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REVIEW

Socio-ecological drivers of multiple zoonotic hazards in highly urbanized cities

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Abstract

The ongoing COVID-19 pandemic is a stark reminder of the devastating consequences of pathogen spillover from wildlife to human hosts, particularly in densely populated urban centers. Prevention of future zoonotic disease is contingent on informed surveillance for known and novel threats across diverse human–wildlife interfaces. Cities are a key venue for potential spillover events because of the presence of zoonotic pathogens transmitted by hosts and vectors living in close proximity to dense human settlements. Effectively identifying and managing zoonotic hazards requires understanding the socio-ecological processes driving hazard distribution and pathogen prevalence in dynamic and heterogeneous urban landscapes. Despite increasing awareness of the human health impacts of zoonotic hazards, the integration of an eco-epidemiological perspective into public health management plans remains limited. Here we discuss how landscape patterns, abiotic conditions, and biotic interactions influence zoonotic hazards across highly urbanized cities (HUCs) in temperate climates to promote their efficient and effective management by a multi-sectoral coalition of public health stakeholders. We describe how to interpret both direct and indirect ecological processes, incorporate spatial scale, and evaluate networks of connectivity specific to different zoonotic hazards to promote biologically-informed and targeted decision-making. Using New York City, USA as a case study, we identify major zoonotic threats, apply knowledge of relevant ecological factors, and highlight opportunities and challenges for research and intervention. We aim to broaden the toolbox of urban public health stakeholders by providing ecologically-informed, practical guidance for the evaluation and management of zoonotic hazards.

KEYWORDS
hazard, landscape, management, mesomammal, mosquito, rodent, spillover, tick, urban, zoonosis

1 | INTRODUCTION

Zoonotic diseases, caused by pathogens transmitted between human and wildlife populations, most often emerge at human–wildlife interfaces where there is an increased likelihood of direct or indirect contact between people and infectious hosts and/or vectors (Hassell et al., 2017; Soulsbury & White, 2015). Urban landscapes are increasingly recognized as habitat for wildlife across both green spaces (e.g., vegetated or natural landcover) and gray spaces (e.g., built structures, impervious surface, and associated infrastructure) leading to increased interactions with human populations (Deplazes et al., 2004; Hansford et al., 2017; Mckinney, 2008; Rothenburger et al., 2017). Globally, cities are growing both in their number of inhabitants—with over 68% of the world's populations expected to be urban-dwelling by 2080 (United Nations, 2018), and in their geographic footprint—with urban land cover steadily increasing (Seto et al., 2012). The process of urbanization contributes to biotic homogenization (McKinney, 2006), invasive species introductions (Blair, 1996; Shochat et al., 2010), and results in a wealth of exploitable resources, which promotes the increased richness and abundance of zoonotic host species and their associated pathogens (Gibb et al., 2020). The COVID-19 pandemic highlighted the risk of zoonotic disease emergence and the unique vulnerability of cities to emerging zoonotic pathogens, emphasizing concerns regarding effective prevention and response to spillover events (Alirol et al., 2011; Bradley & Altizer, 2007; Mackenstedt et al., 2015; Neiderud, 2015). However, there is a persistent need to understand how urbanization alters ecological processes that underlie human zoonotic risk and spillover potential in cities (Karesh et al., 2012) (Figure 1).

Recent discussions of urban zoonoses have focused on factors influencing spillover events (Hassell et al., 2017; Plowright et al., 2017, 2021), pathogen–landscape interactions (Eisenberg et al., 2007; Lambin et al., 2010), and the impacts of urbanization on animal health (Bengis et al., 2004; Bradley & Altizer, 2007; Mackenstedt et al., 2015). The emphasis of these reviews is on the combined influence of environmental change, wildlife biology, and human risk factors (including exposure and vulnerability, see Table 1 for glossary of terms) to broadly illustrate the drivers of zoonotic disease emergence. However, a detailed assessment of the ecological drivers of zoonotic hazards is needed to improve pre-spillover surveillance, research, and management of hazards in cities. Such efforts require collaboration between public health practitioners, wildlife biologists, urban planners, community leaders and others invested in the health of local human communities (hereafter "public health stakeholders") that often go beyond the scope of a single entity. Multi-sectoral partnerships have shown promise for tackling chronic physical and mental health issues and enabling action on climate change adaptation and mitigation (Ramaswami et al., 2016). Similar efforts are essential to prevent urban zoonotic disease, and begin with a thorough understanding of the foundational biology and socio-ecological interactions driving the presence and prevalence of urban zoonotic hazards.

While drivers of urban zoonoses have been mostly studied in tropical regions where health impacts are greatest (Gottdenker et al., 2014; White & Razgour, 2020), the emergence and persistence of these diseases has been overlooked in highly urbanized cities (HUCs) in temperate climates, which also support a diverse suite of zoonotic hazards. These often include human commensal rodents and mesomammals (Feng & Himsworth, 2014; Plumer et al., 2014; Tufts et al., 2021), *Ixodidae* ticks (Adalsteinsson et al., 2018; Mancini et al., 2014; Steere, 1994), *Aedes* spp., and *Culex* spp. mosquitoes (Calhoun et al., 2007; Goodman et al., 2018; Muir & Kay, 1998; Shragai & Harrington, 2019), all of which can harbor and transmit zoonotic pathogens. In our definition, HUCs are those with more than 500 k

FIGURE 1 Socio-ecological drivers influencing zoonotic hazards in HUCs. (a) Individual drivers illustrated across a simplified urban landscape and color coded based on whether they are predominantly related to landscape (blue), abiotic (purple), or biotic (green) factors. (b) Thematic flow chart illustrating how socio-ecological processes drive the intensity of zoonotic hazard, a foundational component of zoonotic risk, which ultimately impacts the likelihood of zoonotic spillover events

TABLE 1 Glossary of terms

Term	Definition
Zoonotic disease	Any disease caused by a pathogen transmitted between non-human animals and humans
Hazard	Potential source of harm (e.g., infected host or vector, shed pathogens) expected to contribute to zoonotic disease, at varying intensities over space and time
Exposure	Likelihood of human contact with hazards from interaction with the environment
Vulnerability	Human or societal condition altering the likelihood of harm, given exposure
Risk	The likelihood of adverse outcomes caused by a hazard, given exposure and vulnerability
Spillover	Event in which zoonotic pathogen enters the human population
Reservoir Host	A species competent to harbor a particular pathogen, such that it sustains the pathogen in the environment and serves as a source of human or vector infection
Vector	An organism capable of transmitting a pathogen between non-human animals and humans
Pathogen	An infectious agent (bacteria, virus, endoparasite, or microorganism) capable of causing disease
Eco-epidemiology	The study of human disease that incorporates information from human populations and societies as well as environmental and biological factors
Ecosystem Disservice	Any consequence of interacting ecological factors or agents that lead to negative outcomes for human and economic well-being
Dilution Effect	Theory that increasing biodiversity results in decreased human disease risk due to increased abundance of lower-competence hosts

residents, citywide sanitation infrastructure, life expectancy above 75 years, as well as a prolonged and pervasive historical conversion of earthen land cover to impervious surfaces. Here, we focus on the ecological conditions and emergent processes accompanying urbanization that drive differences in hazard intensity across HUCs in temperate climates through (1) the distribution and abundance of hosts and vectors and (2) patterns of pathogen prevalence across hosts, vectors, and the environment.

Each HUC supports multiple zoonotic hosts and vectors that experience the heterogeneity of cities differently based on their biological traits and habitat requirements, creating divergent outcomes for the pathogens they harbor and transmit across space, within or among species. Understanding and managing these hazards requires acknowledging several key concepts highlighted throughout this perspective article. (1) There is an inherent ecological tradeoff between green or gray infrastructure and the presence of zoonotic hazards (Diuk-Wasser et al., 2021; Jennings et al., 2019; Lõhmus & Balbus, 2015; Soulsbury & White, 2015; Taguchi et al., 2020). While urban green spaces provide ecosystem services, including climate mitigation and physical and mental health benefits (Gómez-Baggethun & Barton, 2013; Gregory McPherson, 1992; Luederitz et al., 2015), these same spaces produce ecosystem disservices when they increase human exposure to pathogens and act as venues for zoonotic spillover (Shackleton et al., 2016; Vanwambeke et al., 2019). Efforts to increase urban biodiversity or human well-being through urban greening (Fuller et al., 2007) may also alter disease risk, although biodiversity-disease relationships remain widely debated (Ogden & Tsao, 2009; Randolph & Dobson, 2012; Rohr et al., 2020; Salkeld et al., 2013). Similarly, while gray spaces provide human communities and economies room to grow, these spaces support zoonotic hazards that we experience with more direct spatial and temporal overlap. (2) Urban zoonotic hazards are a component of socio-ecological systems; environmental conditions in cities (including the distribution and prevalence of hazards) are co-produced by the interaction of biophysical and social processes (McGinlay et al., 2016). A city's greening or graying process depends on its history, socio-cultural values, and socio-economic drivers of land use (Des Roches et al., 2020; Pickett et al., 2001). Thus, effective and equitable prevention of urban zoonoses is facilitated by an integrated socio-ecological framework for understanding disease emergence. (3) Plans to study and manage hazards should be species-specific. Because of differences in their spatial scale of movement, each host and vector species experiences a unique pattern of landscape connectivity, which depends on traits such as migration propensity, dispersal distance, resource needs, physiological constraints, and response to disturbance and fluctuating population densities (Jetz et al., 2004; Peters et al., 2019; Tucker et al., 2014). Research and management strategies should reflect the scale at which sampling is most informative and management efforts are most effective.

In this article, we first describe how characteristics of urban socio-ecological landscapes, in tandem with their unique abiotic conditions and biotic interactions, determine zoonotic hazards distribution and prevalence. Then using New York City (NYC), USA as a case study, we apply these concepts to evaluate different zoonotic hazards and spillover prevention strategies that incorporate the city's ecological context. Throughout, we discuss implications for pathogen surveillance, research, and mitigation to improve understanding and outcomes of urban zoonotic emergence and persistence (Box 1).

2 | LANDSCAPE CHARACTERISTICS

The intensity of zoonotic hazards exhibits strong spatial heterogeneity across HUCs. Effectively evaluating and managing these hazards requires an understanding of how landscape patterns influence populations of hosts, vectors, and associated pathogens as they interact with one another and the environment. In particular, it is important to address the influence of landscape composition, configuration, and connectivity on specific hazards, and identify the spatial scale at which eco-epidemiological processes take place. But understanding current landscape patterns and their influence on zoonotic hazards necessitates knowledge of their historical and ongoing socio-ecological drivers.

BOX 1 Priority areas for strategic surveillance, research, and mitigation of urban zoonotic hazards

(1) Surveillance:
  a. Identify baseline distribution and abundance of zoonotic hosts and vectors across diverse urban sites (i.e., land use, wildlife community, vegetation characteristics, history, socioeconomic status); balance financial limitations with long-term active samplings of key sites and passive sampling through community reporting.
  b. Leverage molecular approaches to identify variable pathogen prevalence in hosts, vectors, and environment.
  c. Monitor changes in hazard intensity linked to dynamic urban landscape (i.e., greening or degreening of neighborhoods, development).

(2) Research:
  a. Establish multi-sectoral collaborations with diverse public health stakeholders (municipal departments, epidemiologists, community leaders, disease ecologists, social scientists, non-profit groups) to study influence of socio-ecological landscape attributes, abiotic conditions, biotic interactions across local multi-hazard suite.
  b. Create and maintain public data repositories on host, vector, and pathogen distribution, and fine-scale spatial environmental data.

(3) Prevention:
  a. Develop ecologically-informed management strategies by mathematical modeling of habitat, pathogen dynamics, and host/vector connectivity; prioritize interventions on prevalence hotspots in conjunction with societal risk factors.
  b. Implement management strategies at spatial scale relevant to species-specific biology and dispersal.

Urban development is driven by natural ecological processes and biophysical features such as topography, hydrology, and native vegetation, in combination with pervasive social forces (Des Roches et al., 2020; Keeler et al., 2019). Indeed, widespread land cover conversion and patterns of fragmentation among HUCs are largely driven by societal values informed by culture, economics, and local history. During early stages of temperate HUC growth, the adoption of Eurocentric ideals of nature and aesthetics promoted gridded urban forms and open lawns, which greatly contributed to their biotic homogenization (Ignatieva & Stewart, 2009; Loughran, 2020; Shackleton & Gwedla, 2021). During post-industrial growth, systematic racism and classism was institutionalized in many cities through land use policy, development projects, and lending decisions (Schell et al., 2020), which was driven in large part by capitalist systems that prioritized profit and exploited the a-spatiality of marginalized communities (Bledsoe & Wright, 2019). These legacies drive current patterns of habitat suitability for hazards through unequal distribution of green space as well as investment in infrastructure and services across racial- and class-based lines (Schell et al., 2020; Venter et al., 2020). For example, brown rat habitat and elevated pathogen prevalence among adult mosquitos are consistently correlated with low-income areas (Dowling et al., 2013; Harrigan et al., 2010; Johnson et al., 2016; LaDeau et al., 2013; Masi et al., 2010; Rothenburger et al., 2017). Social factors, such as income, education, and employment, also affect people's interactions with the environment through their impact on personal exposure, vulnerability, and coping capacity, but these risk factors are more fully described elsewhere (Hosseini et al., 2017; Solar & Irwin, 2014). We focus here on how public health stakeholders can account for socio-ecologically complex landscape attributes such as composition, configuration, connectivity, and scale in their study and management of zoonotic hazards (Frank et al., 2017; Ostrom, 2018).

Landscape composition describes the identity of patch types and their relative geographic coverage (Ostfeld et al., 2005). The land cover attributes used to define composition and identify suitable niche space may differ for each reservoir host or vector species. For instance, variation in the vegetative understory in patches of urban green space impacts the presence of both mice and ticks (Adalsteinsson et al., 2018), altering local Lyme disease (LD) hazard. Thus, satellite data describing canopy cover may not be as informative as vegetative surveys that directly sample variation in relevant tick and host habitat. Similarly, urban gray spaces differ dramatically in their intensity and type of human use and maintenance, and these characteristics can change between and within neighborhoods. For instance, increasing abandonment rates within neighborhoods correlates to increases in the abundance of rodent hosts and fitness of mosquito vectors (Katz et al., 2020; Peterson et al., 2020a). Such responses impact public health outcomes for spatially adjacent communities (Gulachenski et al., 2016), with homeless populations often experiencing the highest exposure rates to hosts and vectors (Leibler et al., 2018). Identifying zoonotic host habitat in gray spaces may be possible through evaluation of easily recorded, physical attributes like building age or land use; however, ephemeral qualities should also be considered. For example, the likelihood of standing water or solid waste buildup may influence mosquito-borne pathogens and leptospirosis transmission (Murray et al., 2020) by increasing mosquito and commensal rodent presence (Krystosik et al., 2020), respectively. Further, in evaluating when and where to perform surveillance or interventions it is important to consider temporal changes due to seasonality, maintenance frequency, or longer trends of de-urbanization and re-greening (Eskew & Olival, 2018), as well as links between broad-scale habitat attributes and fine-scale patterns of landscape composition.

Landscape configuration reflects the spatial arrangement of patches and their proximity or isolation to one another. In HUCs, patch configuration depend on land use and zoning policies, as well as historical contingencies and natural topography or hydrology that drive local decision making. The degree of landscape fragmentation is metric of configuration that is sometimes used as a proxy for biological community composition and increased potential for zoonotic hazards (Allan et al., 2003; Brock et al., 2019; Diuk-Wasser et al., 2021; Zolnik et al., 2015). Increased landscape fragmentation is associated with increased edges between green and gray spaces that influence hazard distribution and creates increased opportunities for human-wildlife interactions (Barding & Nelson, 2008). For example, in gray spaces, adult mosquitos fly through the landscape (Morlan & Hayes, 1958; Muir & Kay, 1998) and rodents migrate within and between city blocks (Byers et al., 2019), putting residents at risk simply by living within host and/or vector dispersal distance of habitat supporting hazards. While evidence for the impact of green space edges in forests, parks, or yards on vector abundance or pathogen prevalence is mixed (Finch et al., 2014; Hansford et al., 2017; Horobik et al., 2006), assessing the ecology of spillover events at the transition zone between different land covers should be a research priority.

Landscape connectivity results from the integration of composition and configuration and describes both the network of habitable patches available (structural connectivity) and the realized movement of organisms and gene flow among those patches (functional connectivity) (Brooks, 2003). Incorporating connectivity into urban zoonoses mitigation is important because networks of connected habitat permit the flow of pathogens as hosts and vectors move through cities among suitable patches (Ostfeld et al., 2005). For example, taking a species-specific view, habitat connectivity for white-tailed deer based on green space coverage strongly predicts the density and infection prevalence of ticks, and thus LD risk in New York City (Vanacker et al., 2019). In HUCs, linear features like railways, greenbelts, and riverbanks provide movement corridors allowing for rapid dissemination of pathogens across landscapes, suggesting zoonotic disease emergence can occur rapidly via a small number of linked habitat patches. Behaviorally-flexible species like red foxes often use urban infrastructure in unintended ways, for instance by dispersing along roadways (Kimmig et al., 2020), effectively introducing parasitic infections and occasionally the rabies virus to new areas (Mackenstedt et al., 2015; Plumer et al., 2014; Smith et al., 2003). Given the idiosyncratic ways in which different wildlife hosts and vectors navigate urban landscapes, a key research priority should be to understand movement behavior and connectivity for local zoonotic threats through observations, tracking, and spatial modeling (Deplazes et al., 2004; Hemming-Schroeder et al., 2018; Heylen et al., 2019; Richardson et al., 2017).

Networks of habitat connectivity may result in either spatial concentration or spread of zoonotic hosts and their pathogens. This outcome depends on species-specific responses to the distribution of landscape features and should be incorporated into models of zoonotic risk and the development of hazard management programs. Movement barriers reduce connectivity by limiting species movement through physiological limitations (e.g., inability to cross waterways, impervious surface) or behavioral avoidance (e.g., road traffic, noise) (Clark et al., 2010; Fusco et al., 2021; Munshi-South, 2012). Typically, habitat isolation reduces the invasion potential of pathogens, but if pathogens generate immune-dependent responses in host populations, patch isolation can increase future susceptibility. For example, fruit bats forming high-density groups in urban Australia experienced large outbreaks of Hendra virus when decreased connectivity among patches reduced local population immunity (Plowright et al., 2011). Connectivity networks also influence the formation of, and dispersal from, pathogen hotspots, where local hazard intensity is significantly higher than baseline levels, increasing spillover potential (Paull et al., 2012). Prevalence of *Leptospira interrogans* and *Bartonella tribocorum* in urban rats is driven in part by reduced movement among city blocks, leading to high contact rates among high-density groups (Byers et al., 2020). This suggests that zoonotic hazards can persist without widespread movement when infections are endemic and contact rate is high among hosts.

The spatial scale at which the composition, configuration, and connectivity of landscapes is assessed is central to understanding and managing zoonotic hazards (Fischhoff et al., 2019; McGarigal et al., 2016; Richardson et al., 2016). The spatial scale is composed of the scope (i.e., spatial bounds) and grain (i.e., resolution of observed detail) and it must match the resource needs and movement patterns of the particular host(s) or vector(s) (Cushman et al., 2016). For instance, larval mosquito habitat requires only small amounts of standing water that may be perceptible only when composition is characterized at very fine spatial grain, while large mammals or mesomammal host habitat requires larger vegetated patches that are observable at coarser spatial grain. In HUCs, the relevant scale for effective management may differ from the scale at which species sampling or treatments are most practical, creating additional economic and policy hurdles for stakeholders. Brown rats, for example, are often managed across individual properties despite ample evidence that block-level or neighborhood-level management is required to limit host and pathogen presence (Byers et al., 2019, 2020; Combs et al., 2019). Dispersal distance is a key characteristic influencing the potential for human–wildlife interactions, thus spatial grain of analyses must be smaller than this distance to accurately encompass movement dynamics into management approaches (Cushman et al., 2016). A wealth of high-resolution spatial data describing human population, wildlife, and the environment is often available for HUCs, creating tremendous opportunities to assess the links between urban form, biodiversity, and zoonotic disease emergence at appropriate spatial scales.

3 | ABIOTIC CONDITIONS

Landscape changes driven by urbanization significantly alter abiotic conditions, including temperature, light, noise, heavy metal pollution, and hydrology, each of which have downstream effects on wildlife hosts, arthropod vectors, and their associated pathogens (Alberti, 2005). The widespread presence of impervious surfaces (e.g., roads, buildings, parking lots) is a defining characteristic of HUCs. This graying of urban landscapes drastically alters abiotic conditions and presents ecological tradeoffs regarding the presence and intensity of zoonotic hazards, and their impacts on human health. While impervious surfaces may act as a buffer against pathogen transmission when hosts and vectors are restricted to green space, these land cover types support the densification of human settlements, which can increase hazard presence and opportunities for zoonotic spillover by providing high-quality habitat for a suite of urban-adapted commensal rodents and mosquito vectors (Bajwa, 2018; Feng & Himsworth, 2014).

High impervious surface coverage also leads to increased ambient temperatures in urban landscapes, known as the "heat island" effect (Rizwan et al., 2008). Elevated temperature in cities has a strong direct effect on populations of small ectothermic arthropods (LaDeau et al., 2015; Youngsteadt et al., 2017), including observed increases in *Aedes* spp. mosquitos (de Azevedo et al., 2018) and increasing overwintering survival of *Phlebotomus* sand flies, the vector for leishmaniasis (Trajer et al., 2014). Heat island effects may have a strong impact in temperate HUCs specifically, by increasing the number of days above threshold activity temperatures for vectors like *Ixodes* ticks, though this mechanism requires further study (Duffy & Campbell, 1994; Gray, 2008). Underground infrastructure in cities also provides a geothermally stable environment that supports arthropod and rodent populations year-round (Bajomi et al., 2013; Byrne & Nichols, 1999; Channon et al., 2006). Green infrastructure (e.g., parks, green roofs, plantings) offers climate mitigation for humans while also providing thermal refugia for vectors by buffering against extreme temperatures (Venter et al., 2020), presenting a tradeoff between ecosystem services and disservices. Cities should seek to better characterize the thermal landscape at scales relevant to hosts and vectors of concern, as well as integrate future warming conditions due to climate change and expected consequences on species activity and range shifts (Gray, 2008; Ryan et al., 2018).

Impervious surfaces can also drastically influence hydrology by reducing drainage and restructuring watersheds (Pickett et al., 2001; Shuster et al., 2005). At broad spatial scales, this can increase the risk of flooding events, which is correlated with *Leptospira* spp. infection in humans (Naing et al., 2019) and contaminated drinking water, though this phenomenon is more likely in cities lacking robust sanitation systems (Ko et al., 1999; Lau et al., 2010; Rydin et al., 2012). Impervious surfaces also cause environmentally acquired pathogens to concentrate downstream along urban watersheds, increasing hazard exposure (Mallin et al., 2000; VanWormer et al., 2016). At fine spatial scales, impervious surfaces increase opportunities for standing water, which provides breeding habitat for urban mosquitoes and has been correlated with increased *Leptospira* spp. infection in brown rats due to environmental persistence of bacteria shed in urine of infected hosts (Murray et al., 2020).

Urban environments can alter urban wildlife behavior and host–parasite interactions through light and noise pollution (Francis et al., 2011; Francis et al., 2015; Singh et al., 2014). Migrating birds are attracted to regions with more artificial light at night, which may result in increased deposition of bird-fed ticks and associated pathogens around urban areas (Brinkerhoff et al., 2011; Ogden et al., 2008). Light and noise have variable effects on arthropod activity in non-temperate cities (McMahon et al., 2017; Pacheco-Tucuch et al., 2012) and alter gene expression in *Culex pipiens* (Honnen et al., 2016), though downstream consequences of these genomic effects for zoonoses are currently unknown. Furthermore, artificial light at night has been linked to increased West Nile Virus (WNV) exposure in Florida (Kernbach et al., 2021), a pattern that may hold true in temperate HUCs as well. These forms of pollution are pervasive in HUCs and should be recognized for their potential impacts on zoonotic hazards.

Zoonotic systems in HUCs may be influenced by heavy metal pollution, which has historically tainted cities and may have persistent physiological and immune effects, despite ongoing cleanup efforts (Perugini et al., 2011; Rodríguez Martín et al., 2015; Swaileh & Sansur, 2006). Heavy metal contamination is spatially aggregated in post-industrial sites, often positively correlated with neighborhood poverty (Aelion et al., 2013), and can have varied downstream influences on reservoir host immunity and pathogen dynamics (Sánchez et al., 2020). For example, urban pigeons with higher lead concentrations suffered higher intensities of blood pathogens, but those with increased zinc concentrations experienced protective effects against *Chlamydiaceae* infection, a family of potentially human zoonotic bacteria (Gasparini et al., 2014). Lead exposure and cadmium exposure have been found to increase susceptibility of brown rats to bacterial challenge, suggesting that heavy metal pollution could increase their capacity to host zoonotic agents (Cook et al., 1975). In contrast, a recent study of white-footed mice on polluted sites showed no evidence of reduced immunocompetence (Biser et al., 2004). Further work is needed to elucidate how pollution-mediated variation in host susceptibility impacts zoonotic disease risk across urban landscapes.

4 | BIOTIC INTERACTIONS

Species interactions in wildlife communities and their reactions to abiotic factors and socio-ecological landscape features structure the presence of zoonotic hazards in HUCs, their pathogen burden, and human–wildlife interactions that may result in spillover events (Plowright et al., 2017). Identifying and managing zoonotic hazards is thus contingent on understanding (i) how species traits influence their distribution, (ii) how intra- and inter-species interactions, including indirect effects of community diversity, influence pathogen prevalence, and (iii) how resource availability modifies these processes. With this knowledge, public health stakeholders can better implement both direct interventions (e.g., species removal, pathogen-targeted vaccinations) and indirect management solutions (e.g., habitat modification, policy changes).

For reservoir hosts in HUCs, behavioral traits, particularly flexibility to resource shifts and human disturbance, allow colonization and population persistence in habitable patches of either green and/or gray space (Lowry et al., 2012). Generalist species often dominate urban wildlife communities, and typically exhibit a dependence on humans for resources (i.e., human commensal ecology) and high spatial overlap with urban residents (Pickett et al., 2011). Intense urbanization can also filter for individuals with increased boldness and reduced stress responses, possibly increasing opportunities for human–wildlife interaction (Atwell et al., 2012; Carrete & Tella, 2017; Lowry et al., 2012). Additionally, behavioral and phenotypically plastic traits interact with landscape heterogeneity to determine species-specific dispersal success and home ranges (Baguette et al., 2013). Generally, host movement is restricted in cities compared to non-urban habitats due to patchy distribution of suitable habitat (Tucker et al., 2018); however, those species capable of surviving within and traversing the urban matrix can play a major role in the presence and prevalence of zoonotic pathogens across the landscape (Firth et al., 2014; Vanacker et al., 2019). By modeling both habitat suitability and dispersal pathways of hosts in HUCs, public health stakeholders can better understand the ecological determinants of their distribution and incorporate these findings into targeted management solutions that reflect the spatial scale relevant to the target species.

Arthropod vectors usually require bloodmeals, providing direct links between the distribution of habitat, hosts, and the patchy distribution of mosquitos and ticks across green and gray space (Bajwa, 2018). For example, *Culex* mosquitoes are attracted to breeding habitats high in organic matter and bacteria (Burkett-Cadena & Mullen, 2007), and preferentially feed on avian hosts (Bernard et al., 2001). This limits them to avian habitats, which may consist of relatively small patches of green space compared to mammal habitat and is often interspersed across human-populated areas, creating opportunities for host shifts from avian to human populations (Kilpatrick et al., 2006). In contrast, *Ae. aegypti* and *Ae. albopictus*, important vectors of arboviruses, exploit small artificial container habitats in cities (e.g., rainwater in tires, tree holes, etc.) (Hawley, 1988), and blood feed largely on mammals (Faraji et al., 2014; Valerio et al., 2008), including humans (Rose et al., 2020). As a result, these mosquitoes are typically distributed across a broader range of green and gray spaces (Pless et al., 2021). Ticks are an increasingly important vectors of bacterial, viral, and parasitic pathogens in cities globally (Dautel & Kahl, 1999; Hansford et al., 2017; Heylen et al., 2019; LaDeau et al., 2015; Lydecker et al., 2019; Steere, 1994; Vanacker et al., 2019). Pathogen prevalence in urban ticks has been linked to green space structure, including understory composition (Adalsteinsson et al., 2018), and its influence on the movement and community dynamics of hosts (see discussion of dilution effect below).

Though available niche space for zoonotic hazards in urban landscapes may remain unoccupied when landscape barriers and species traits limit successful colonization, urbanization often facilitates introductions (Reed et al., 2020). HUCs are often global and regional hubs of interconnectivity through trade and travel, providing opportunities for the movement of hosts, vectors, and pathogens into and between cities (Padayachee et al., 2017; Reed et al., 2020). Ports of entry in HUCs are particularly vulnerable to invasion given the daily flow of people, goods, and biota moving through them. Pathogen prevalence and diversity in urban rats is often higher around ports, suggesting periodic introductions (Rothenburger et al., 2017). In some scenarios, ecological priority effects may buffer the threat of new invasions if niches are filled such that increased competition limits the successful establishment of additional species or populations (Fraser et al., 2014). However, high propagule pressure (a composite measure of the number of non-native individuals dispersing into a region), continued anthropogenic disturbance, and increased resource availability may allow invasion despite high occupancy and competition with established populations. Additionally, elevated frequency and intensity of human–wildlife interactions due to high human density in HUCs may allow spillover to occur rapidly upon arrival such that population establishment is not always necessary for introduced species to act as important zoonotic hazards. Prioritizing targeted screening for introductions where zoonotic potential is high (e.g., where high propagule pressure and high human density overlap; Little et al., 2017) as well as protocols for rapid identification of potential threats, can provide crucial and cost-effective strategies for limiting zoonotic hazards in HUCs.

The role of biodiversity and abundance of hosts in habitat patches has become an increasingly important and debated factor in the study of zoonotic hazards (Randolph & Dobson, 2012; Wood & Lafferty, 2013). The dilution effect hypothesis posits that increased vertebrate diversity begets an increasing proportion of low-competence hosts that reduce overall environmental prevalence of specific pathogens and thus the hazard or risk to humans (Keesing et al., 2010; LoGiudice et al., 2003). Direct population regulation of zoonotic hosts or vectors through competition or predation is also possible through increases in diversity (e.g., predator reduction of vector mosquito abundance; Dambach, 2020), though this differs from canonical dilution effects based on indirect interactions. The dilution effect has spurred a strong public health impetus for managing urban environments to maximize biodiversity. However, several arguments suggest these effects are not experienced in many temperate HUCs.

First, we must note that the diversity–risk relationship is often depicted as nonlinear, whereby risk increases in low diversity systems and only decreases after a diversity threshold is met (Diuk-Wasser et al., 2021; Kilpatrick et al., 2017; Rohr et al., 2020; Wood & Lafferty, 2013). Across most small and isolated habitat patches in HUCs, host diversity often remains too low to reach a dilution threshold (Diuk-Wasser et al., 2021). Second, while the classic dilution hypothesis predicts higher diversity systems results in an abundance of "dilution" hosts, a recent meta-analysis revealed that the increased diversity in cities is composed of a large proportion of zoonotic hosts, resulting in pathogen amplification rather than dilution (Gibb et al., 2020). Indeed, species experiencing global abundance increases by adapting to human-dominated landscapes pose the greatest risk of viral spillover (Johnson et al., 2020). Furthermore, while re-greening through de-urbanization in HUCs may create natural experiments by increasing urban diversity, recent work indicates hosts in these environments harbor increased pathogen loads and infection prevalence (Peterson et al., 2020). Third, transmission mode (i.e., frequency dependent vs. density dependent) can dramatically impact infection rates, suggesting changes in diversity in HUCs will lead to different pathogen-specific outcomes depending on underlying biology (Dobson, 2004; Faust et al., 2017). Finally, diversity increases in HUCs are associated with greater beta diversity through increased number of unique niche types rather than alpha diversity from species sharing common habitats (Mckinney, 2008). Given trends of reduced movement and concentrated resources in cities (Tucker et al., 2018), this suggests many urban species do not co-occur or interact with the same suite of vectors and pathogens, which is an assumption of the dilution effect. Thus, increases in biodiversity, either through natural dispersal or human-assisted colonization into these areas, may be more likely to increase human disease risk by increasing abundance of competent zoonotic hosts and facilitating greater diversity of pathogenic hazards.

Practical guidance for public health stakeholders in HUCs regarding biodiversity will require a local perspective and context, as outcomes for human disease may be idiosyncratic (Salkeld et al., 2013). Rather than blanket promotion of biodiversity as a buffer against infectious disease (Randolph & Dobson, 2012), each HUC should seek to understand the unique suite of species and ecological processes driving hazards locally and then balance the value of ecosystem services provided by increasing biodiversity against costs of species-specific zoonotic risks.

Urban areas often exhibit increased availability of anthropogenic food resources, either from household and commercial trash or intentionally provided food subsidies, with clear consequences for zoonotic hazards (Altizer et al., 2018; Becker et al., 2018). These ample and clumped resource distributions directly influence zoonotic hazards by increasing host density (Becker & Hall, 2014; Murray et al., 2016), affecting host immune response and thus pathogen susceptibility (Murray et al., 2016), increasing host aggregation, and altering host movement patterns (either increasing dispersal to, or decreasing dispersal from, high-resource sites) (Becker et al., 2018). High-resource density can drive local pathogen load and prevalence in hosts indirectly by altering behavior and interspecific and intraspecific interactions among species (Becker et al., 2018; Moyers et al., 2018). For example, raccoons feeding at clumped resources exhibited higher endoparasite prevalence and parasite diversity (Wright & Gompper, 2005). The dynamics of pathogen–host interactions and resultant zoonotic hazards will depend on specific host immune responses and changes in dispersal (Becker & Hall, 2014; Becker et al., 2018), suggesting a need for further research across local contexts in HUCs. Ultimately, human activity drives the distribution of clumped anthropogenic resources in HUCs, suggesting policy decisions and cultural attitudes around trash containment and wildlife feeding remain important levers in the toolbox of public health stakeholders. Ideally, waste and wildlife managers can develop plans to reduce access to supplemental anthropogenic resources because it increases the likelihood of spatial overlap among hosts and humans, but effective economical waste management remains a major challenge for cities globally.

5 | CASE STUDY: NEW YORK CITY, NEW YORK, UNITED STATES

New York City (NYC) supports the largest human population (8.4 M) and highest density (28k people/mi^2) of any city in the United States. NYC has also been a hub for international travel and trade for centuries, serving as an entry point for the invasion of zoonotic reservoirs, such as brown rats (Armitage, 1993), and pathogenic agents such as West Nile Virus (Sejvar, 2003). The five boroughs of NYC exhibit strong socioeconomic disparities and differences in land use history that drive differential hazard presence (Figure 2). NYC supports a spectrum of green and gray space connectivity, from the large, connected forest patches of Staten Island and Bronx to the intensely developed urban core of Manhattan (Figure 2a). Furthermore, a wealth of research by academic institutions and municipal agencies actively document the distribution and pathogenicity of several zoonotic hazards across NYC (Figure 2c–f) (Bajwa, 2018; Johnson et al., 2016; Little et al., 2017; Vanacker et al., 2019; Walsh, 2014). These attributes make NYC a useful case study to understand how urban eco-epidemiological processes influence zoonotic disease emergence and the roles of diverse stakeholders in surveillance, research, and identification of relevant ecological drivers.

5.1 | Rodent-borne zoonoses

Brown rats and house mice host a diverse community of zoonotic pathogens (Table 2). While city agencies track disease outbreaks, genetic and observational studies by academics provide detailed

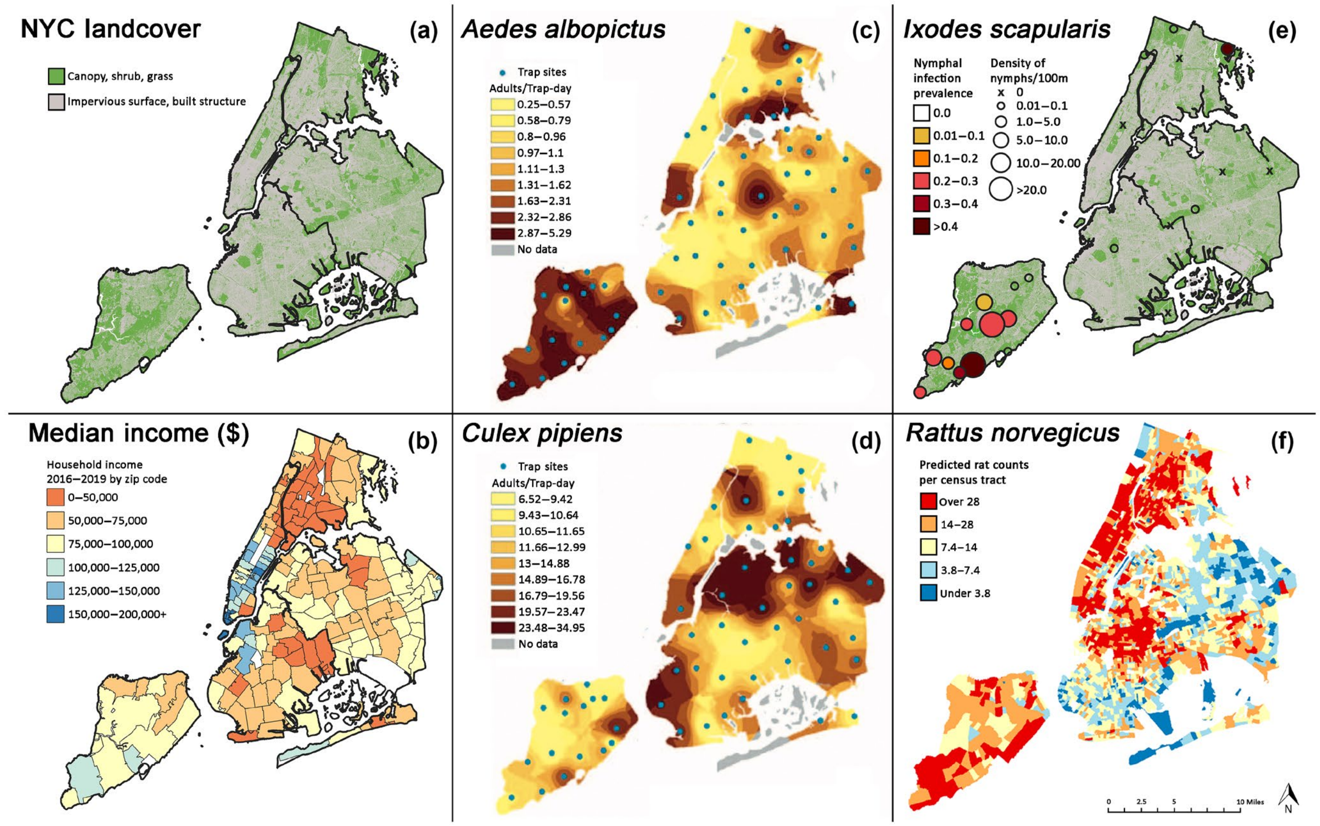

FIGURE 2 Eco-epidemiology of zoonotic hazards in New York City described by: distribution of green and gray land cover (a), median household income (b), density of *Aedes albopictus* (c) and *Culex pipiens* (d) mosquitos interpolated from citywide sampling points, *Ixodes scapularis* density and infection prevalence with *Borrelia burgdorferi* (e), and predicted abundance of *Rattus norvegicus* (f). Land cover data sourced from https://opendata.cityofnewyork.us/. Income data mapped by zip code, sourced from the American Community Survey. *Aedes* and *Culex* density adapted from Bajwa (2018) reproduced with permission from the American Mosquito Control Association. *Ixodes* and *Borrelia* data provided by authors of Vanacker et al. (2019). *Rattus* data adapted from Walsh (2014)

characterization of pathogen and ectoparasite threats (Firth et al., 2014; Frye et al., 2015; Williams et al., 2018). Of most concern in NYC is *Leptospira interrogans*, which is shed through rodent urine and environmentally transmitted, with 58 local cases of Leptospirosis reported between 2006 and 2021 (Bassett, 2017; Chokshi, 2021).

Modeling efforts led by city agencies and various academic groups help identify drivers of rodent habitat and exposure (Childs et al., 1998; Johnson et al., 2016; Walsh, 2014), informed by public datasets of approximately 1.8 million city inspections and 23 million reported complaints between 2010 and 2020, highlighting the role of government and community engagement. Lower socioeconomic wealth is consistently identified as driving rat abundance, as are the characteristics of abiotic structures including building age, vacancy rates, and sewer and subway infrastructure (Johnson et al., 2016; Walsh, 2014). NYC recently began neighborhood-based management approaches (i.e., vs property-level treatments) to match the spatial scale of rodent activity (Mayor, 2017). Studies outside of NYC clearly identify biotic factors such as anthropogenic food and vegetated areas as key sources of rodent resources and habitat (Feng & Himsworth, 2014; Traweger et al., 2006; van Adrichem et al., 2013), though rats in HUCs do not require green space and regularly live at high densities in gray space environments.

5.2 | *Aedes*-borne zoonoses

Surveys led by city and state agencies and academics help track the diverse community of *Aedes* spp. mosquitos and their associated pathogens in the NYC area (Table 2), where *Ae*. albopictus is the most epidemiologically-significant vector (Bajwa, 2018; Little et al., 2017; McMillan et al., 2020). While most *Aedes*-borne zoonoses in NYC are imported, laboratory studies reveal *Ae*. *albopictus* from NY State are competent for Zika virus transmission (Chouin-Carneiro et al., 2016) and in a European HUC a researchers from non-profit, for profit, and government researchers reported local chikungunya transmission (Grandadam et al., 2011), suggesting potential spillover and transmission risks in NYC.

Surveys reveal widespread *Aedes* spp. distribution across Staten Island with localized hotpots in other NYC boroughs with both green and gray spaces. While standing water availability provides necessary larval habitat, modeling efforts suggest *Ae*. *albopictus*

TABLE 2 Major zoonotic hazards of New York City

	Host or vector	Zoonotic pathogens	Socio-ecological drivers in NYC
Rodents	*Rattus norvegicus* *Mus musculus*	*Bartonella spp.*, *Leptospira interrogans*, *Clostridium difficile*, Seoul Hantavirus, others *Shigella spp.*, *Salmonella spp.*, *Clostridium difficile, and Leptospira interrogans*, others	L: High-poverty areas linked to increased host abundance and pathogen prevalence; neighborhood-scale treatments match spatial scale of rodent activity A: Built structures and underground infrastructure constitutes major habitat. Older buildings and higher vacancy rates increase abundance B: Human food waste is major and abundant resource. Reducing trash limits local carrying capacity
Aedes spp. mosquitos	*Aedes albopictus* *Ae. canadensis*, *Ae. vexans*, *Ae. trivittatus*	Zika virus, dengue virus, chikungunya viruses Eastern equine encephalitis virus, Jamestown Canyon virus, La Crosse virus	L: *Aedes* found across all urbanization levels; abundance increases in low- to medium-intensity development A: Standing water availability limits larval habitat (natural and artificial containers). Macroclimate variation influences population survival, microclimate variation influences individual behavior and survival B: Vegetation offers sugar meals, resting habitat, and habitat for animal host
Culex spp. mosquitos	*Culex pipiens f. pipiens* *Culex pipiens f. molestus*	West Nile Virus (WNV), St. Louis encephalitis	L: WNV incidence higher in high-poverty areas. Neighborhood-scale management targets known disease hotspots (e.g., northern Queens). Stronger association with green space habitat than *Aedes* spp., especially for aboveground inhabiting *C.p. pipiens*; *C.p. molestus* preferentially inhabits underground habitats A: Temperature influences vectorial capacity. Macroclimate variation influences population survival, microclimate variation influences individual behavior and survival B: Canopy and vegetation offer habitat for avian hosts, resting habitat, and useful targets for preventative insecticide treatments
Mesomammals	*Felis catus* *Procyon lotor*	*Bartonella* spp. and *Toxoplasma gondii* *Baylisascaris procyonis*, rabies lyssavirus, *T. gondii*	L: Use green-space habitat but survive across gradient of connectivity. Cats survive in smaller patches in mix of green and gray space. High poverty linked to higher cat density and *Toxoplasma gondii* contamination A: Mesomammals are robust to normal range of climate variation B: Clumped food resources from intentional feeding or human food waste increase local density, increase pathogen transmission within/between co-feeding species

TABLE 2 (Continued)

	Host or vector	Zoonotic pathogens	Socio-ecological drivers in NYC
Ticks	*Ixodes scapularis* *Dermacentor variabilis* *Amblyomma americanum*	*Borrelia burgdorferi*, *Babesia microti*, *Anaplasma phagocytophilum*, Powassan virus *Rickettsia rickettsii* *Ehrlichia chaffeensis*, *Ehrlichiia ewingii*	L: Ticks restricted to green land cover. *Ixodes* more limited to forest with leaf litter, *Amblyomma* survives on mowed lawns. Increasing green space connectivity increases *Borrelia* prevalence and tick density. Broad scale required for hazard assessment A: Temperature influences tick activity. Microclimate variation influences fine-scale distribution during questing and resting. B: Influence of host community on vector and pathogen. Deer required for tick reproduction; small mammal reservoir diversity may influence pathogen prevalence.

Note: Hazards are separated by taxa groups and include relevant host or vector species, zoonotic pathogens of importance, and ecological drivers of hazard intensity broken up by type (L: landscape characteristics, A: abiotic conditions, B: biotic interactions).

abundance correlates with increasing low- and medium-intensity urban development (Kache et al., 2020) as well as seasonal meteorological conditions (Little et al., 2017), highlighting both landscape and abiotic drivers of this hazard. Critical biotic factors include presence of vegetation for sugar meals and resting habitat (Fikrig et al., 2020; Samson et al., 2013), as well as distributions of mammalian hosts that are themselves structured by the socio-ecological landscape (Faraji et al., 2014; Goodman et al., 2018).

5.3 | *Culex*-borne zoonoses

In NYC, the most important and prevalent *Culex* spp. mosquito-borne pathogen is West Nile Virus (WNV), which is vectored locally by the *Culex pipiens* complex. City agencies lead vector surveillance and track human cases. Across the five boroughs, 381 WNV cases have been reported between 2000 and 2019, with the highest case counts in Queens where WNV was first detected in 1999 (NYC Department of Health and Mental Hygiene, 2019).

Both *Culex pipiens* f. pipiens and *Culex pipiens* f. molestus are locally abundant (Bajwa, 2018) but exhibit diverse activity patterns, physiology, and spatial distribution across subterranean and aboveground environments (Vinogradova, 2000), allowing them to inhabit a wide range of conditions across NYC's green and gray spaces. Academic studies continue to reveal cryptic biological variation in *Culex* species, which helps inform municipal surveillance, identification, and management efforts (Kilpatrick et al., 2010).

Despite few studies describing ecological drivers of *Culex*-borne hazards in NYC, others have identified a correlation between WNV cases and urbanization and poverty (Andreadis et al., 2004; Poh et al., 2020), though the causal mechanisms remain poorly characterized. Temperature is the key abiotic driver of *Culex* spp. populations and vectoral capacity (Ciota et al., 2014; Reisen, 2013). In NYC, passerine birds are the major WNV reservoir and pathogen prevalence may be linked to host-specific competency and preference by vectors (Bernard et al., 2001; Kilpatrick et al., 2006; Kramer & Bernard, 2001; Nasci et al., 2002). The role of increasing avian diversity for WNV hazard is debated; it appears negatively correlated at broad scales (Allan et al., 2009), but found to be uncorrelated for passerine birds and at fine spatial scales in Chicago, USA (Ezenwa et al., 2006; Loss et al., 2009).

5.4 | Mesomammal-borne zoonoses

NYC supports a community of native and introduced mesomammals (WildlifeNYC, 2021). While few mesomammal-borne zoonoses are reported in NYC, local studies of raccoons and feral cats conducted by city agencies and academics have identified a diverse group of zoonotic pathogens and vectors from hosts and their environment (Table 2; Bassett, 2018; Rainwater et al., 2017; Tufts et al., 2021; Tyungu et al., 2020). These hosts are under-surveyed and associated zoonotic spillover events are underreported, but recent but unreviewed estimates suggest NYC supports tens of thousands of free roaming cats, and Central Park alone supports around 500 raccoons (Slavinski et al., 2012).

Supplemental feeding by local residents appears to be the main biotic driver of mesomammal populations, causing dense and clumped populations that may allow increased transmission within and between co-feeding species (Bozek et al., 2007; Rainwater et al., 2017). They are robust to most climactic conditions, suggesting little role for abiotic variation. Their capacity for long-distance movements enables mesomammals to survive across a gradient of green connectivity, from networks of forested patches to small and isolated parks or gardens surrounded by the gray spaces. Socio-ecological landscape characteristics are useful predictors of mesomammal zoonotic hazard, given studies of *Toxocara cati*, a cat-borne parasite, reveal higher levels of egg contamination in soils of lower-income NYC neighborhoods (Tyungu et al., 2020).

5.5 | Tick-borne zoonoses

NYC supports four major Ixodid tick species including the black-legged tick (*Ixodes scapularis*), the American dog tick (*Dermacentor variabilis*), the lone star tick (*Amblyomma americanum*), and the recently introduced Asian longhorned tick (*Haemaphysalis longicornis*) (Barbot, 2020; Tufts et al., 2021). Their distributions, densities, and pathogen communities are surveyed by city and state agencies as well as academic researchers through yearly observational sampling (e.g., tick dragging, carbon dioxide traps, microscopy) and molecular approaches (e.g., qPCR). LD remains the most common tick-borne disease in NYC with 812 cases between 2010 and 2019, though human babesiosis is becoming increasingly prevalent (average 62 cases/year; Barbot, 2020).

Sampling indicates tick populations are largely restricted to urban green spaces and adjacent neighborhoods in Staten Island and Bronx in NYC. Modeling efforts further emphasize the critical role of biotic factors for urban tick-borne hazards, revealing positive associations between NYC canopy cover connectivity and both *I. scapularis* density and prevalence of *Borrelia burgdorferi*, the etiological agent of LD (Vanacker et al., 2019). Evidence for dilution effects in HUCs like NYC remains mixed (Salkeld et al., 2013) and an area of active research. Neighborhood greenness and biodiversity are correlated with economic wealth in HUCs and linked to racist development policies (i.e., the luxury effect) (Schell et al., 2020), illustrating strong links between tick-borne hazards socio-ecological landscape drivers. Community science reporting further enables research of human behavior and demographics on tick-borne hazard exposure (Bron et al., 2020). Abiotic factors ultimately govern survival of individual ticks via species-specific tolerances for humidity and temperature in HUCs (Diuk-Wasser et al., 2021), where microclimate conditions are often linked to fragmentation and land use patterns (Tuff et al., 2016).

6 | CONCLUSION

The COVID-19 pandemic put a spotlight on the potential devastating human health impacts of zoonotic pathogen emergence, reinforcing the importance of identifying local hazards and understanding their ecological relationships with diverse environments to prevent future spillover events. The persistent risk of known and novel zoonotic diseases in close proximity to high-density human settlements in HUCs should be a call to action to reassess the ecological factors that influence both the distribution of hazards and their varying pathogen prevalence to improve active assessment and mitigation of potential human zoonoses. In this article, we have provided an assessment of how factors relating to the socio-ecological landscape, abiotic conditions, and biotic interactions influence multiple zoonotic hazards in HUCs and provided examples of these how these patterns and processes play out in NYC.

Each city has its unique suite of hazards and socio-ecological landscape patterns to consider, as well as its own practical limitations in available budget, labor, and political support for wildlife management and spillover mitigation. Effective zoonotic spillover prevention requires key collaborations among public health stakeholders, a strategy suggested by a chorus of zoonoses research groups (Eskew & Olival, 2018; Gottdenker et al., 2014; Hansen et al., 2017; Hassell et al., 2017; Magle et al., 2019; Plowright et al., 2021; Vanwambeke et al., 2019). Municipal departments of health and city biologists can work with disease ecologists and modelers to improve surveillance networks and better understand local host/vector distributions, connectivity networks, and interactions with heterogeneous landscapes. Social scientists and community leaders provide necessary context to socio-ecological frameworks, help prioritize programs toward high-risk communities, and promote local engagement for community-based surveillance and reporting efforts. Urban planners, non-profit public health advocates, and policy specialists will also be key partners for developing feasible mitigation goals and securing political support and funding. Establishing these multi-sectoral partnerships and promoting a common understanding of the ecological drivers of local zoonotic hazards are crucial steps toward pre-spillover prevention in HUCs.

We recommend several steps for surveillance that can inform city-specific hazard assessment and response plans. First, it is critical to establish baseline information on the geographic distribution of hazards through field surveys, community reporting, and local expertise. Multi-city information networks can bolster these efforts by promoting methodological standardization and enabling comparative research that informs local efforts (Magle et al., 2019). Given that exhaustive surveys are often unfeasible, sub-sampling areas of interest and leveraging predictive models of habitat distribution can provide valuable information on hazard intensity across complex urban landscapes. Second, this information must be paired with molecular approaches to identify variable pathogen prevalence and eco-epidemiological modeling approaches to predict how they might change over time (Fountain-Jones et al., 2018; Lloyd-Smith et al., 2009). Incorporating community science in aspects of surveillance (e.g., reporting wildlife sightings and encounters with vectors) would also supplement efforts where resources are limited.

While this article does not focus on variable zoonotic exposure (i.e., the likelihood of human–pathogen contact from human interaction with the environment) or risk factors (i.e., the likelihood of adverse effects, given exposure and vulnerability) across HUCs, we recommend management plans also assess these metrics to focus efforts and limited resources on the most at-risk communities. Together, data on hazards, exposure and vulnerability allows for a comprehensive assessment of risk and the creation of quantitative risk maps, which are key tools to facilitate public education of local hazards and develop actionable and targeted management plans (Beard et al., 2018; Morandeira et al., 2019; Ostfeld et al., 2005;

vonHedemann et al., 2015). Finally, management plans should seek to implement integrated pest management approaches when possible, to reduce local densities and sustainably limit hazard intensity but may often require rapid and/or cost-effective measures to directly reduce hazards, especially when faced with urgent needs (Witmer, 2007).

Reducing zoonotic risk across HUCs is challenging for many reasons. Urban landscapes have dynamic demographic, environmental, cultural, and political conditions, suggesting risk maps along with public health programs should be frequently updated to reflect changes over time. Additionally, the basic biology of many hosts, vectors, and pathogens remains understudied, particularly in the context of hyper-local and novel conditions presented within each city, indicating a continued need for collaborative research. Given the continued growth in the number, density, and geographic footprint of HUCs globally, ensuring prevention and preparedness through biologically informed strategies to surveille, research, and manage zoonoses is key to reducing the burden of these preventable human diseases.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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