ANNUAL REVIEWS

Annual Review of Entomology

Tick-Borne Diseases in Urban and Periurban Areas: A Blind Spot in Research and Public Health

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Annu. Rev. Entomol. 2026. 71:615–34

First published as a Review in Advance on December 2, 2025

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-121423-013702

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Keywords

Lyme, urban, *Ixodes*, *Borrelia*, tick, risk

Abstract

Tick-borne zoonotic diseases continue to emerge in North America and Europe. Of particular concern are pathogens transmitted by *Ixodes* ticks, such as *Borrelia* spp., the causal agents of Lyme disease (Lyme borreliosis). Because *Ixodes* ticks are adapted to forested habitats with high humidity and depend on wildlife for feeding and movement, research has focused on natural or rural landscapes. Demographic and land-use transitions, however, have created novel ecosystems in urban and periurban areas with high potential for human exposure. We describe post–World War II land processes giving rise to these ecosystems and explore resource-based habitat concepts and top-down community ecology perspectives aimed at predicting tick-borne disease (TBD) risk. We review studies in Europe and North America that demonstrate TBD risk in urban areas and potential drivers for TBD emergence. We identify missed opportunities for data measurements and reporting and propose metrics to quantify landscape connectivity to facilitate future syntheses or meta-analyses.

1. THE ROLE OF URBAN AND PERIURBAN AREAS FOR TICK-BORNE DISEASE RISK

Urban: characterized by higher concentrations of continuous buildup, population, and activities than the surrounding areas

Periurban: characterized by a mix of urban and rural environmental or socio-economic features not necessarily spatially associated with a city

Suburban: describes areas at the fringe of cities characterized by lower density buildup and often dominated by detached housing

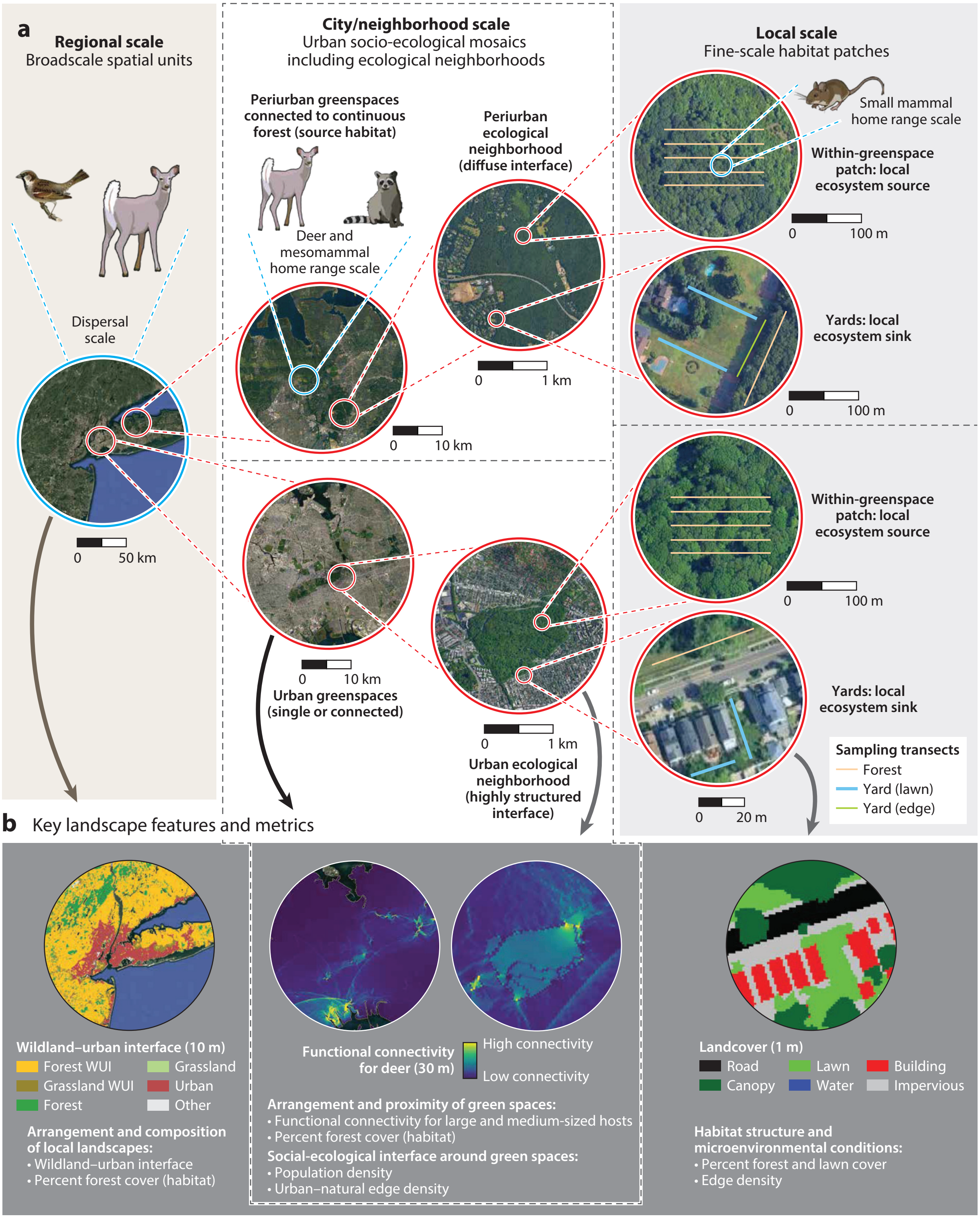
Novel urban ecosystem: an ecosystem persisting or arising in cities that is structured by intentional or indirect management actions and has a unique species composition providing ecosystem services and disservices

Urban and periurban areas are key locations for zoonotic disease emergence and circulation, as they support close interactions between humans, domestic animals, and wildlife (2, 20, 26, 63). Urban and periurban landscapes have seen extreme growth since World War II (130), with 68% of the human population expected to live in urban areas by 2050 (140). While landscapes are becoming more (sub)urban globally, urban areas are attracting efforts to create greener environments for climate-change mitigation and adaptation and human well-being. As cities become greener, their surroundings become more urbanized, and wild vertebrates adapt to live in the vicinity of humans, tick-borne diseases (TBDs) can become a public health threat in urban ecosystems where they have been less studied.

Tick-borne zoonoses—and in particular some *Ixodes*-borne diseases—are well-suited to explore the impact of greening on zoonotic risk in urban and suburban settings, given their strong dependence on natural habitats and differential linkages to wildlife species. In the Northern Hemisphere, the genus *Ixodes* [277 species (41)] includes the most important tick vector species (*Ixodes ricinus*, *Ixodes scapularis*, *Ixodes pacificus*, and *Ixodes persulcatus*), which transmit *Borrelia burgdorferi* sensu lato, the bacterial agents of Lyme disease (also known as Lyme borreliosis), in addition to other bacterial, protozoan, and viral pathogens (126). These members of the *Ixodes* genus also cause noninfectious conditions such as tick paralysis, which is caused by neurotoxins secreted by the salivary glands of certain female or male ticks (31). We focus on *I. scapularis* and *I. ricinus* in this review, and therefore primarily on Eastern North America and Western Europe, given the more extensive literature on urban and suburban settings; findings can sometimes be generalizable to other *Ixodes* species and metastriate tick vectors (56).

Ixodes ticks have been documented in urban areas as early as the late 1980s in the United States (42) and the late 1990s in Prague, Czech Republic, and Helsinki, Finland (8, 76, 113). Since then, many urban areas have been assessed for the presence and abundance of ticks and/or tick-borne pathogens (TBPs) although there is no comprehensive database presently available. Research on the ecology of emerging human TBDs has focused, until recently, on sampling habitats favorable for ticks during off-host periods, i.e., forests and woodlands (18, 95). Forests have been expanding in many regions in the United States and Europe, and, along with climate change, this has been linked to the expansion of TBDs in the United States (151) and Europe (106). However, at the landscape scale, it is the fragmentation—or perforation (34)—of these expanded woodlands by agriculture or urbanization that has been increasingly linked to TBD hazard (measured as the density of infected vectors) as well as increasing likelihood of human exposure to the hazard, both reinforcing risk (34). Biodiversity loss driven by habitat fragmentation has been proposed as the mechanism mediating TBD emergence in urban areas, as it leads to community dominance of highly competent hosts for TBPs in the most urbanized settings [a dilution effect (3, 107)]. However, rather than considering urban ecosystems as impoverished versions of other landscapes or analogous versions of fragmented agricultural landscapes, we propose to consider them as novel ecosystems (66). These novel urban ecosystems are characterized by a unique host and tick community composition that is driven by the extreme barriers imposed on wildlife, novel resources, and intense overlap of wildlife with domestic animals and humans, which, in combination, can drive human exposure to TBDs (**Figure 1*a***).

Recognition of the unique nature of urban ecological interfaces for TBDs has expanded the focus from primary tick and tick-host habitats to areas combining such habitats with high human exposure, including periurban and urban areas. However, characterizing habitat features



(*Caption for* ***Figure 1*** *appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Tick-borne disease risk in novel urban ecosystems, shown at nested spatial scales. (*a*) Spatial scales [regional (50 km), city/neighborhood (1–10 km), local (20–100 m)] relevant to the presence and density of ticks in sampled transects at the local scale. Scales correspond to host home range sizes (*small blue circles*). (*Top*) Periurban settings. (*Bottom*) Urban greenspaces. Transects are the smallest sampling unit across homogeneous habitats [e.g., forest (*orange lines*), lawn (*blue lines*), edge of forest and lawn (*green lines*)]. (*b*) Key landscape features and metrics to assess tick-borne disease risk at multiple scales: regional scale (wildland–urban interface), city/neighborhood scale (landscape connectivity based on circuit theory), and local scale (e.g., percent forest cover). Abbreviation: WUI, wildland–urban interface.

maximizing TBD risk in urban environments has proved challenging. Here we undertake a scoping review that uses the references listed in **Table 1** and other references to inform a conceptual framework characterizing and quantifying the risk for TBDs in novel urban and periurban ecosystems. After a brief history of urban landscapes in Europe and the United States (Section 2), we describe the novel TBD urban ecosystem across scales and with bottom-up and top-down perspectives (Section 3) and end with some forward-looking directions to study TBP ecosystems (Section 4).

Table 1 Studies comparing the density of *Ixodes* spp. nymphs and/or *Ixodes* spp. infection prevalence with *Borrelia burgdorferi* sensu lato across urban gradients or categories of urbanization as defined by the authors

Reference	Comparisons covered in the study, as defined by the authors	Land cover where density of *Ixodes* nymphs was greatest	Land cover where *B. burgdorferi* s.l. infection prevalence in nymphal *Ixodes* was greatest
16	Urban gardens and parks versus periurban forests	U	–
19	Urban parks versus protected forest	R	R
24	Urban parks versus urban forests	–	NS
80	Urban versus natural sites	R	NS
147	Urban versus natural ecosystems	–	NS
4	Urban forest patches of different sizes and distances among them	U	U
60	Woodlands in urban, periurban, and rural zones	NS	NS
112	Urban core, suburban, and periurban areas	R	–
131	City parks versus nonurban residential and recreational areas	NS	NS
154	Forested sites in an urban-to-rural gradient	–	NS
65	Gradient in green space isolation from periphery to urban center	R	R
116	Gradient in urbanization grade (% urbanized area)	NS	U
143	Gradient in greenspace connectivity for deer movement	R	R
91	Gradient in greenspace connectivity for deer movement	R	R

Abbreviations: –, not reported; NS, no significant differences in *Ixodes* spp. density or infection prevalence between U and R; R, rural or low-fragmentation land cover; U, urban or high-fragmentation land cover.

2. A BRIEF HISTORY OF ANTHROPIC LANDSCAPES IN EUROPE AND NORTH AMERICA

2.1. Post–World War II: Urbanization, Rural Abandonment, and Urban Sprawl

For most of human history, cities represented a small fraction of land and population, well differentiated from their rural surroundings. However, over the course of the nineteenth and twentieth centuries, many largely rural, agrarian societies transformed into largely urban, industry- or service-based economies, a phenomenon called the urban transition. Our areas of focus underwent the urban transition between the 1950s and 1970s (129). By 1960, 58% of the population of the current 27 member states of the European Union and 70% of the North American population were urban, and these figures reached 75 and 83%, respectively, as of early 2025 (137). Similarly, the amount of built-up land increased continuously, going from 6.61 Mha to 14.77 Mha and from 7.21 Mha to 26.21 Mha from 1950 to 2020 in Europe and North America, respectively (40, 70). While urban land remains a small fraction of global land surface, it is the land cover that has increased most since 1700, from an estimated 0.01% to 40 times more in 2000 (40, 70).

Urbanization is strongly associated with urban sprawl (48) permitted by rising spatial accessibility (5), first with mass public transit and then with the advent of individual car ownership, which opened up new areas to urbanization. While land governance diversity generates diverse landscapes, urban sprawl is commonly found in countries that underwent the urban transition: increases in urban population correspond to proportionally greater use of land. Urban sprawl concerns not only housing but also the infrastructure needed to serve new or more distant communities and a diversity of economic activities.

Urban sprawl: an increase in per capita land consumption that is often haphazard, fragmented, and car-oriented; associated with the loss of agricultural land and wildlife habitat

Urban greening: increasing the presence of vegetation in cities to reduce urban heat island effects, support human well-being, and sometimes support wildlife conservation

The forest transition represents another major landscape change in Europe and North America. Forest transition describes regions moving from net deforestation to an increase in forest cover (124), which here strongly relates to agricultural intensification, marginal land abandonment, industrialization, and urbanization (84). The forest transition increased habitat availability for wildlife, and reduced hunting and predation pressure led ungulate populations to recover. Deer recolonized most of eastern North America by the 1950s (138, 151). In Europe and the United States, wild ungulate populations returned so successfully as to become a concern in relation to damage to forestry and agriculture, collisions, and zoonotic disease transmission (21, 22, 120, 138). Suburbanization and the forest transition have resulted in the creation of extensive ecological interfaces, with urbanization taking place in the vicinity of (re)natured areas. The term periurbanization captures the essence of such socio-ecological interfaces by focusing on landscape composition rather than its location and by acknowledging the hybrid character of landscapes that are neither fully urban nor fully rural.

2.2. Into the Twenty-First Century: Urban Greening for Climate Mitigation and Sustainability

Providing green space in cities has been advocated for a long time, as demonstrated by the prominence of green spaces and gardens in plans elaborated by Ebenezer Howard in his garden city vision early in the twentieth century (28). Used throughout the twentieth century in various forms, planning principles integrating green spaces have reappeared in contemporary urban challenges in relation to air pollution, urban heat island effects, and extreme event mitigation (150). Urban greening is now envisaged in multiple forms such as urban forests, parks, and gardens but also green roofs and walls (6, 81, 88). Differences may exist between long-existing green spaces (e.g., tree cover age, heritage value) and newly established ones, but all such spaces share strong anthropic pressure and the need to conciliate recreation with other objectives such as conservation or production (81, 88).

Urban and periurban land uses cannot be defined simply but vary greatly in their wildlife–human interfaces based on their wildlife composition, density, range, and movement, depending on urban landscape constraints, human population density, and configuration (45). As such, we believe examining urban and periurban landscapes as novel ecosystems would help identify ecological features that modify TBD risk.

3. URBAN AREAS AS NOVEL ECOSYSTEMS FOR TICK-BORNE DISEASES

Novel ecosystems for TBPs have an important human footprint and are highly fragmented, with heterogeneous land covers and land uses, and they retain or have expanded vegetation and wildlife habitats that are no longer exclusively natural landscape features. An example typology for novel urban ecosystems based mostly on plant biodiversity and vegetative structures and the type and intensity of human intervention or management classifies them into remnant (high biodiversity and low management; e.g., urban forests); restored (high biodiversity and high management; e.g. native meadow restoration), abandoned/ruderal (low biodiversity and low management; e.g. vacant lots, railway edges), and horticultural/formal (low biodiversity and high management) (1). These classes occur along urban gradients that are strongly affected by the surrounding ecological matrix. To determine key features of these novel urban ecosystems that can sustain wildlife communities, TBP persistence, and human exposure, we delineate the study extent and the spatial resolution (geographic scale) of published studies of urban TBPs (Section 3.1); describe known resources for TBPs, tick vectors, and hosts that can define hazardous interfaces (**Figure 2**), i.e., use a bottom-up perspective (Section 3.2); and discuss the applicability of a top-down perspective on how urban structure drives wildlife community composition with cascading effects on TBP emergence along urban gradients (Section 3.3).

3.1. Definitions, Boundaries, and Critical Scales for Tick-Borne-Pathogen Novel Urban Ecosystems

Many published studies describe their study area as urban, suburban, and/or periurban. The use of these terms, in the absence of formal definitions, is often idiosyncratic, sometimes using administrative boundaries (13, 123), functional proximity to a city with a documented or assumed high visitation rate by city residents (24, 32, 100), quantitative variables used on an ad hoc basis (11, 35), or land-cover classification (59). The terms used in individual studies are locally relevant but inconsistent across studies. Furthermore, studies of ticks in urbanized landscapes cover a broad diversity of vegetated areas at multiple scales ranging from sizable forests to private gardens and well-kept lawns in public parks and sometimes sampling across several types of green spaces. Site description is also variable, from broad descriptions including lawn, urban greenery, urban parks, and urban forests (24) to more systematic inventories of potential habitat features (56). Some studies report on the size of green spaces or the distance to an assumed source habitat (65).

A first challenge to comparisons across urban studies of TBDs is that system boundaries and scale are often defined poorly or not defined at all. TBP circulation can be conceived as a hierarchical system and studied at various aggregation levels, spatial resolution, and extents (152), similarly to other ecosystem processes (**Figure 1*a***). Sampling ticks in a garden or a spot in a park would correspond to a fine scale, whereas serological studies in aggregate human populations defined by administrative boundaries would correspond to a coarse scale. Fine-scale studies can cover a large extent (e.g., using replicated sampling of multiple gardens across a region), but aggregated data can shed light only on broadscale ecological processes.

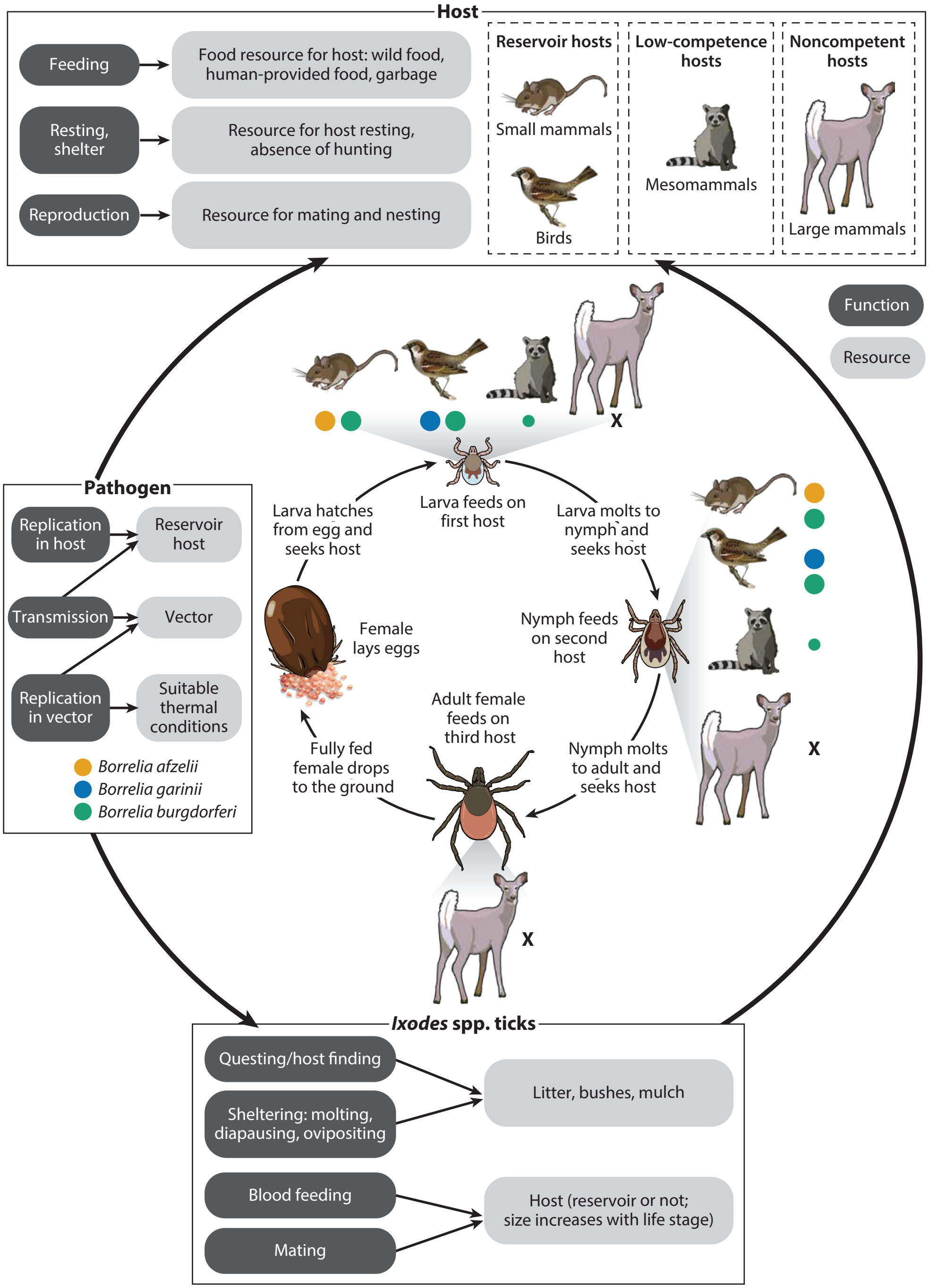


Figure 2

Generalized life cycle for *Ixodes* ticks and *Borrelia burgdorferi* sensu lato (three genospecies are illustrated with their host associations). Each organism concerned (pathogen, vector, and host) is described with its functions and associated resources, with a focus on resources relevant to the periurban and urban environment.

Ecological neighborhood: an area within which an ecological process of interest occurs, taking into account the focal organism(s)'s activity during a specified time scale

We illustrate three representative scales that would impact the probability of finding a tick and TBPs in a sampling transect or point sample, i.e., at the smallest scale (**Figure 1*a***). The regional scale captures the spatial arrangement of major land uses and covers (e.g., forest, urban, agriculture), shaped by large-scale ecological and land management processes. This scale provides the backdrop of novel ecosystems, where human and natural systems are deeply intertwined and influence the broadscale distribution and dispersal movement of hosts for ticks from source locations to urban habitats that may act as sinks (9, 56). The city/neighborhood (intermediate) scale involves urban socio-ecological mosaics with mixed land uses and land covers including urban greenspaces, residential areas, and periurban zones that support host communities and shape tick–host dynamics. At this scale, ecological neighborhoods are defined by greenspaces and surrounding residential areas that capture the scale of home ranges and movement patterns of large and medium tick and pathogen hosts, as well as humans. Residents in areas surrounding urban greenspaces would be most likely to visit the focal parks (people most frequently visit areas within 500 m of their home) or be exposed to ticks deposited by wildlife visiting their yards, if these are permeable and suitable (9, 56).

Many studies were conducted at this neighborhood scale by comparing tick and pathogen populations in forests in the periphery and small (17) or large (94) parks in the urban core. In addition, the local scale involves the fine-scale habitat patches of relatively homogeneous vegetation–soil units (e.g., forest patches, lawns, or yards) where ticks are typically sampled in transect or grid formats. These patches are embedded in urban matrices, where anthropogenic effects directly interact to affect tick survival, host activity, and human exposure.

3.2. A Bottom-Up Perspective: The Resource-Based Habitat Concept for Describing Tick-Borne Disease Risk Interfaces

The resource-based habitat concept (RBHC) can describe TBD novel ecosystems by defining functional habitats for TBPs (62, 145). The RBHC identifies all functions of the organism and what resources are needed for each. Resources need to be within the movement capacity of the organism so that all functions can be fulfilled. Connectivity is thus key when not all resources are found in one place. The RBHC uses a niche concept to identify, in a bottom-up manner, the resources needed by the pathogen to persist and thus also those needed by the other organisms involved; here we apply the concept to *Ixodes* ticks and their vertebrate hosts. We use the RBHC to explore how local urban ecosystems may differ from primary tick habitat making them novel ecosystems (**Figures 1** and **2**).

3.2.1. Resources needed by the pathogen. Spirochaetes associated with Lyme disease form a species complex known as *B. burgdorferi* sensu lato, which comprises more than 20 named species, among which *B. burgdorferi* sensu stricto, *Borrelia garinii*, and *Borrelia afzelii* are known human pathogens (135). Assuming a suitable climate for populations of ectothermic vectors, ecological functions of *B. burgdorferi* s.l. are replication and transmission, for which resources are hosts and vectors. Because *Ixodes* ticks are host generalists (78), *B. burgdorferi* s.l. genospecies are exposed to multiple host environments, which vary in reservoir competence (83, 92). *B. burgdorferi* s.l. genospecies vary in host range and may differentially associate with specific hosts. *B. burgdorferi* s.s., the dominant human-infectious genospecies in North America, is a host generalist, infecting small mammals, birds, and some mesomammals. The wide host range of *B. burgdorferi* s.s. has been postulated to have allowed Lyme disease to spread rapidly across the northeastern United States as afforestation progressed during the twentieth century (57). *B. burgdorferi* s.s. is less abundant in Europe (8), where *B. burgdorferi* genospecies tend to be associated with different host species. *B. afzelii* is associated with rodents, *B. garinii* with birds (83), and *Borrelia lusitaniae* with lizards, while *Borrelia valaisiana* is less host associated (82); the human infectiousness of *B. lusitaniae* and *B. valaisiana* is debated (134). The host associations of *Borrelia* genospecies mean that the composition and abundance of vertebrate hosts are expected to be key in shaping the hazard. However, the greater prevalences of *B. afzelii* in continental Europe (33, 54, 116) and *B. garinii* and *B. valaisiana* in the UK (58) as well as the Czech Republic (110) have not been reliably linked to host species composition. Introduced rodents in Europe [e.g., Siberian chipmunk (*Eutamias sibiricus*) and gray squirrel (*Sciurus carolinensis*)], an important feature of novel urban ecosystems, can also impact TBP ecology, and some of these species were associated with three species of *B. burgdorferi* s.l. (93, 101, 118).

3.2.2. Resources needed by the tick vector.

Tick-species vectors of *B. burgdorferi* s.l. belong to the *I. ricinus* species complex, which are exophilic, three-host, generalist ticks. They include *I. ricinus* and *Ixodes hexagonus* (Western Europe), *I. scapularis* (Eastern North America), *I. pacificus* (Western North America), and *I. persulcatus* (Eurasia). The ecological functions required to complete the life cycle of *Ixodes* ticks are sheltering, host questing, blood feeding, mating, and ovipositing. *Ixodes* spend the majority of their life cycle off-host, sheltering or host questing (**Figure 2**). Sheltering, during molting or diapausing, is typically done in forest leaf litter, hence deciduous forests are considered favorable habitats. Leaf litter provides humid conditions and protection from harsh temperatures (above 35°C and below freezing) and desiccation (19, 97). In urban settings, mulching material has been assumed to be a possible tick shelter (136), along with leaf litter accumulated from leaf blowers (74). Lawns are generally assumed to provide insufficient shelter, although in the presence of shade (96), under the canopy (60), or in humid climates such as coastal areas or islands (14, 46), *Ixodes* ticks can be found on lawns, although generally at a lower abundance.

Ticks quest for a host, mostly above 10°C (78), by climbing on a support, typically forest undergrowth such as ferns, brambles, grasses, or leaf litter. Different tick life stages usually quest at different heights, and this has been linked to attachment to differentially sized hosts (7, 115). Urban forests provide sheltering and host questing resources in abundance, but parks and gardens differ. Ornamental or berry bushes and groundcover plants have been associated with tick presence or abundance (9, 56, 96, 117, 136), suggesting that urban parks and gardens can offer suitable habitat for *Ixodes* ticks.

Immature stages can obtain a blood meal on most hosts available in urban areas, including small mammals and birds; adult *Ixodes* can feed and mate only on intermediate and larger hosts, particularly ungulates (34, 118). Some intermediate-sized hosts have become very abundant in urban areas, and the presence of ticks in places where ungulates are absent suggests that ticks may persist in the absence of ungulates (12, 17, 122, 123, 149). In Europe, species adapted to the urban environment that can support the adult stage of *I. ricinus* are hedgehogs (*Erinaceus* spp.) (17, 38, 39, 47, 51, 69, 71, 133), hares (*Lepus timidus*) (76), wild boars (*Sus scrofa*) (32, 148, 153), and red foxes (*Vulpes vulpes*) (99, 141); some of these mesomammal host species can also act as hosts for *B. burgdorferi* s.l. (111, 118). In contrast, ungulates—mainly white-tailed deer (*Odocoileus virginianus*)—are the only significant tick maintenance host in North America (120), with raccoons (*Procyon lotor*) and other mesomammals rarely hosting adult *I. scapularis* (44, 139). This ecological difference significantly impacts the habitat requirements and landscape structure needed to maintain tick and pathogen populations.

3.2.3. Resources needed by vertebrate hosts.

Because *Ixodes* ticks are generalist feeders, it is not feasible to examine the detailed ecological resources shaping the habitat of each possible tick and pathogen host. We focus here on generic functions and ecological resources that may be specific to the urban and periurban environment such as resource subsidies in the form of food (e.g., human-provided feed or garbage, food-producing plants) or shelter (e.g., wood piles or stone walls) (9, 29, 49, 56, 96). Resource subsidies in urban settings can lead to smaller home-range sizes for most hosts (105). However, small green areas such as gardens, parks, or urban forests may not be able to support middle- and large-sized hosts, such as ungulates, which are essential for tick maintenance. Landscape connectivity for host movement links resources at multiple scales and becomes a limiting factor with increased urbanization. Barriers reducing connectivity for hosts span from fencing around residences at the local scale (9, 56, 96) to transport infrastructure, which impedes movement between urban areas and neighboring rural landscapes or limits access to larger forest fragments that serve as sources of wildlife populations. Many studies have investigated what authors call urban forests, which can be large enough to support populations of hundreds of large mammals (125), emphasizing that areas described in the literature as urban can cover a wide range of host habitat quality.

3.2.4. Humans as incidental hosts in urban and periurban settings. People are incidental hosts for *Ixodes*-borne pathogens, so they are not included in an RBHC for the pathogen. However, as humans are the target population (sensu 64) for public health interventions, they are a critical component of novel ecosystems when evaluating TBD risk (23, 87). Humans may become exposed to TBPs recreationally when traveling to natural parks or forests or peridomestically, i.e., in ecological neighborhoods (**Figure 1*a***; see also Section 3.1).

Many studies account for the human dimension when selecting study sites (35, 39, 47) or interpreting risk (53, 56). Few studies specifically compare tick abundance between places where humans are more or less susceptible to being exposed in a green space (but see 142). There is ample documentation of visitor preferences in green spaces (127, 132), and many larger parks, in particular forests, channel visitors through an organized infrastructure (parking lots, picnic areas etc.), but few tick or TBP studies have used that information in their sampling set up or analysis (but see 142). Dumas et al. (36) produced a risk map by combining trail use and density of infected nymphs in a periurban park in Montréal, Québec, and found a strong contrast in risk for different habitat types, similar to studies on Staten Island, New York (63), and in Stockholm, Sweden (72). Studying the incidence of tick bites in three Scandinavian countries, Jore et al. (75) found that periurban municipalities (where many urbanites enjoy the outdoors) were most often reported as the site of tick bites.

3.3. A Top-Down Perspective: Can Urbanization Metrics Predict Tick-Borne Disease Hazard?

The RBHC describes how overlapping resources required for the pathogen, tick, and hosts determine the persistence of TBP foci in novel urban ecosystems. A complementary approach rooted in community and landscape ecology aims to predict, in a top-down manner, how urbanization drives the composition of whole wildlife communities and cascading effects on TBP distribution. Because immature *Ixodes* ticks are host generalists and bite according to their hosts' relative availability, the proportion of competent and noncompetent hosts determines the proportion of infected nymphal ticks after molting (while tick abundance is driven by adult *Ixodes* host abundance) (43). This frequency-dependent transmission mode led to the proposal that increased biodiversity would be protective for human health, as more diverse wildlife communities may host a larger proportion of noncompetent hosts, reducing infection prevalence in the tick population (92, 107). This concept attracted significant attention as a win-win proposal for conservation and human health (25, 90) but also attracted calls to acknowledge complex, nonlinear associations (34, 79, 121, 151). Given the challenge of sampling a complete host community in even a single location, many studies have used proxies for host diversity, such as habitat fragmentation across urbanization levels, with the assumption that more fragmented forests have lower biodiversity.

3.3.1. Using proxies: Is tick-borne-disease hazard higher in most urbanized areas? We identified a range of outcomes in studies explicitly comparing the two components of the hazard—the density of *Ixodes* nymphs and infection prevalence with *B. burgdorferi* s.l.—between urban and rural sites (16, 19, 24, 59, 80, 112, 131, 147) or across urban gradients (4, 65, 91, 116, 143, 154) (**Table 1**). The density of *Ixodes* nymphs was most often greater in low fragmentation/rural sites, while *Ixodes* infection prevalence with *B. burgdorferi* was most often not significantly different between urban and rural sites. A study that quantified fragmentation metrics found increased *Ixodes* density and infection prevalence in the most urbanized sites (4), defined based on patch size and isolation metrics, while others found decreased *Ixodes* density and prevalence when using continuous measures of greenspace connectivity (65, 91, 143). Utilizing consistent metrics of urbanization and habitat fragmentation across studies would facilitate systematic comparisons (**Figure 1*b***). We discuss next how the complex TBD ecology may lead to these divergent outcomes.

3.3.2. How does the relative abundance of urban adaptor hosts shift across urban gradients? The expectation from the dilution effect theory that competent hosts will dominate in the most urbanized areas is based on an assumed positive association between traits linked to resilience to human disturbance and those linked to reservoir competence. Both traits are hypothesized to be linked to fast life-history traits of small bodied species (e.g., rodents), leading to high reproductive output and lower investment in survival and adaptive immunity (3, 52, 108, 114). Indeed, cities experience a substantial decrease in the diversity of many taxonomic groups, accompanied by a rise in urban exploiters—primarily human commensals that are almost entirely dependent on human subsidies, such as pigeons or rats (61, 98). In contrast, most TBP hosts are considered urban adaptors, which are (mostly) native species that favor disturbed edge habitats such as urban forest fragments and rely on a combination of wild-growing and human-derived resources (98). Urban forest fragmentation often increases the abundance of highly competent rodent hosts of *B. burgdorferi* such as white-footed mice (30, 102, 103). However, the abundance of mesomammals potentially acting as dilution hosts is highly variable (45, 61) and can be highest in the most urbanized settings, potentially leading to reduced transmission there.

3.3.3. A focus on host community structure: how resource availability and species interactions shape host community composition and abundance in urbanized landscapes. Given the limitations of the trait-based approach, there is increasing interest in how species interactions structure host community composition, focusing on how predators shape prey community structure, abundance, and composition through top-down regulation via consumptive and nonconsumptive effects (67). For example, in North America, the elimination of top predators in urban environments can result in an increased abundance of mesopredators (i.e., mesopredator release) (10, 89, 109), which may decrease the hazard (89, 109) by reducing tick feeding on small mammals through consumptive (predation) and nonconsumptive (landscape of fear) (86) interactions. However, invasion of coyotes into urban areas can reverse dilution effects by mesopredators by competitively displacing red foxes (89), which consume large numbers of small mammals, resulting in higher small mammal abundance and higher tick burdens.

3.3.4. Nonlinearities due to a two-host system: one for the tick vector, one for the pathogen. A unique feature of *Ixodes*-borne pathogens (compared to other vector-borne or directly transmitted pathogens) is the requirement for (at least) two host species—a reproductive host for the tick that is often not pathogen competent and one for the pathogen—creating nonlinearities in the relationship between hazard and urbanization. Modeling studies predict that transmission increases as deer populations increase but eventually plateaus or decreases as the role of deer as dilution hosts becomes dominant over its role as tick host (50, 68, 73, 104).

3.3.5. Variable *Borrelia burgdorferi* sensu lato host range: Does host diversity beget pathogen diversity? A key assumption of the dilution effect is that hosts vary in their reservoir competence, which generally applies to host competence for *B. burgdorferi* s.s. in the United States (92). In contrast, differentiation into host-associated species or ecotypes of *B. burgdorferi* s.l. (see Section 3.2.1) in Europe may violate this assumption, potentially leading to increases rather than decreases in pathogen abundance with increased host diversity.

Furthermore, differentiation of *B. burgdorferi* s.s. species into mouse- and bird-adapted genotypes in the United States may result in a positive response to biodiversity (27). The limited role of reservoir host diversity in driving a dilution effect has led most European studies to focus on dilution by deer, which has low competence for all genospecies, rather than dilution by biodiversity.

4. TOWARD A TYPOLOGY OF NOVEL URBAN ECOSYSTEMS FOR TICK-BORNE PATHOGENS

To address scale dependence and nonlinearities in the relationship between urbanization and TBDs, we propose that research on the ecology of *Ixodes*-borne pathogens in urban and periurban landscapes would benefit from a more systematic specification of the study area and a more explicit consideration of ecological interfaces at various scales (**Figure 1*b***). Because urban and periurban landscapes are so diverse, in the absence of globally accepted classifications of TBD novel ecosystems, study designs and published studies should identify and report, at a minimum, the geographic coordinates of the study sites, the scale of the study (the extent of the sampling sites and study area and the resolution of sampling units), the dominant land-cover type for sampling transects for tick collection, and a summary of the host resources available, in particular whether ungulates are present, if known. Considering the challenges involved in studying hosts and covering heterogeneous urban landscapes, the potential for data compilation, for example, using the Global Biodiversity Information Facility (55), for host community composition should be explored further, as well as using citizen science data, including data concerning ticks or tick bites (37, 77, 96, 119).

Most published studies reported landscape composition as a vegetation cover type; a few reported landscape metrics such as patch size, isolation, distance, and edge; and only some reported landscape connectivity metrics (**Figure 1*b***; **Table 1**). Quantification of connectivity metrics at multiple scales can identify, for example, thresholds for ungulate connectivity driving tick establishment (65, 91, 143). At a regional scale, globally standardized databases that characterize the interface between urban and wild areas such as the wildland–urban interface (WUI) (128) would allow comparisons across systems. The WUI is qualitatively defined as a place where humans and their development meet or intermix with wildland fuel; it combines metrics of housing density and vegetation cover and has been linked to regions with high Lyme disease incidence (15). At a city/neighborhood scale, tick and TBP occupancy in local patches should be linked to metrics of connectivity, such as those based on electronic circuit theory (85) operationalized in the Circuitscape (used in 143) or Omniscape (used in 91) platforms. For studies that include the peridomestic interface, quantifying the connectivity of the residences/yards to the surrounding natural landscapes in an ecological neighborhood is necessary to characterize the full human–wildland interface (9, 56, 96). In addition, process-based approaches derived from invasion/metacommunity dynamics—for example, those used to construct agent-based models (e.g., 146)—would provide a fuller understanding of the underlying dynamics driving TBPs in urban novel ecosystems.

The concept of novel ecosystems draws focus to the different resources and host species assemblages and the complex spatiotemporal overlap between humans and infected ticks. The effects of these parameters on the resulting risk are hard to predict, which justifies approaching urban areas with a dedicated framework. The role of scale cannot be emphasized enough here, as the use of space by hosts differs considerably between species and depends on the urban constraints and opportunities for each. Cities and their surroundings are dynamic landscapes that are in constant evolution, as are their human and wildlife inhabitants. As cities get greener, identifying challenges inherent in combining the multiple objectives human societies may hold for the land will be key, as providing ecosystem services such as urban heat islands, recreation and well-being, and conservation may come with ecosystem disservices imposing trade-offs (144).

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

M.A.D.-W. and P.F. were partially supported by the National Science Foundation's Coupled Natural Human Systems 2 (CNH2) program (award #1924061) and Cooperative Agreement Number U01CK000509-01 between the Centers for Disease Control and Prevention and the Northeast Regional Center for Excellence in Vector Borne Diseases. This article's contents are solely the responsibility of the authors and do not necessarily represent the official views of the Centers for Disease Control and Prevention, the Department of Health and Human Services, or the National Science Foundation. Some ideas presented in this paper were first elaborated while S.O.V. was hosted by the Center for International Earth Science Information Network (CIESIN) and the Earth Institute, Columbia Climate School, Columbia University, New York, NY, USA.

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