cases reported annually and hundreds of thousands of unreported infections estimated each year in the United States (U.S.) alone (Steere *et al.*, 2004; Kilpatrick *et al.*, 2017). In North America, it is caused by *Borrelia burgdorferi* (Ostfeld and Keesing, 2000) and in Europe and Asia by *B. afzelii* and *B. garinii* (Steere *et al.*, 2004). The main vectors are *Ixodes* ticks, including *I. scapularis* and *I. pacificus* in North America (Ostfeld and Keesing, 2000) and *I. ricinus* and *I. persulcatus* in Eurasia (Steere *et al.*, 2004). Small mammals, such as white-footed mice and voles, serve as primary reservoirs, while deer sustain tick populations but are not a source of the pathogen (Ostfeld, 2011). In the U. S., reported the number of Lyme disease cases have roughly tripled over the past two decades (Kilpatrick *et al.*, 2017), couples with a steady expansion of the geographic range (Levi *et al.* 2012). Similar trends are observed in Europe, where Lyme borreliosis is endemic across many countries (Steere *et al.*, 2004).

Lyme disease imposes a significant public health burden in the U.S., with estimated annual direct healthcare costs ranging from $712 million to $1.3 billion (Adrion *et al.*, 2015). Many patients suffer rom persistent symptoms, including fatigue and cognitive issues, even after antibiotic therapy (Aucott *et al.*, 2013), a condition referred to as Post-Treatment Lyme Disease Syndrome

(PTLDS) (CDC, 2025a). These lingering effects can lead to substantial losses in productivity and work absenteeism. A study found that 42% of individuals with PTLDS report being unable to work full-time, with about 25% of individuals reporting cut-back on work hours or modifying job responsibilities because of symptoms (Johnson *et al.*, 2014). These significant statistics, along with Lyme disease's expanding range, has elevated Lyme disease into a serious public health concern, sparking interest in the underlying causes of its emergence.

Much Lyme disease research has focused on examining a range of potential explanatory factors, including ecological, climatic, and social influences that shape disease patterns and transmission dynamics. While such individual factors are clearly important in efforts to explain Lyme disease emergence, it is increasingly evident that no single driver fully accounts for the dramatic rise and expanded range of this disease. Instead, Lyme disease arises from a *system* of interacting ecological and social processes (Kilpatrick *et al.*, 2017; Couper *et al.*, 2021). The pathogen *B. burgdorferi* exists in a complex enzootic cycle involving ticks and multiple host species, all embedded within changing environments and human communities. Thus, a more *systems-level understanding* of Lyme disease emergence is needed: one that can accommodate climate trends, ecological dynamics (land cover habitat changes and wildlife ecology) as well as human behaviour simultaneously. Recent analyses show that Lyme disease incidence exhibits spatial synchrony influenced by combined ecological and social factors, further emphasizing the need for an integrated perspective (Ali *et al*., 2024). Recent geospatial and vector-borne disease studies further reinforce the need to examine disease risk as a product of interacting environmental, demographic, socioeconomic and spatial processes rather than isolated ecological variables (Y. Lin *et al.*, 2025; Nuñez Murillo *et al.*, 2026). These findings strengthen the case that Lyme disease emergence results from interacting domains rather than isolated drivers.

In this context, we draw on the concept of "eco-syndemics" as a framework, adapted from syndemic theory, which was first used to describe "synergistically related" diseases such as HIV and tuberculosis that cluster and arise from harmful social conditions (Singer, 1996). In this case, we expand the theory to explain how environmental and societal forces interact to intensify Lyme disease. Rather than treating climate change, ecological conditions, or human behaviour separately, this framework emphasizes their collective feedbacks. Lyme disease emerges as an eco-syndemic given that its emergence represents a convergence and amplification of drivers creating greater transmission risk than the simple sum of individual factors.

Previous Lyme disease ecology reviews have provided important syntheses of tick biology, host communities, land cover change, climate suitability and prevention challenges. However, many of these reviews primarily organize the evidence by individual domains of risk or emphasize broad integrative approaches such as One Health. Our review differs by using the eco-syndemic framework to explain Lyme disease emergence as a process of mutual amplification among climatic, ecological and social drivers. Rather than treating climate change, habitat fragmentation, biodiversity loss, host dynamics, tick ecology, and human behaviour as parallel contributors, we examine how these processes interact, reinforce one another and produce non-linear patterns of disease risk. This adds conceptual value by shifting attention from the identification of risk factors to the pathways through which those factors converge, compound, and sustain Lyme disease emergence across coupled human–environment systems. In this sense, the eco-syndemic framework not only complements One Health but extends it by emphasizing feedbacks, amplification and the social–ecological conditions, through which disease risk becomes entrenched.

Since the concept, Singer, helped reshape our understanding of disease beyond biomedical models, we took an interest of. Singer (1996, 2009, 2023) introduced the term *syndemic* while analyzing the interconnected epidemics of substance abuse, violence and AIDS within impoverished urban communities. We applied this thinking since we felt that this concept would have an application also for Lyme's disease. Indeed, expanding this perspective, Singer (2009) defined the *syndemic* approach as "a concentration and deleterious interaction of two or more diseases or other health conditions in a population, especially as a consequence of social inequity and the unjust exercise of power," emphasizing the ways political, economic, and environmental forces shape disease clustering. Rooted in the *One Health* perspective, this framework highlights the inseparable links between human, animal and environmental health reflecting how disruptions in one domain reverberate across the others (Singer, 2023). This theoretical grounding is empirically reinforced by a study demonstrating that El Niño–driven climatic anomalies in Peru triggered overlapping outbreaks of cholera, malaria and respiratory infections illustrating how environmental shocks can simultaneously intensify multiple diseases in socially marginalized regions (Ramírez *et al.*, 2018). Similarly, Tallman *et al.* (2022) apply the eco-syndemic lens to the Amazon Basin, showing that infrastructural expansion and deforestation through projects like the Belo Monte Dam and the Southern Interoceanic Highway gave rise to compounded burdens of infectious disease, psychosocial stress and sexual health risks. Together, these works advance *eco-syndemics* as a framework that binds health inequity to planetary instability, revealing that the wellbeing of human populations and the stability of the Earth's ecosystems are profoundly intertwined. In the case of Lyme disease, transmission requires the intersection of pathogen, vector, reservoir and humans, with each component shaped by external forces (Steere *et al.*, 2004; Killilea *et al.*, 2008; Coburn *et al.*, 2021). For example, the spatial distribution of Lyme disease risk depends on where infected ticks, reservoir hosts, and people coincide – a pattern governed by climate suitability, forest cover, wildlife community composition and human presence on the landscape as described by Killilea *et al.* (2008) and Couper *et al.* (2021). An eco-syndemic approach is justified by evidence that reductionist single-factor explanations for Lyme disease are inadequate. Earlier hypotheses highlighted the role of the 20th-century deer rebound for the widespread expansion of tick populations and the subsequent intensification of Lyme disease transmission (Steere *et al.*, 2004). Yet incidence have kept climbing without connection to deer density (Ostfeld, 2011; Levi *et al.*, 2012) or the current climate warming (Killilea *et al.*, 2008; Couper *et al.*, 2021), a fact that makes an integrative eco-syndemic view of Lyme disease essential.

This review synthesizes evidence on Lyme disease's synergistic drivers through an eco-syndemic lens, focusing on climate conditions, ecological change, and human behaviour. Building on peer-reviewed studies, we argue that Lyme disease emergence is best understood not simply as the result of multiple co-occurring drivers, but as the outcome of interacting and mutually reinforcing processes. By clarifying these pathways, the review highlights how eco-syndemic thinking can strengthen Lyme disease surveillance, prevention and intervention strategies by linking environmental management, wildlife ecology, public health outreach and human behaviour within a unified explanatory framework.

Concept

In this model, three major domains—climate, ecological conditions and human practices—form an interacting network of the ecological processes that enable *B. burgdorferi* to circulate among hosts, vectors and humans. Rising temperatures and changing precipitation regimes affect tick survival, development and activity patterns, directly altering infection risk (S. Lin *et al.*, 2019; Giesen *et al.*, 2024). Landscape alteration within vector and host habitat such as reforestation, suburban development, and fragmentation creates the environmental context in which ticks and host thrive or decline (Steere *et al.*, 2004; Ostfeld *et al.*, 2018). Ecological dynamics, including the loss of predators and the dominance of efficient reservoir hosts, mediate pathogen transmission rates (Levi *et al*., 2012; Keesing & Ostfeld 2021). Human behaviour and societal factors ultimately determine the frequency of human–tick contacts (Beck *et al.*, 2022; Tamari *et al.*, 2024). The multifaceted linkages show that Lyme disease emerges from *coupled natural and human systems*, which are processes where human actions and environmental changes continuously influence one another through feedbacks rather than simple linear chain of events as discussed by Ali *et al.* (2024). While such work acknowledges multi-domain interactions, it does not yet situate these processes within a syndemic or eco-syndemic framework. Our review extends this emerging evidence by explicitly theorizing Lyme disease as a coupled ecological–social–climatic system as depicted in Figure 1.

Study selection and inclusion criteria

To ensure coherence with the review's objectives, each article was first subjected to a preliminary relevance check based on its title, abstract, and introductory materials. Inclusion criteria were broadly defined to capture studies that examined Lyme disease (or closely related tick-borne diseases) through ecological, climatological, socio-demographic or landscape lenses. Studies had to present original data or syntheses that elucidated relationships between environmental or human-related variables and tick dynamics, Lyme disease incidence, or disease risk patterns. All studies included were published in English and had appeared in peer-reviewed academic journals spanning disciplines such as geography, epidemiology, and disease ecology.

For each article, we extracted core details into a review matrix to provide a standardized basis for cross-study comparison and thematic organization. Key elements included: i) geographic context and spatial scale, such as regional studies, continental models or localized community-based surveys; ii) methodological approach, such as field surveys, GIS-based risk mapping, statistical modelling, qualitative interviews or literature synthesis; iii) focal variables, included those analyzed in relation to Lyme disease or tick vectors, such as land cover types, forest fragmentation, deer or small mammal host abundance, temperature and humidity indices, socio-economic characteristics and prevention behaviours; iv) key findings, regarding risk drivers, tick ecology, disease emergence patterns and any reported interactions or feedback mechanisms. After data extraction, an inductive thematic analysis was conducted to identify recurring conceptual patterns and clustering of related findings. We iteratively grouped studies based on their dominant focus, resulting in three overarching thematic domains: i) climate change and weather variability; ii) ecology, including biodiversity, host dynamics, land cover and habitat alteration; and

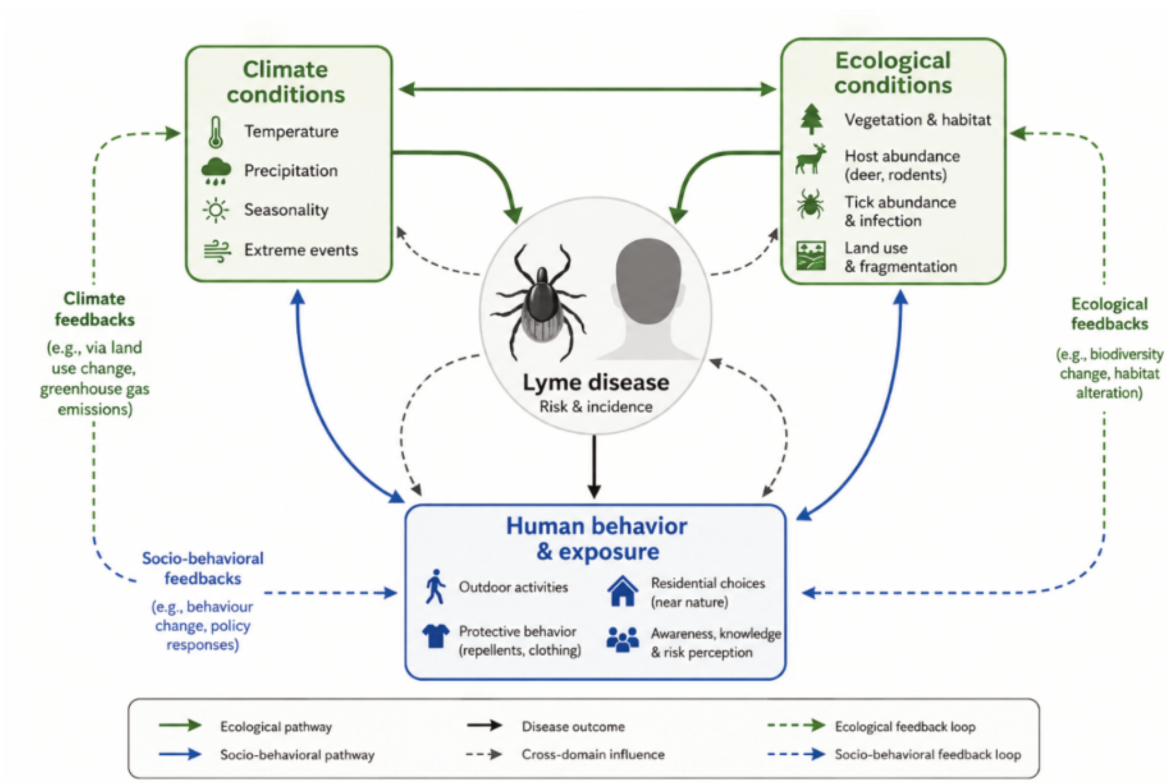

Figure 1. Conceptual image of eco-syndemic system for Lyme disease emergence.

iii) human behaviour and exposure risk. Special attention was paid to studies that reported interdependencies or synergies between these domains, for example, climate-mediated effects on host populations or land cover changes modulating human contact with tick habitats.

Rather than conducting a quantitative meta-analysis, we employed a qualitative comparative approach. This method emphasized convergence and divergence in findings across study contexts and identified where multiple environmental and social drivers acted in concert to shape disease risk. The synthesis also explored potential feedback loops, compounding effects, and cross-scale dynamics relevant to an eco-syndemic framework.

Core synergistic drivers

Lyme disease arises from a confluence of core drivers, which, following our thematic analysis, could be grouped into three broad categories: i) climate conditions; ii) ecological conditions; and iii) human behavior. These drivers do not operate in isolation as their effects often amplify one another, which is key within an eco-syndemic framework.

Climate

Climate change is widely implicated in the expanding incidence and range of Lyme disease as ectotherms accelerate development under higher temperatures, in part because climate influences behaviour, metabolism and molting (Giesen *et al.*, 2024). In addition, the life cycle of *Ixodes* spp. is highly sensitive to temperature and humidity (Couper *et al.*, 2021; Giesen *et al.*, 2024). Warmer average temperatures and milder winters increase tick abundance and prolong the transmission season (Giesen *et al.*, 2024). In New York State, for example, a study found that mild winter temperatures, extended springs and hotter summer days are each followed by higher Lyme disease case counts (S. Lin *et al.*, 2019). These phenological shifts put humans and animals at risk of tick bites for longer periods of the year than previously.

Climate warming also pushes the Lyme disease frontier northward and to higher elevations. Over the past few decades, *Ixodes scapularis* has steadily expanded into more northerly latitudes in Canada and into previously cooler regions of the Upper Midwest and New England, tracking areas that are becoming climatically suitable (Clow et al., 2017; Couper et al., 2021). In Ontario, Canada, field surveillance documented a northward advance of established tick populations as fast as 45–50 km per year, closely matching predictions by climate-based models (Clow *et al.*, 2017). County-level Lyme case data have been found annual temperature increases to be strongly associated with rising incidence in the north-eastern U.S., the region with the currently heaviest Lyme disease burden (Couper *et al.*, 2021). Their model projected that under a Representative Concentration Pathway (RCP) of 8.5, the most extreme of the predictions of the Intergovernmental Panel on Climate Change (IPCC), the Northeast could experience tens of thousands of additional Lyme disease cases already by this mid-century (Couper *et al.*, 2021). Although other regions showed more subtle climate effects, the warming has opened the door for Lyme disease in formerly unsuitable areas (Ogden *et al.*, 2014).

Humidity and precipitation play pivotal roles in shaping tick ecology and the transmission potential of tick-borne diseases (Giesen *et al.*, 2024). Moist, shaded microhabitats created by consistent rainfall or elevated relative humidity enhance tick survival by reducing desiccation and prolonging host-seeking activity, whereas drought and low humidity suppress questing behaviour and increase mortality (Giesen *et al.*, 2024). Indeed, suitable humidity have been identified as a key factor facilitating the northward expansion of *I. scapularis* populations in Ontario, Canada (Clow *et al.*, 2017). Similarly, analyses across the U.S. indicate that humidity alongside temperature exerts a strong positive influence on tick phenology and Lyme disease incidence (Dumic and Severnini, 2018). In Europe, shifts in precipitation patterns and atmospheric moisture have been linked to wider tick distributions and longer transmission seasons, particularly under conditions of warming and higher saturation deficits (Voyiatzaki *et al.*, 2022). Collectively, these findings show that changes in rainfall and humidity critically mediate how climate change reshapes tick dynamics and the spatial ecology of Lyme disease risk (Clow *et al.*, 2017; Dumic and Severnini 2018; Voyiatzaki *et al.*, 2022; Giesen *et al.*, 2024).

Mild winters enhance deer and small-mammal survival, increasing hosts for ticks and raising infection prevalence. At the same time, warmer conditions keep people outdoors longer, heightening exposure. Together, these ecological and behavioural shifts reinforce one another, amplifying Lyme disease risk. A key example is acorn mast years in oak forests: rodent booms following mast events elevate tick infection rates, and climate anomalies influence mast frequency through plant phenology (Ostfeld *et al.*, 2018) Thus, climate acts as a *threat multiplier*—expanding tick habitat and intersecting with host and habitat dynamics. The eco-syndemic framework recognizes climate as a critical yet interdependent factor in Lyme disease emergence.

Ecological conditions

Disease emergence is rarely a sudden biological anomaly but instead reflects long-term disruptions to the dynamic equilibrium linking society, land use and ecological systems (Mayer, 2000). The environmental history of land cover change in the Northeast explains Lyme disease's emergence. Here, post-agricultural reforestation and suburbanization were pivotal drivers (Steere *et al.*, 2004). During the 19th century, widespread clearing of New England's forests for farming reduced habitat for deer and ticks, and by the early 20th century deer were nearly eradicated in certain areas (Steere *et al.*, 2004). As marginal farms were abandoned, forests regenerated, creating favourable conditions for hosts. Legal protections and restocking then fuelled a deer population explosion, while, suburban growth placed homes at forest edges, producing "wooded suburbs" with abundant deer (Steere *et al.*, 2004). These environments proved ideal for *I. scapularis* and *Borrelia* transmission reflecting how land development and population redistribution create repeated spatial coincidences between hosts, vectors and humans, transforming everyday residential landscapes into sites of persistent exposure (Mayer, 2000). The environmental history of the Northeast thus shows how landscape alteration set the stage for Lyme disease; housing expansion into rural forests brings humans into close contact with tick habitat (Patel and Puli, 2024). This recent study reaffirmed that urban and suburban development is a major driver of human exposure through habitat encroachment.

Key features of areas at higher risk of Lyme disease are habitat fragmentation and associated edges. Small forest patches and abundant edge habitat tend to favour certain species like white-footed mice (*Peromyscus leucopus*) and white-tailed deer, while disadvantaging others such as predators and less disturbance-tolerant wildlife, a recipe for efficient *B. burgdorferi* transmission (Keesing and Ostfeld, 2021). Fragmentation also creates more edge habitat, which is typically characterized by dense underbrush and higher levels of light, promoting plant growth that can support rodents, while edges often serve as travel corridors for deer. Ticks thrive in edge environments, which provide humid leaf litter and abundant blood hosts. Human activities frequently concentrate around edges too, making them prime sites for human-tick encounters. Fragmented suburban landscapes thus actively engineer these encounters through their configuration and use (Mayer, 2000). These factors combine to explain why residential fragmentation and patchy suburban landscapes correlate with elevated Lyme disease rates in many regions (Kilpatrick *et al.*, 2017; Leibovici *et al.*, 2021; Ballard and Bone 2021). In short, the way we shape and configure our landscapes by cutting forests, creating residential lots, and altering plant and animal communities has direct repercussions for the Lyme disease system.

Deforestation and logging may initially reduce habitat for ticks and hosts, but subsequent regrowth can create dense thickets ideal for ticks and hosts. Logging roads and forest clearings create edges and increase human access, raising long-term exposure. In Europe, agricultural and forestry conversion has shifted host distributions and tick-borne disease patterns (Giesen *et al.*, 2024). Recreation infrastructure (e.g., parks, trails, campgrounds) also focalizes encounters, as ticks thrive along trail edges and in peri-urban parks. Recent work similarly shows that urban tick and Lyme disease hazards may be shaped not only by conditions within cities, but also by surrounding hinterland tick abundance and land cover, emphasizing the importance of cross-scale rural–urban landscape connections in Lyme disease risk (Gandy *et al.*, 2025). On Staten Island, New York, for example, significant tick populations emerged in city green spaces alongside expanding deer populations in predator-free refuges (Tamari *et al.*, 2024). These examples reinforce how land management, development decisions, and human mobility collectively form part of the causal chain driving Lyme disease emergence and persistence (Mayer, 2000).

The wild-land–urban interface is a space of constant tension, where expanding neighbourhoods press against forests and fields, increasing ecological disturbance. In this zone, human activity and natural processes collide, reshaping landscapes, habitats, and patterns of exposure. Land use/land cover changes drive Lyme disease emergence by creating interfaces between humans and tick habitat. Wooded suburbs, fragmented forests, and urban parks blend living space with tick–host cycles, increasing exposure during daily activities (e.g., children playing at yard edges) or recreation (e.g., hiking, hunting). A recent study noted that urban encroachment into natural habitats has drawn communities closer to ticks (Patel and Puli 2024). Thus, landscape alteration can outpace health response, enabling hotspots to expand. Thus, environmental history reveals how land-use and settlement patterns repeatedly align humans, vectors, and pathogens, transforming routine landscapes into sustained disease risk (Mayer, 2000). In the eco-syndemic framework, land cover change is a vital driver; fragmentation and encroachment not only benefit ticks but also compound biodiversity loss, reducing ecological checks and amplifying transmission.

Biodiversity plays a central role in Lyme disease dynamics. The dilution effect hypothesis posits that high biodiversity dilutes pathogen transmission by spreading vectors across a variety of hosts, including less competent hosts (Keesing and Ostfeld, 2021). For Lyme disease, host species vary widely in competence: white-footed mice, chipmunks, and shrews infect a high proportion of feeding ticks, whereas squirrels and deer are poor or dead-end hosts (Keesing and Ostfeld, 2021). In intact, species-rich ecosystems, ticks are more likely to feed on these non-competent hosts, lowering overall infection prevalence. Biodiversity loss, however, often favours species that are efficient reservoirs. Human-disturbed landscapes like suburbs and farms disproportionately support small, fast-lived mammals, while predators and larger, long-lived species decline (Keesing and Ostfeld, 2021). The result is reservoir-dominated communities where most tick meals come from highly competent hosts. Long-term studies support that reduced predator diversity correlates with higher infection prevalence in ticks (Ostfeld *et al.*, 2018). Fragmentation and simplified food webs allow mice to reach high densities unchecked, amplifying infected tick numbers (Ostfeld *et al.*, 2018). Likewise, a grounded study has shown that Lyme disease risk closely tracked small mammal abundance, with years with high mouse and chipmunk populations resulting in spikes in infected nymphs (Levi *et al.*, 2012). Thus, biodiversity loss elevates Lyme disease risk through reservoir dominance in such ecosystems. However, high biodiversity may dilute transmission, while degraded ecosystems dominated by usual reservoirs such as mice, chipmunks, and deer elevate risk (Keesing and Ostfeld, 2021).

Deer and wild boar also disperse ticks by carrying engorged females into new areas, helping establish Lyme disease and other tick-borne diseases in previously tick-free patches (Steere *et al.*, 2004; Castillo-Contreras *et al.*, 2022). However, as described previously, deer abundance has limits to the support of tick populations; beyond moderate density, more deer do not yield more Lyme disease, as ticks become constrained by larval and nymph host availability (Levi *et al.*, 2012; Kilpatrick *et al.*, 2017). Deer removal experiments confirm their pivotal role, with drastic reductions in tick numbers, but adding deer to saturated areas brings diminishing returns (Kilpatrick *et al.*, 2017). In fragmented landscapes, deer and mice act synergistically; deer boost tick abundance while mice amplify infection prevalence. Other secondary hosts (e.g., birds, raccoons) also shape Lyme disease dynamics (Ostfeld *et al.*, 2018). For instance, birds may play a subtle but important role in the geographic expansion of Lyme disease. As they can be mobile hosts for immature ticks, some bird species can transport infected ticks over long distances, introducing them into new habitats and facilitating the establishment of *B. burgdorferi* in previously uncolonized regions (Ostfeld *et al.*, 2018).

Changes in predator communities are a crucial but sometimes underrated element of the Lyme disease eco-syndemic. Top predators, like wolves and foxes, and even mesopredators can regulate rodent populations through predation pressure, e.g., the decline of red foxes in eastern North America due to the rise of coyotes (Levi *et al.*, 2012). This study presents a theoretical model and empirical data suggesting that a range-wide decline in red fox abundance coincident with coyote expansion is correlated with increase in Lyme disease explained by fewer foxes leading to growing mouse populations, which in turn has led to more infected ticks. Similarly, another study found that areas with a functionally-diverse predator community had significantly lower infection prevalence in ticks compared to areas where key predators were absent (Ostfeld *et al.*, 2018). In their study, the presence of bobcats, a top carnivore in the New York region, was associated with reduced *B. burgdorferi* infection in ticks, presumably because bobcats help keep rodent numbers in check. Interestingly, they also observed that if smaller predators, such as foxes, are missing and coyotes are present, tick infection prevalence moves higher, which reinforces the idea that specific predator composition matters (Ostfeld *et al.*, 2018). Many human-altered landscapes have lost their top-down control. For instance, suburban and peri-urban areas rarely have large predators such as wolves or cougars and limited numbers of coyotes or bobcats, and even mid-sized predators may be scarce due to road deaths and intentional culling by humans. Thus, human influence often simplifies food webs in a way that favours prey species like rodents and deer, thus also favouring ticks. Restoring predators or controlling mesopredator dynamics could, in theory, help reduce Lyme disease risk (Ostfeld *et al.*, 2018; Keesing and Ostfeld, 2021). Human-driven changes often restructure entire species networks, and a consistent theme across studies is that biodiversity loss tends to increase human exposure to zoonotic pathogens, Lyme disease included (Keesing and Ostfeld, 2021). This situation suggests that conserving and restoring biodiversity could be a tool for disease mitigation, an idea that aligns well with an eco-syndemic approach. In fact, Keesing and Ostfeld (2021) argue that "restoration of biodiversity is an important frontier in the management of zoonotic disease risk" highlighting that protecting natural ecosystems may yield health benefits by re-establishing the ecological interactions that keep pathogens in check. This kind of changes often amplify the effects of climate and land cover drivers reaffirming the need to view Lyme disease emergence through an eco-syndemic lens.

Human behaviour and exposure

Human behaviour links environmental risk to Lyme disease. Even in tick-rich areas, cases occur only when people encounter infected ticks and are bitten. Rising recreation, suburban expansion, and yard use place more individuals at woodland edges, increasing exposure. Farmers, hunters, and outdoor enthusiasts face elevated risk, while pet ownership heightens contact at vegetation edges (Tamari *et al.*, 2024). Urban parks and community gardens have also served as transmission sites (Tamari *et al.*, 2024). Seasonality matters; peak outdoor activity in late spring and summer coincides with higher activity levels among ticks at the nymphal stage. Behaviour thus dynamically amplifies or buffers ecological risk through choices and precautions.

Public health campaigns emphasize personal protective measures; repellent, tick checks and prompt removal of attached ticks have been shown to reduce infection incidence, yet adoption is inconsistent (Beck *et al.*, 2022; Cuadera *et al.*, 2023). Surveys in endemic regions show varied awareness and uneven practice. In the U.S. Upper Midwest, 98% of respondents had heard of Lyme and knew the pathogen is transmitted by ticks, yet this knowledge did not result in consistent prevention methods (Beck *et al*., 2022). Common gaps included irregular tick checks, infrequent repellent use or reluctance to wear protective clothing. Misconceptions persist with some respondents assuming risk only exists deep in forests, or that absence of deer populations ensures safety, ignoring or misunderstanding the role of reservoir hosts.

Risk perception strongly shapes behaviour; people who view Lyme disease as serious or know affected individuals are likelier to adopt precautions (Beck *et al.*, 2022; Cuadera *et al.*, 2023). By contrast, newcomers to an endemic area or those in communities where Lyme disease is just now emerging often lack awareness until incidence rises. Patel and Puli (2024) note critical gaps in identification and management in regions without clinical familiarity, leading to underdiagnosis. Socioeconomic and cultural factors also matter; fencing and specific landscaping measures reduce risk but are costly, leaving lower-income groups less protected, while affluent communities may have greater access to such measures, though such communities are more often near high-risk wooded edges. Fear of Lyme disease can motivate behaviour changes that actually reduce risk. Communities with heavy Lyme disease burdens often develop a culture of vigilance in which tick checks become routine and schools educate children on ticks.

In addition to its effects on exposure, human behaviour also affects how diseases are detected and reported. If people do not seek medical care or recognize a tick bite, cases may go unreported, contributing to underestimation of true incidence. The Centers for Disease Control and Prevention (CDC) in the U.S. estimates that actual Lyme infections are an order of magnitude higher than reported cases, partly due to underreporting (Kilpatrick *et al.*, 2017; CDC 2025b. This underreporting can be exacerbated by lack of awareness in both the public and medical community, mainly in emerging areas. Conversely, heightened public awareness and clinician education can improve case detection. Heightened clinical awareness is noted as one factor behind increasing Lyme case numbers – as more doctors look for and test for Lyme, more diagnoses and reports are made (Patel and Puli, 2024).

Community-scale interventions to reduce human–tick contact show mixed results. Integrated tick management programs have been attempted in some neighbourhoods (Ostfeld and Keesing, 2023). A multi-year study in New York tested rodent bait boxes with acaricide and fungal yard sprays but found no statistically significant reduction in human–tick encounters or Lyme disease cases, even if tick densities dropped by about 50% in treated sites (Ostfeld and Keesing, 2023). This paradox suggests that ecological risk reduction alone may be insufficient; people may still be exposed in untreated areas, or fail to adopt personal precautions, sustaining infection rates, and the authors conclude that neighbourhood-scale interventions are insufficient on their own. This reinforces the eco-syndemic principle that lasting progress requires coupling ecological measures with behavioural change, community awareness and the broader insights highlighted in other studies (Steere *et al.*, 2004; Ostfeld *et al.*, 2018; Couper *et al.*, 2021; Keesing and Ostfeld, 2021; Patel and Puli, 2024;)

Synthesis: interactive and non-linear dynamics

This review employed a structured, narrative approach to synthesize current scientific understanding of the synergistic drivers of Lyme disease emergence, using an eco-syndemic framing. We drew from a curated collection of peer-reviewed scholarly articles that were selected to represent the intersection of ecological, climatic, and socio-behavioural factors relevant to Lyme disease transmission, particularly within the context of North America. Because the same climatic, ecological, and social drivers operate across multiple parts of the Lyme disease system, this synthesis revisits selected concepts only to synthesize their interactions, feedbacks, and non-linear effects rather than to restate them as independent risk factors.

No single driver operates in isolation; the emergence of Lyme disease is characterized by *interactive and non-linear dynamics* among climate, ecological conditions, and human factors. The recent study by Ali *et al.* (2024) finding that Lyme disease incidence exhibits opposing spatial synchrony patterns driven by combinations of environmental and social variables, rather than by any single factor alone, reinforces the eco-syndemic principle that climate, ecological structure, and human behaviour interlock to produce non-linear, region-specific risk patterns. The cumulative impact of these drivers is often greater than the sum of their parts in terms of Lyme disease risk. The core drivers of Lyme disease, climate change, ecological dynamics, and human behaviour, operate through interwoven feedbacks that magnify disease risk beyond the influence of any single factor. Climate warming extends the seasonal activity and geographic range of ticks, but its effect depends heavily on the surrounding land cover and host community. In fragmented suburban forests, warmer winters coincide with abundant deer, fewer predators, and dense rodent populations, forming ideal conditions for tick proliferation and *B. burgdorferi* transmission (Levi *et al.*, 2012; Ostfeld *et al.*, 2018; Couper *et al.*, 2021). Land cover alteration, including reforestation, suburban expansion, and edge creation, shape both ecological dynamics and human exposure; fragmentation simplifies food webs, favoring competent reservoirs like white-footed mice while discouraging predators that help regulate them (Steere *et al.*, 2004; Keesing and Ostfeld, 2021). These ecological imbalances amplify the effects of climatic suitability.

Human behavior then translates ecological risk into realized disease burden. Warmer temperatures and wooded residential settings encourage more outdoor recreation and yard use, increasing contact with infected ticks (Tamari *et al.*, 2024; Beck *et al.*, 2022). At the same time, gaps in awareness and uneven adoption of preventive measures sustain vulnerability even where ecological interventions have reduced tick densities (Ostfeld and Keesing 2023). Feedback loops emerge; high incidence spurs behavior change and management responses, but these often lag behind environmental shifts. Collectively, these interactions exemplify an *eco-syndemic system* in which climate, ecological conditions, and human behavior continuously reinforce one another, entrenching Lyme disease as a persistent coupled human–environment challenge (Kilpatrick *et al.*, 2017; Giesen *et al.*, 2024; Patel and Puli, 2024). The main drivers of Lyme disease identified in this study often reinforce each other. Climate change expands tick-suitable areas, but outcomes depend on ecological conditions. Warming temperatures in an area characterized by suburban fragmentation would likely magnify Lyme disease risk with abundant deer, fewer predators, and edge habitats, whereas intact wild areas may see only modest increases in Lyme disease risk even under warming temperatures. When ecological conditions that support the zoonotic Lyme disease transmission cycle, human behaviour then translates risk into illness; for example, gardening or hiking in an at-risk setting without precautions can lead to human cases. Rising incidence can prompt application of preventative practices or management decisions (e.g., deer culls, insecticides), but feedbacks to dampen the risk to humans naturally lag, allowing the drivers to compound in reinforcing cycles.

The north-eastern U.S. exemplifies an eco-syndemic system where states, such as Connecticut and Vermont show converging risks driving Lyme disease to record levels. Reforestation created fragmented forests and suburbs with thriving deer (Steere *et al.*, 2004), low biodiversity, and abundant mice (Levi *et al.*, 2012; Ostfeld *et al.*, 2018). Warming winters lengthen tick seasons and extend ranges northward (Brownstein *et al.*, 2005; Burtis *et al.*, 2016; Clow *et al*., 2017; S. Lin *et al*., 2019; Deshpande *et al.*, 2024).

A hallmark of eco-syndemic systems is their non-linear behaviours; small changes can trigger large effects once thresholds are crossed. Deer abundance illustrates this point. Once deer densities surpassed a critical threshold, tick populations flourished and Lyme disease incidence rose exponentially as farmland across the north-eastern U.S. reverted to woodland, albeit in a fragmented configuration, deer populations rebounded, white-footed mice remained abundant, while moist, shaded environments near rivers and coastal areas created favourable conditions for tick survival and persistent transmission 2004). Host diversity reveals a similar tipping point; when previously-diverse communities collapse to a few competent hosts, such as white-footed mice, tick infection rates surge disproportionately (Ostfeld *et al.*, 2018). Climate change may also produce thresholds; several mild winters can suddenly permit tick survival in previously unsuitable regions, catalyzing invasion and amplification that is not easily reversed by a single cold year.

These dynamics create entrenched high-incidence equilibria. In parts of New England, Lyme disease remains persistent despite decades of public awareness and deer control, as the eco-social system now strongly favours transmission (Ostfeld, 2011). This author emphasizes feedback loops that complicate matters further, while rising incidence may spur yard treatments or avoidance of risky habitats, potentially reducing exposure. Awareness may increase case reporting, amplifying apparent incidence even without heightened transmission. Thus, thresholds and feedbacks reinforce the resilience and complexity of Lyme disease emergence.

The New England case shows Lyme disease as a coupled human–natural system, not purely ecological or social. Effective reduction requires multi-level action: deer and predator management, restoration of dilution species, tick-unfriendly landscaping, and vigilant personal protection. This approach aligns with an eco-syndemic view. Communities are piloting multi-level action approaches, such as One Health Lyme disease programs that integrate animal, human, and environmental surveillance to better understand and manage disease risks (Giesen *et al.*, 2024). These programs track ticks, wildlife infection, and human cases to reveal leverage points where interventions can most effectively interrupt transmission and reduce Lyme disease risk. Because drivers interact nonlinearly, single measures (e.g., repellents or deer culls) rarely suffice, holistic strategies are essential.

To further synthesize the review, Figure 2 presents the reinforcing eco-syndemic pathways through which climate conditions, land cover alteration, biodiversity loss, host dynamics, tick ecology, and human behaviour interact to shape Lyme disease emergence. Rather than operating as independent drivers, these domains form a connected system in which environmental change alters habitats and host communities, ecological shifts influence tick abundance and infection prevalence, and human behaviour determines realized exposure. The figure highlights the feedbacks and non-linear relationships emphasized throughout this review, illustrating how Lyme disease risk emerges from the convergence of climatic, ecological, and social processes.

Limitations

As a structured narrative review, this study has several methodological limitations. First, although the literature was selected to capture major climatic, ecological, and socio-behavioural drivers of Lyme disease emergence, the review did not follow a formal systematic review protocol or conduct a quantitative meta-analysis. As a result, some relevant studies may have been missed, and the synthesis may reflect selection bias toward studies most directly aligned with the eco-syndemic framing. Second, the review was limited to English-language, peer-reviewed literature, which may exclude relevant studies published in other languages or in gray literature. Third, we did not conduct a formal quality appraisal or risk-of-bias assessment of individual studies. Therefore, the findings should be interpreted as a conceptual and thematic synthesis rather than a comprehensive quantitative assessment of the strength of evidence for each driver. Despite these limitations, the structured narrative approach was appropriate for integrating diverse evidence across climate, ecology, land cover, host dynamics, tick ecology, and human behaviour.

Research gaps and future directions

Significant research gaps hinder our ability to predict and control Lyme disease, especially gaps that involve bridging ecological and social dimensions. This section outlines research gaps and future directions for Lyme disease and other tick-borne diseases. In particular, we recommend greater focus on developing integrated, cross-scale models that link climate, landscape, ecological, and human factors; incorporating human behaviour, socioeconomic context, and equity into Lyme disease surveillance; establishing joined ecological–social monitoring systems and strengthening Health Impact Assessments (HIAs) to anticipate and mitigate dis-

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ease risk from environmental change; and advancing adaptive, community-centred interventions that ensure accessibility and effectiveness across diverse populations.

One major gap is the lack of integrative models spanning micro-scale tick processes, broad-scale landscape ecology, and regional climate factors, while also incorporating human behavioural factors. Most epidemiological models correlate Lyme incidence with climate or land cover factors, but rarely both, and they seldom include human behaviour or socioeconomic factors. Thus, no unified predictive model exists for Lyme under future environmental change. Researchers urge One Health and socio-ecological approaches (Pfäffle *et al*., 2013; Giesen *et al*., 2024), both of which complement an eco-syndemic framework by recognizing that human, wildlife, and environmental health are inseparable in shaping Lyme disease risk. Interdisciplinary teams could build simulations linking ticks, hosts, humans, land cover and climate to identify tipping points, test combined strategies and forecast hotspots, which would represent moving beyond correlative work toward truly integrative prediction. Another notable gap is the limited use of human behavioural data in Lyme disease risk mapping and forecasting. Most maps rely on environmental predictors, such as tick presence, host distribution, or climate suitability, and assume uniform human exposure. Yet cases are often patchy even in high-tick areas due to differences in community behavior, awareness, and healthcare access. Some studies provide valuable data on knowledge, attitudes, and practices, but such social metrics are rarely integrated with ecological surveillance (Beck *et al.*, 2022; Tamari *et al.*, 2024). Consequently, public health officials may know where ticks are but not how vulnerable or prepared local populations are.

Future efforts should build integrated surveillance systems that couple tick monitoring with resident surveys on tick knowledge and prevention. Citizen science and smartphone apps show promise by recording human–tick encounters; Patel and Puli (2024) also noted that such initiatives help bridge gaps but remain underutilized, especially in resource-poor regions. Socio-economic analyses are also needed to uncover disparities in who gets sick and why, informing targeted outreach. Broader geospatial health research also suggests that urban change, housing conditions, and neighbourhood transformation can shape infectious disease vulnerability, reinforcing the need to integrate socio-spatial inequities into future Lyme disease surveillance and prevention research (Kiani *et al*., 2025). In short, embedding the human factor into risk models is essential, ensuring interventions reach the right people and do not miss vulnerable communities.

A promising avenue for strengthening Lyme disease prevention and control lies in adopting HIAs as a formal decision-support tool. CDC (2025c) defines HIAs as a structured process that combines scientific data, health expertise, and stakeholder input to evaluate the potential health effects of policies, projects, or plans before they are implemented. In the context of Lyme disease, HIAs could be used to anticipate how land development, forest management, or urban expansion may alter tick habitats, host populations, and human exposure risks. Building on established frameworks that emphasize equity, sustainability, and community participation (Harris-Roxas *et al.*, 2012), HIAs can operationalize the eco-syn-

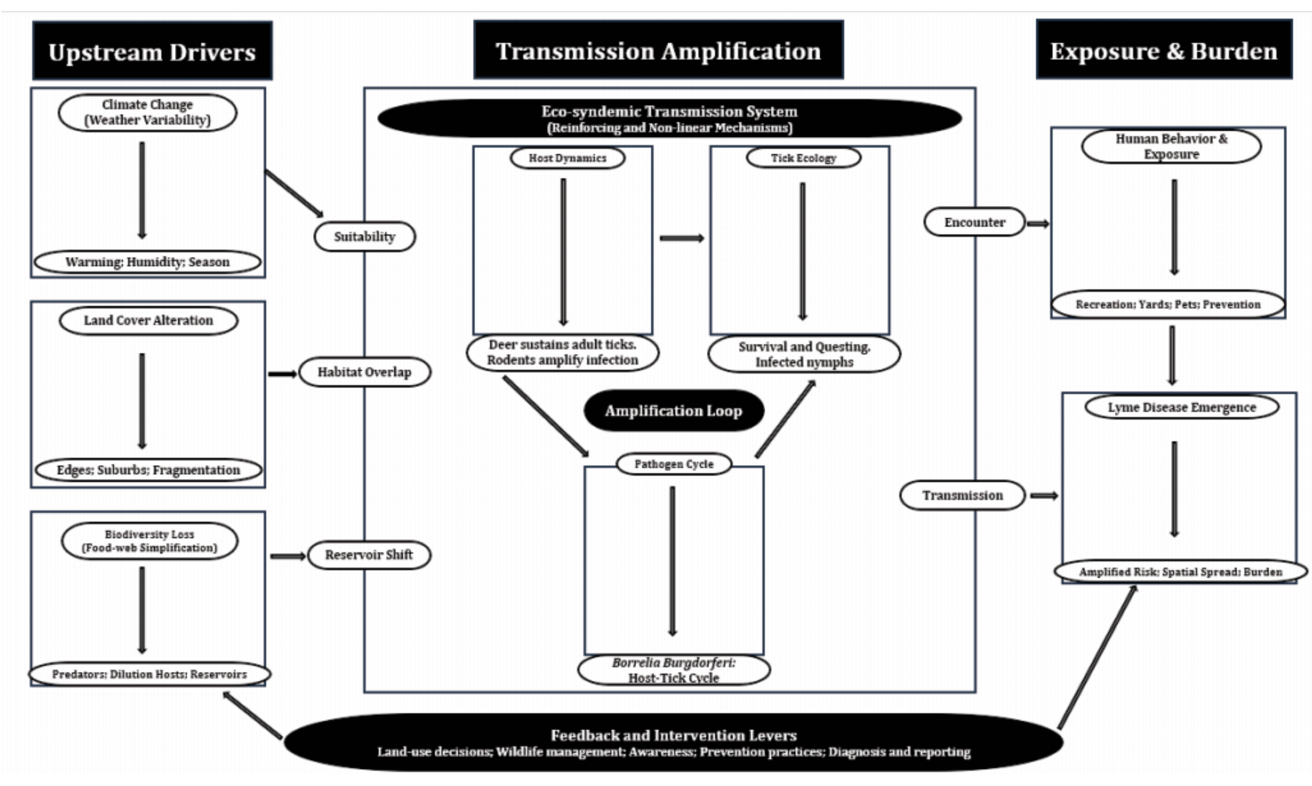

Figure 2. Visual synthesis of reinforcing eco-syndemic pathways driving Lyme disease emergence.

demic and One Health perspectives by systematically linking environmental change, wildlife ecology, and public health outcomes. This approach would allow policymakers to compare alternative land-use strategies or intervention programs not only in terms of economic feasibility but also long-term health implications. Conducting localized HIAs could further ensure that prevention measures such as vegetation management, housing design, or recreation planning protect vulnerable groups and reduce health inequities. Overall**,** integrating HIAs into Lyme disease planning provides a structured, anticipatory framework for decision-making that aligns with the eco-syndemic vision: addressing disease emergence through proactive, multi-sectoral collaboration that considers the full human–environment system.

Finally, future Lyme research must consider ecological adaptation and equity. Adaptive measures like controlled burns, habitat management, or novel tick control technologies (e.g., anti-tick vaccines designed to prevent ticks from successfully feeding on hosts (Abbas, Muhammad Nadeem, Mohamed Amine Jmel, Imen Mekki, Ingrid Dijkgraaf, and Michail Kotsyfakis. 2023) may disrupt transmission. With respect to equity, ensuring that interventions, such as a hypothetical vaccine, are accessible and that public health messaging reaches diverse populations is crucial. Research should proactively address how to implement solutions in a way that reduces, rather than exacerbates, existing health disparities. For instance, if tick control relies on individual yard treatments, renters or low-income households might be excluded unless community-level solutions are provided.

Conclusions

In conclusion, this eco-syndemic review highlights both knowledge gained and persistent uncertainties. The future of Lyme disease research and control lies in embracing complexity and connectivity. As Kilpatrick *et al.* (2017) emphasize, substantial uncertainty still exists on fundamental aspects, such as tick population regulation, that hamper predictive models. Filling these gaps will require multi-scalar, integrative studies. The conceptualization of Lyme disease as an eco-syndemic pushes us to ask integrative questions and to build the scientific and public health infrastructure for integrated answers. By doing so, we do not only improve our understanding of Lyme disease but also strengthen our capacity to handle other vector-borne and zoonotic diseases that are driven by similarly complex socio-environmental interactions.

Lyme disease has become a persistent public health challenge not because of a single cause, but through the convergence of multiple environmental and societal changes. Its rise reflects coupled ecological and human forces; climatic warming, evolving land covers, shifting wildlife communities, and human behaviours have combined to create landscapes of heightened risk. This review applied the eco-syndemic framework to capture this reality, viewing the Lyme epidemic as the outcome of interacting epidemics in climate, ecology with biodiversity loss, and society as tied to suburbanization and outdoor lifestyles. This framing is more than conceptual; it has practical implications for how we monitor, prevent, and respond to emerging diseases.

An eco-syndemic perspective emphasizes that siloed approaches are inadequate. Public health strategies must move beyond isolated interventions, and research must move into true transdisciplinary spaces that involve academic disciplines ranging from ecology, entomology, geography, climate science, and sociology, as public health, which effectively serves as a connection between academic research and community stakeholders, such as veterinarians, park services, and the general public. Holistic monitoring involving surveillance systems that integrate environmental indicators with human behaviour data to anticipate outbreaks is needed. Integrated planning is equally important; urban planners, wildlife managers, and health officials must design communities that balance human use of green space with tick control. Educational campaigns should extend beyond personal protection, promoting yard management, pet care, and community-level actions like deer management policies.

The eco-syndemic lens also highlights that no single biomedical solution will suffice. Vaccines and diagnostics are invaluable, but their impact will be maximized only when embedded within broader environmental and behavioural strategies. For example, a human vaccine might reduce cases, but without addressing ecological drivers, people would still face tick bites and risks of other tick-borne infections. Long-term goals should focus on rebalancing human–nature relations by restoring ecological checks (e.g. predators, diverse hosts), managing lands to reduce tick habitat near homes, and normalizing tick awareness akin to sun protection or road safety. This approach aligns with the One Health paradigm, recognizing human health as intertwined with animals and ecosystems. It also reflects the eco-syndemic perspective, which emphasizes how social, ecological, and environmental processes interact to shape disease dynamics. Lyme disease control likely requires the One Health approach, with collaboration between veterinarians, environmental agencies, health departments, park services, and schools.

Ultimately, Lyme disease illustrates a larger lesson: we live in a world of accelerating, intersecting changes in climate, land, wildlife, and human behaviour. Its eco-syndemic nature calls for a panoramic, One Health–aligned systems approach that transcends disciplinary boundaries, fostering resilience not only against this disease but against the growing web of vector-borne and zoonotic threats driven by our changing planet.

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Received: 23 December 2025; Accepted: 16 June 2026.

Contribution: Michael F. Ojo and Korine N. Kolivras jointly contributed to the conceptualization and overall framing of the review. Michael F. Ojo conducted the literature search, led the synthesis and analytical integration of findings, and prepared the original draft of the manuscript. Korine N. Kolivras provided methodological guidance, critical evaluation, and substantive revisions that refined the structure, clarity, and scholarly rigor of the review. Both authors contributed to the interpretation of the findings, participated in the revision process, and approved the final version of the manuscript.

Conflict of interest: the authors declare no competing interests.

Availability of data and materials: all data generated or analyzed during this study are included in this published article.

Acknowledgements: the authors acknowledge the academic environment and support that facilitated the development of this review article.

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