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The ecological foundations of transmission potential and vector-borne disease in urban landscapes

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Summary

1. Urban transmission of arthropod-vectored disease has increased in recent decades. Understanding and managing transmission potential in urban landscapes requires integration of sociological and ecological processes that regulate vector population dynamics, feeding behavior, and vector-pathogen interactions in these unique ecosystems. Vectorial capacity is a key metric for generating predictive understanding about transmission potential in systems with obligate vector transmission. This review evaluates how urban conditions, specifically habitat suitability and local temperature regimes, and the heterogeneity of urban landscapes can influence the biologically-relevant parameters that define vectorial capacity: vector density, survivorship, biting rate, extrinsic incubation period, and vector competence.

2. Urban landscapes represent unique mosaics of habitat. Incidence of vector-borne disease in urban host populations is rarely, if ever, evenly distributed across an urban area. The persistence and quality of vector habitat can vary significantly across socio-economic boundaries to influence vector species composition and abundance, often generating socio-economically distinct gradients of transmission potential across neighborhoods.

3. Urban regions often experience unique temperature regimes, broadly termed urban heat islands (UHI). Arthropod vectors are ectothermic organisms and their growth, survival, and behavior are highly sensitive to environmental temperatures. Vector response to UHI conditions is dependent on regional temperature profiles relative to the vector's thermal performance range. In temperate climates UHI can facilitate increased vector development rates while having countervailing influence on survival and feeding behavior. Understanding how urban heat island (UHI) conditions alter thermal and moisture constraints across the vector life cycle to influence transmission processes is an important direction for both empirical and modeling research.

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Data Accessibility
This paper is a review of existing research and does not use new data.

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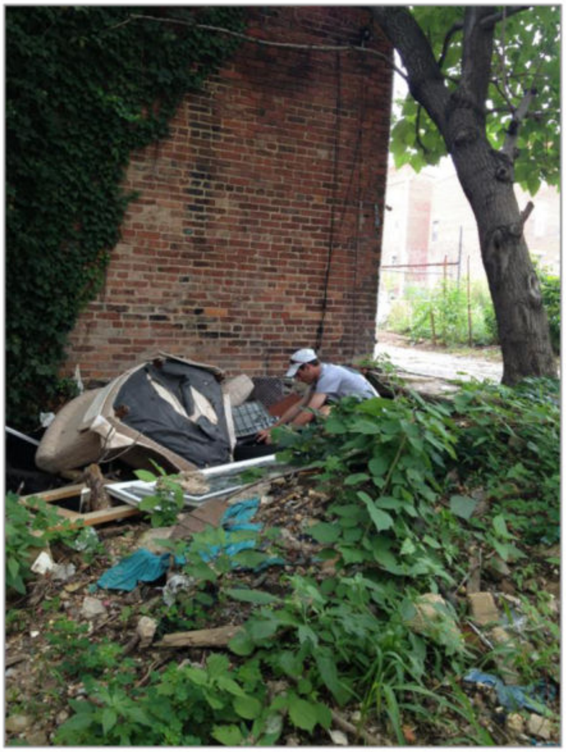
4. There remain persistent gaps in understanding of vital rates and drivers in mosquito-vectored disease systems, and vast holes in understanding for other arthropod vectored diseases. Empirical studies are needed to better understand the physiological constraints and socio-ecological processes that generate heterogeneity in critical transmission parameters, including vector survival and fitness. Likewise, laboratory experiments and transmission models must evaluate vector response to realistic field conditions, including variability in sociological and environmental conditions.

Graphical Abstract



Pathogens transmitted by the bite of arthropod vectors pose a significant human health burden worldwide, and mosquito-vectored diseases alone cause more than 1300 deaths each day (WHO 2013). The landscape of vector-borne disease risk has changed dramatically in recent decades, due in part to global exchanges of goods and people. This is evident in the spread of tick-borne disease across the eastern United States and in the emergence of mosquito-borne chikungunya virus in temperate Italy. Urban regions are often a focus for arrivals and pathogens transmitted by biting arthropods have been increasingly reported in urban areas across the temperate zone.

This paper reviews how urban climate and habitat conditions influence population density, biting behaviour, and vector-pathogen interactions across a range of arthropod-pathogen systems. Predictive capacity needed to manage transmission risk is often limited to broad spatial and temporal scales, yet disease incidence in urban regions is fundamentally patchy. Urban landscapes represent unique mosaics of habitat. The persistence and quality of vector habitat can vary significantly across socio-economic boundaries to influence vector species composition and abundance. The changes in the environmental temperature and moisture regimes observed in

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urban systems can dramatically influence predictions for vector population growth and transmission potential. Synthesis of research highlights the heterogeneity in transmission potential across urban landscapes, created in part by socio-economic conditions that can influence both vector species composition and fitness to generate distinct gradients of risk across neighborhoods.

There remain persistent gaps in understanding of vital rates and drivers in even the most studied mosquito-vectored disease systems, and vast holes in understanding for other arthropod vectored diseases. Empirical studies are needed to better understand the physiological constraints and socio-ecological processes that generate landscape heterogeneity in transmission. Likewise, laboratory experiments and transmission models must evaluate vector response to realistic field conditions, including variability in sociological and environmental conditions.

Keywords

arthropod; climate; disease; mosquito; pathogen; socio-ecology; tick; triatomine; urban heat island; vector; vectorial capacity

Introduction

Human activities have facilitated the emergence and resurgence of many vector-borne diseases (Gratz 1999; Lounibos 2002; Wilcox & Gubler 2005; Kilpatrick & Randolph 2012; Weaver 2013). Although once considered rural diseases, local transmission of suburban and urban cases of malaria (Keiser *et al.* 2004), Chagas disease (Guzman-Tapia, Ramirez-Sierra & Dumonteil 2007; Medrano-Mercado *et al.* 2008; Delgado *et al.* 2011), Leishmaniasis (Jeronimo *et al.* 1994; Harhay *et al.* 2011), have increased in recent decades, often challenging public health responses and management strategies (Geissbuhler *et al.* 2007; Levy *et al.* 2010). Likewise, increases in cases of locally-transmitted arboviruses in suburban and urban populations have increasingly raised public health concern even in temperate regions (Rezza *et al.* 2007; Kyle & Harris 2008; Rey *et al.* 2010; Leisnham & Juliano 2012; Weaver 2013). The processes that facilitate pathogen emergence and rises in urban transmission are complex but changes in the abiotic and biotic quality of habitat supporting vector populations and host exposure in urban landscapes are critical (Leisnham & Slaney 2009; Kilpatrick & Randolph 2012; Weaver 2013).

Here we review current understanding of the ecological properties of urban landscapes that regulate local transmission of vector-borne pathogens. We define a vector-borne disease as a pathological condition in humans, domestic animals, or wildlife that is caused by an etiological agent (i.e, pathogen) that is transmitted by another organism, the vector. This review is focused on arthropod-vectored diseases because a vast majority of important disease-vectors around the world are hematophagous (blood-feeding) arthropods. Arthropod vectors are capable of transmitting viral (e.g., dengue, West Nile virus (WNV)), rickettsial (e.g., typhus, ehrlichiosis), bacterial (e.g., plague, Lyme), protozoan (e.g., malaria, trypanosomiasis) and nematode (i.e., filariasis) pathogens between vertebrate hosts. Likewise, a majority of the studies we discuss are focused on understanding vector transmission to humans. This reflects the distribution of published literature that can inform a mechanistic understanding of transmission parameters in urban systems, although both

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domestic animals and wildlife can also experience changes in prevalence (Bradley & Altizer 2007; Kellner *et al.* 2012; Jennett, Smith & Wall 2013; Giraudeau *et al.* 2014; Paras, O'Brien & Reiskind 2014) and increased susceptibility to some pathogens in urban habitat (Bradley & Altizer 2007; LaDeau *et al.* 2011; Giraudeau *et al.* 2014).

The most unpredictable influence on vectorial capacity in urban ecosystems is humans. Socio-economic variability, cultural practices, and human behavior all help shape the biotic and abiotic components of urban ecosystems and the species interactions underlying ecological disease systems (Leisnham & Slaney 2009; Levy *et al.* 2014a). Urban infrastructure can alter habitat availability and quality, affecting fundamental rates of vector and host life cycles and interactions (Joshi *et al.* 2006; Reisen *et al.* 2009; Leisnham, LaDeau & Juliano 2014; Levy *et al.* 2014b). For example, poverty and degraded urban infrastructure are associated with high mosquito production in two temperate U.S. cities (LaDeau *et al.* 2013), but human behavior can also effectively decouple mosquito population growth from environmental regulation when residents water urban gardens during dry periods (Becker, Leisnham & LaDeau 2014).

Urban areas can have temperature (Oke 1982; Arnfield 2003) and precipitation regimes (Lacke, Mote & Shepherd 2009; Shepherd *et al.* 2010; Niyogi *et al.* 2011) that are distinct from the surrounding region (Pierce and Negri 2002), with important consequences for all organisms that use city habitats. The replacement of natural soil and vegetation with built surfaces in cities can elevate temperatures several degrees above the surrounding region (Oke 1982). In the continental United States researchers found that urban areas were on average 2.9°C warmer than surrounding areas, except in arid biomes where differences could be reversed (Imhoff *et al.* 2010). This is evident in Baltimore, Maryland (Figure 1) where both monthly temperature and numbers of days with maximum temperatures over 32.2°C were higher in urban versus nearby suburban sites. Urban heat island (UHI) effects can also lead to reduced daily temperature ranges (DTR) due to higher night temperatures in cities relative to forested surroundings (Kalnay & Cai 2003). Arthropod vectors are small ectothermic organisms and their growth, survival, and behavior are highly sensitive to environmental conditions (Thomas & Blanford 2003; Paaijmans *et al.* 2013). However, the specific responses of arthropod vectors to UHI conditions are dependent on regional temperatures relative to the vector's thermal performance range (Huey *et al.* 2012a).

The predominance of research on mosquito-vectored systems in this paper reflects a dominance of mosquito studies in the published literature. Mosquito-vectored diseases pose a significant human health burden worldwide (Lounibos 2002) and cause more than 1300 deaths each day (WHO 2013). However, there are other vector-borne systems that represent considerable and growing health threats in and around urban environments, including Chagas disease (*Trypanosoma cruzi*), transmitted by dozens of triatomine insect species (Reduviidae) (Levy *et al.* 2006; Guzman-Tapia, Ramirez-Sierra & Dumonteil 2007; Medrano-Mercado *et al.* 2008) and a growing number of pathogens with tick (Ixodidae) vectors (Maetzel, Maier & Kampen 2005; Hamer *et al.* 2012; Queirogas *et al.* 2012; Uspensky 2014). An incomplete understanding of the ecological processes that regulate mosquito and non-mosquito vector population growth and pathogen transmission continues

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to limit predictive capacity needed to effectively manage vector-borne diseases, especially in urban systems.

We organize the remainder of this review around the mechanistic components of vectorial capacity (Garrett-Jones 1964), *V*, a key metric for generating predictive understanding about transmission potential in systems with obligate vector transmission (Figure 2). Unlike the widely used basic reproductive number, R0 (MacDonald 1957), *V* is derived from entomological parameters and is not dependent on knowledge of host incubation and/or recovery rates. *V* can also be estimated and evaluated for locations and times with or without pathogen presence (Anderson & May 1992) to evaluate spatio-temporal heterogeneity in transmission potential. Although constrained by important and often unrealistic assumptions such as homogenous transmission and constant mortality and biting rates, see (Wonham *et al.* 2006; Bellan 2010; Smith *et al.* 2014), *V* still provides a useful framework for evaluating the constituent processes and environmental variables that define transmission potential. While the vectorial capacity equation (Figure 2) was formulated specifically to characterize transmission of malaria causing *Plasmodium* by *Anopheles* mosquitoes to humans, we use it here as a conceptual roadmap for investigating how various ecological processes associated with urbanization can affect transmission potential of diverse pathogens with obligate arthropod vectors. For recent and thoughtful reviews of the derivation of these epidemiological metrics and application to mosquito control (see Smith *et al*. 2012 and Reiner *et al.* 2013). For each of the parameters below we evaluate current understanding of how arthropod vectors respond to urbanization, and specifically to urban heat island and habitat conditions. In Figure 3 we provide a conceptual framework to evaluate current understanding of vectorial capacity in urban landscapes.

Vector Density (m)

Urban conditions can effectively limit vector populations and pathogen transmission in some systems. Drainage of wetlands and stream burial during urbanization can reduce habitat for *Anopheles* mosquitoes and may reduce malaria incidence (Hay *et al.* 2005; Tatem *et al.* 2013), although urban malaria can persist when agricultural ecosystems are present (De Silva & Marshall 2012). Similarly, deforestation can result in changes to vector access to wildlife hosts, reducing development rates of *Ixodid* ticks (Horobik, Keesing & Ostfeld 2006). However, there are increasing reports of established tick and pathogen populations in even small remnant forests within urban environments (Magnarelli *et al.* 1995; Jobe *et al.* 2007; Jennett, Smith & Wall 2013). Quantifying urban influences on vector density often requires a full evaluation of impacts at different life-stages, which may differ radically in habitat requirements. For example, adult mosquitoes transmit pathogens between hosts, but food web processes and abiotic conditions at the egg and aquatic juvenile stages are important for regulating adult emergence and subsequent density (Juliano 2007; Beck-Johnson *et al.* 2013).

Urban microclimates and UHIs have a large impact on spatio-temporal patterns of arthropod population growth. In regions where vector growth rates and fitness are already at the peak thermal performance, warmer urban conditions should limit vector populations (Huey *et al.* 2012b; Paaijmans *et al.* 2012). However, in temperate regions especially, warmer urban

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environments could facilitate overwinter survival and speed vector development (Alto & Juliano 2001; Ogden *et al.* 2004) to alter population growth rates. Even small shifts in microclimate near impervious surfaces can lead to substantial changes in vector development rates and population growth (Beck-Johnson *et al.* 2013). For example, models using malaria vector and climate data from Africa found that a 0.5 °C increase in mean temperature could lead to a 30–100% increase in mosquito abundance (Pascual *et al.* 2006). Model's parameterized with data from different sites often show differences in relative importance of environmental conditions (Johansson, Dominici & Glass 2009), demonstrating that the influence of the abiotic environment on vector density is a function of the temperature or moisture regime currently limiting vector fitness. There is growing recognition of the need to investigate vector performance under field conditions, where thermal conditions can fluctuate more widely and rapidly than is easily reproduced in laboratory settings and when vector responses are conditionally dependent on regional climate (Cator *et al.* 2013; Mordecai *et al.* 2013; Paaijmans *et al.* 2013).

The vector species that feed on humans are often the species that are best able to adapt to environmental changes associated with urbanization. Urban habitats, both terrestrial and aquatic, can offer high resources (e.g., food, resting sites) with sparse populations of competitor and predator species that regulate vector population growth in more natural systems (Chase & Shulman 2009; Freed & Leisnham 2014). The viral pathogens that cause dengue, yellow fever and the emergent chikungunya virus are transmitted by *Aedes* spp. mosquito vectors that are well-adapted to human-dominated landscapes (Gratz 2004; Hammond *et al.* 2007). Immature development occurs in artificial water-filled containers (e.g., trash receptacles, garden pots) or ephemeral pools (e.g., drainage ditches, bioswales) associated with human activities (Bartlett-Healy *et al.* 2012; Quintero *et al.* 2014; Townroe & Callaghan 2014). Likewise, subterranean urban storm water drains can support population growth for a range of mosquito species and may account for as much as 78% of the resident urban mosquito population in the dry season in Australian cities (Kay *et al.* 2000). Habitat permanence, size and nutrient status are important characteristics of larval mosquito habitat and can influence species composition and vector abundance (Silver 2008). Unmanaged container habitat supporting immature mosquito development is often more abundant around vacant lots in lower socio-economic neighborhoods (LaDeau *et al.* 2013), while more permanent habitat such as garden water features and ponds are more likely to be found in higher income neighborhoods (Bartlett-Healy *et al.* 2012; Dowling *et al.* 2013). The aggressive human-biting Asian tiger mosquito (*Aedes albopictus)* is especially capable of exploiting unmanaged container habitat and is a superior competitor to the predominant WNV vector, *Culex pipiens*, in small to medium sized containers (Carrieri *et al.* 2003; Costanzo *et al.* 2011). However, the heterogeneous availability and quality of aquatic habitat across socio-economically diverse neighborhoods in the mid-Atlantic region of the United States appears to support local-scale coexistence of *Ae. albopictus* and *Cx. pipiens* (LaDeau et al. 2013). The mosaic of land use and socio-economic status at both local and regional scales is important. Vector management actions can effectively limit population density, although socio-economic and political boundaries influence which regions and neighborhoods can institute effective control strategies (Tedesco, Ruiz & McLafferty 2010). The intersection of agricultural and urban landscapes can create geographic overlap between

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vector species and human populations (Ljumba & Lindsay 2001; Afrane *et al.* 2004; Mackenzie, Gubler & Petersen 2004; Matthys *et al.* 2006) and the process of urbanization can facilitate pathogen emergence when urban areas expand into natural areas of existing high vector densities (Bradley & Altizer 2007; Leisnham & Slaney 2009; Brearley *et al.* 2013). The greatest number of human cases of Lyme disease in the northeastern and north-central regions of the United States occurs most often in the suburban and exurban communities that intersect with forest ecosystems containing hosts, vectors and pathogen (Steere, Coburn & Glickstein 2004; Bacon, Kugeler & Mead 2008; Tran & Waller 2013).

Strategies for prevention and control of vector-borne disease generally focus on reducing the density of vector populations. Positive associations between the abundance of arthropod vectors and disease incidence has been demonstrated across numerous systems (Gratz 1999; Andreadis *et al.* 2004; Walk *et al.* 2009; Levy *et al.* 2011), although this association does not hold in all locations even for a specific pathogen (Scott *et al.* 2000). Habitat availability is certainly a prerequisite for vector population growth, but the timing and quality of available habitat have complex impacts on vector populations. For example, reduced availability of larval habitat during droughts can cause female mosquitoes to retain eggs, which has been associated with reduced fitness and propensity to take a second blood meal in some *Aedes* and *Anopholes* species (Dieter, Huestis & Lehmann 2012; Charlwood *et al.* 2013) but has relatively low fitness cost in *Cx. pipiens* (Johnson & Fonseca 2014). Persistent gaps in mechanistic understanding of what regulates vector population growth rates in built environments continue to limit predictive capacity for managing transmission risk.

Vector Survival (p)

Vector survival is necessary to achieve high vector density. However, it is important to note that the duration of vector survival (longevity) is a critical determinant of *V* in itself. Even highly abundant and competent vectors are unlikely to pose a transmission risk if their lifespan is shorter than the time required for extrinsic incubation (*n*) and subsequent host feeding. Urban conditions can have complex impacts on vector survival that transverse life-stages. While temperatures can directly influence survival of adult mosquitoes (Alto & Bettinardi 2013), environmental conditions at the larval life-stage can also affect adult longevity (Delatte *et al.* 2009; Alto 2011; Araujo, Gil & e-Silva 2012). Larval mosquitoes reared at warm mean temperatures (26°C) had slower development, decreased survival and reduced adult reproduction when daily temperature fluctuations were large (Carrington *et al.* 2013c, but see Ciota et al. 2014). Juliano and colleagues used both laboratory experiments and field collected female *Ae. aegypti* to demonstrate that intraspecific competition in larval habitat produced smaller females that had reduced survival and were less likely to be infected with dengue (Juliano *et al.* 2014). Thus, heterogeneity in habitat persistence, size and quality across urban landscapes is likely to generate important variability in vector survivorship and transmission potential.

There are few studies of survivorship in non-mosquito vectors that are relevant to urban landscape comparisons, yet local urban transmission is evident in sand fly (Harhay *et al.* 2011), triatomine (Guzman-Tapia, Ramirez-Sierra & Dumonteil 2007; Medrano-Mercado *et al.* 2008) and tick-borne systems (Schwartz *et al.* 1991; Buczek *et al.* 2014; Uspensky

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2014). In general, tick survival is negatively related to temperature (Bertrand & Wilson 1996) but most sensitive to low or variable humidity conditions (Nieto, Holmes & Foley 2010; Buczek *et al.* 2014). Similarly, a principal vector of Chagas disease, *Triatoma infestans*, is sensitive to shifts in both temperature and relative humidity in laboratory studies (Lorenzo & Lazzari 1999) and is typically found in human residences where building materials dampen variation in these factors (Vazquez-Prokopec *et al.* 2002). The malaria vector *An. stephensi* was also found to prefer indoor resting habitat where daily temperature ranges were moderated, even though these were on average warmer than ambient (outdoor) temperatures (Cator *et al.* 2013).

The physiological constraints on arthropod survival through temperature or humidity extremes are clear, but further research is needed to better understand how variability in survival and its interaction with the extrinsic incubation period (EIP) across urban landscapes can contribute to heterogeneous transmission risk. Despite the importance of mosquito survivorship, there are relatively few studies that have evaluated mosquito age in the field (Harrington *et al.* 2008) and many models assume constant population mortality rates (see references in Bellan 2010). Advances in use of transcriptional profiles to estimate adult mosquito age (Cook et al. 2006, Cook and Sinkins 2010, Hugo et al. 2010) provide an opportunity for estimating adult mosquito age from field-collected samples and make this an exciting and critically important direction for future work. Likewise, empirical data informing understanding of overwinter or inter-seasonal vector survival are generally sparse, although those studies available suggest egg and adult survival between seasons may be important determinants of seasonal population dynamics and pathogen persistence (Andreadis, Armstrong & Bajwa 2010; Lounibos *et al.* 2010; Fischer *et al.* 2011; Andreadis, Dimotsiou & Savopoulou-Soultani 2014). The classical assumption of constant mortality rates is not supported by empirical studies, meaning that common transmission models overestimate the efficacy of control strategies aimed at reducing survival rates (Bellan 2010).

Host Feeding or Biting Rate (a)

Most human vector-borne pathogens and all arboviruses originated as zoonoses and many still function as multi-host systems that require vectors to consume bloodmeals from more than one vertebrate species. *Borrelia burgdorferi* (Lyme) and WNV require non-human (zoonotic) hosts for pathogen amplification and persistence, and any human infection indicates spill-over from zoonotic cycles. The pathogens causing malaria and dengue virus in humans originated through similar zoonotic cycles (Wolfe, Dunavan & Diamond 2007), although most forms of these pathogens are now effectively adapted to mosquito transmission exclusively between humans.

In the vectorial capacity (V) equation the parameter a is the number of human bites per mosquito per day. To encompass our focus on diverse arthropod vectors, we interpret the biting rate more broadly to evaluate feeding activity across available host species. Thus, the biting rate for a given host species is a function of both the time needed to find (i.e., composition and density of available host species) and process the blood meal (e.g., gonotrophic cycle in mosquitoes). In V, the parameter a is squared to reflect the fact that a

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vector must feed twice to transmit a pathogen: first to acquire it and then a second time to pass it on to a new host. These sequential host feeding probabilities may be equal (i.e., a^2), although systems in which transmission to humans relies on occurrence of a previous zoonotic bloodmeal (e.g., WNV, Lyme) could be represented by separate feeding parameters. In some cases, infection with a pathogen may also influence vector host-seeking behavior (as in human malaria (Cator *et al.* 2014)). Likewise, there are many studies demonstrating that mosquito biting rates vary across individuals in host populations (Ansell *et al.* 2002; Harrington *et al.* 2014), although models and derived control strategies generally assume constant biting rates.

As with other parameters, urban habitat modification and temperature regimes potentially have strong impacts on host-seeking and biting behavior across arthropod vectors. Laboratory studies have shown that *Anopheles* mosquitoes reared at lower temperatures take more time between emergence and initial blood feeding (Paaijmans, Cator & Thomas 2013) and that temperature-dependent feeding rates vary among important WNV vector *Culex* species (Ciota *et al.* 2014). Similarly, thermal preferences are evident in the spatial distribution, feeding activity and dispersal of *Triatoma* species (Guarneri *et al.* 2003; Minoli & Lazzari 2003), and host-seeking activity in many tick species is negatively associated with temperature and sensitive to humidity (Ogden *et al.* 2004; Berger *et al.* 2014).

The composition of potential host species is often a critical determinant of pathogen transmission. The suite of host animals required to support persistent (endemic) pathogen transmission can be complex community networks (LoGiudice *et al.* 2003; Keesing, Holt & Ostfeld 2006; Kilpatrick *et al.* 2006; Garcia *et al.* 2007; Hamer *et al.* 2011). Human infection is often the event that motivates research and management in disease systems, but humans are not always an active player in transmission (i.e., pathogens with a non-human reservoir host). The human malaria parasite *Plasmodium* is effectively transmitted to and from humans through sequential mosquito feeding (Service & Townson 2002). Thus, the density of susceptible human hosts and their availability to biting mosquitoes is an important determinant of mosquito feeding rates and human transmission potential for malaria-causing *Plasmodium*. Control strategies such as the use of bednets to prohibit biting can effectively limit transmission and ultimately, local pathogen persistence (Lindblade *et al.* 2004; Muller *et al.* 2006). Mosquito feeding behavior varies substantially across sites, due both to differences in host availability and to geographic differences in host preference (Apperson *et al.* 2004; Kilpatrick *et al.* 2006; Molaei *et al.* 2006; Hamer *et al.* 2009; Faraji *et al.* 2014b). *Aedes albopictus* host-use includes ten to twenty percent avian species in some regions (Richards *et al.* 2006; Sawabe *et al.* 2010), although most published studies report few to no bird bloodmeals (Munoz *et al.* 2011; Faraji *et al.* 2014a). High densities of non-human animals may divert some vector species from biting humans (Franco *et al.* 2014). The presence of outdoor pets (dogs and cats) in an urban New Jersey neighborhood was associated with a decrease in *Ae. albopictus* human feeding rates relative to nearby suburban sites where pets were generally kept indoors (Faraji *et al.* 2014a). Heterogeneity in feeding preferences across populations is, however, also evident. For example, *Ae. albopictus* preference for human hosts despite availability of other mammalian host species is reported

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from studies in the southern U.S. (Richards *et al.* 2006), Cameroon (Kamgang *et al.* 2012), and Spain (Munoz *et al.* 2011).

By comparison, transmission and persistence of the etiological agents of Lyme borreliosis rely on a complex sequence of ticks feeding on multiple animal reservoir species (LoGiudice *et al.* 2003). Although humans may be infected by a tick bite, they are not infectious to subsequent biting ticks. The relative density of zoonotic host species is an important determinant of *Borrelia burgdorferi* infection in ticks and human disease risk. Small forest fragments, including those that occur in urban landscapes, may pose elevated risk of exposure to tick-borne Lyme disease due to high densities of a key tick host and pathogen reservoir, the white-footed mouse (*Peromyscus leucopus*), and low densities of predators and competitors (Rosenblatt *et al.* 1999; Nupp & Swihart 2000; Logiudice *et al.* 2008). As a result, tick density and infection prevalence with the Lyme pathogen have been shown to negatively correlate with forest fragment area or vertebrate host species richness in both empirical and theoretical studies (Allan, Keesing & Ostfeld 2003; Brownstein *et al.* 2005; Logiudice *et al.* 2008). Recent studies suggest that invasion by exotic shrubs, which are widespread in urban ecosystems, may also increase tick-borne disease risk via changes in reservoir host abundance (Williams *et al.* 2009; Allan *et al.* 2010). *Trypanosoma cruzi* (the etiological agent of Chagas disease) falls somewhere in between—humans can transmit the parasite, but other animal hosts are usually implicated in areas of high incidence and host species composition near human residences is an important component determining human exposure (Gurtler *et al.* 2014).

Creation of vector habitat close to humans and domestic animals can dramatically influence host feeding success and disease transmission, although human behavior can be the largest determinant of feeding success in these situations (Guillet *et al.* 2001; Gurtler *et al.* 2014). Triatomine bugs are particularly adept at finding resting places in the cracks and crevices that occur between bricks and stones (Levy *et al.* 2006) close to the humans and domestic animals that support persistent local *T. cruzi* transmission during and after the urbanization process in Peru (Levy *et al.* 2006; Foley *et al.* 2013; Gurtler *et al.* 2014; Levy *et al.* 2014b). In a study of tick-borne ehrlichiosis in the metropolitan area of St. Louis, MO, where tick-borne disease risk increases with distance from the urban core, prevention measures taken by humans were greatest in exurban habitats (Bayles, Evans & Allan 2013). Thus while vector density and corresponding disease risk may change along human land-use gradients, human knowledge and prevention of disease may change as well, necessitating an interdisciplinary approach to the study of vector-borne disease dynamics in human-dominated ecosystems.

Vector Competence (b)

A vector ingests a pathogen while feeding on an infected host, and, in many cases, the pathogen must pass through the gut and enter the salivary glands before the vector is infectious (exceptions include *T. cruzi* and *Typhus* systems in which transmission occurs via the vector's feces). A pathogen's interaction with the vector's gut epithelium is often specific to vector physiology and many species can ingest pathogens but fail to become infectious. In triatomine vectors it may be the chemical make-up of the feces that define

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variation in *T. cruzi* competence across species (Antunes *et al.* 2013). Species competence across a taxonomic group (or across populations within a species) can vary from not competent to fully competent for pathogen transmission according to vector physiology, environmental conditions, and interactions between vector and pathogen genetics (Weaver *et al.* 2004).

Arboviral competence can vary among mosquito populations within a species (Kilpatrick *et al.* 2010; Charan *et al.* 2013; Fansiri *et al.* 2013; Tabachnick 2013) and are often temperature-sensitive (Dohm, O'Guinn & Turell 2002; Reisen, Fang & Martinez 2006; Kilpatrick *et al.* 2008; Carrington *et al.* 2013b). Dengue virus infection and transmission rates increase at higher temperatures (Halstead 2008), although a growing body of models and laboratory experiments suggest that fluctuations in daily temperature modify this relationship (Lambrechts *et al.* 2011; Carrington *et al.* 2013a). Adult mosquitoes held at 26°C mean temperature were less likely to have midgut infections when DTR was large (Carrington *et al.* 2013b), while infection and transmission probability were increased when DTR was large at lower mean temperature (20°C) (Carrington *et al.* 2013a). Vector immunity (Murdock *et al.* 2012) and interactions between vector and viral genetics (Zouache *et al.* 2014) can be important determinants of vector competence in mosquitoes. Immune function and genetic interactions may explain some of the mechanism for temperature regulation of vector competence, as both are influenced by environmental temperatures (Kilpatrick *et al.* 2008; Murdock, Moller-Jacobs & Thomas 2013; Zouache *et al.* 2014). Empirical studies that evaluate the role of vector immunity and the role of vector-pathogen genetics in vector competence across urban landscapes are an important research priority. Relatively few studies examine vector competence across species of ticks feeding on the same hosts (Henning *et al.* 2014). The influence of ambient temperature on vector competence in tick species was not existent for Venezuelan equine encephalomyelitis (Dohm & Linthicum 1993) and temperatures above 27°C were not conducive to vector competence for *B. burgdorferi* (Shih, Telford & Spielman 1995).

For vectors with complex life-cycles such as mosquitoes, environmental conditions experienced in the larval life-stage can also influence the vector competence of adults. For example, larval competition between *Ae. albopictus* and *Ae. aegypti* increases the susceptibility of *Ae. albopictus* to infection by dengue-2 virus as adults (Alto *et al.* 2008). Similarly, larval *Ae. aegypti* raised at higher temperatures in the presence of the pesticide malathion experienced increased virus dissemination as adults (Muturi & Alto 2011), indicating potential for complex interactions between UHI and environmental pollutants to influence vector competence in urban landscapes.

Extrinsic Incubation Period (n)

The EIP describes the number of days between the time a vector acquires an infectious pathogen and when it is capable of transmitting the pathogen to a subsequent host. Pathogen transmission can only occur if the vector bites a host after sufficient time for parasite development (e.g., malaria) or replication (infection by viruses, *T. cruzi*, etc.). Urban heat island characteristics, including both high temperatures and reduced daily temperature variation, may directly influence the rate of pathogen development inside vectors.

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Nymphal ticks reared at warmer temperatures (33–37°C) were less likely to be infected with *B. burgdorferi* (Shih, Telford & Spielman 1995). Likewise, the development of *T. cruzi* within the triatomine bugs is highly temperature dependent (Neves 1971); the presence of infectious parasites in the vector *Rhodnius prolixus* was observed in 2 versus 7 days when the temperature was increased from 20°C to 30°C (Phillips 1960; Brener 1973).

Much of our current understanding about how environment influences EIP is once again derived from mosquito models, primarily in malaria and dengue systems. In regions where temperature means are generally below the thermal peak for EIP performance, urban heat island conditions will generally shorten EIP, although dampening of daily temperature fluctuations may have contrasting effects (Blanford *et al.* 2013; Carrington *et al.* 2013a). The extrinsic incubation of the malaria parasite for example, was faster when daily temperature range (DTR) was large at cooler mean temperatures but large DTR slowed EIP when mean temperatures were already high (Blanford *et al.* 2013). More rapid viral replication (and shortened EIP) in response to increased temperature has been demonstrated for many (Dohm, O'Guinn & Turell 2002; Reisen, Fang & Martinez 2006; Richards *et al.* 2012), although not all arboviruses (Kramer, Hardy & Presser 1983) and some evidence suggests that cooler temperatures may increase vector susceptibility to infection (Adelman *et al.* 2013). Likewise, cooler larval habitat has been shown to increase vector susceptibility to dengue (Alto & Bettinardi 2013).

Discussion

The ability to predict and effectively manage arthropod-vectored disease outbreaks depends critically on how well we understand the mechanistic components of vectorial capacity. The emergence and re-emergence of vector-borne diseases in urban areas across the globe is occurring in parallel with a surge in urban populations and public health challenges will continue to increase (Patz *et al.* 2004; Leisnham & Slaney 2009; Myers & Patz 2009). Our review demonstrates that while there is much we do know, there remain persistent gaps in understanding of critical rates and drivers in mosquito vectored systems, and vast holes in knowledge for other arthropod vectored diseases.

A majority of arboviruses lack effective vaccines, while clinical diagnosis and treatments of other vector-borne diseases (including those caused by parasites and bacteria) are limited. Thus, managing the entomological exposure risk is critical. The most effective management of vector-borne disease in humans has often focused on limiting the distribution and abundance of vector populations and thus, processes regulating vector density are the most studied component of vectorial capacity. However, predicting and managing transmission of even well-studied, mosquito-vectored pathogens is often difficult due to limited understanding of the processes controlling vector-pathogen interactions and vector-host contacts in real environmental conditions.

Vectorial capacity captures many important aspects of vector-borne disease transmission but the simple formulation lies atop of a number of assumptions, such as homogenous mixing of vectors and hosts and the absence of migration. These assumptions were never meant to be realistic, even for idealized rural environments (Smith *et al.* 2012). For cities they can be

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especially misleading. Urban areas typically serve as regional transport hubs and are often the point of entry for exotic organisms (Lockwood, Cassey & Blackburn 2009). Indeed *Aedes* mosquito species have spread to urban areas worldwide (Lounibos 2002; Tatem, Hay & Rogers 2006). The establishment of these species in cities has been a determining factor in the spread of chikungunya and dengue viruses (Delatte *et al.* 2008; Lambrechts, Scott & Gubler 2010). Likewise, neither vector nor host populations within cities are likely to be ‘well-mixed’. Vector density can vary significantly across neighborhoods within a city (Foley *et al.* 2013; LaDeau *et al.* 2013) but current understanding of urban dispersal barriers and heterogeneity in vector fitness at this scale is limited. City streets can serve as a barrier to insect dispersal, as some species may be unwilling or unable to cross a swath of unprotected pavement or asphalt (Hemme *et al.* 2010; Barbu *et al.* 2013). Variation in temperature and humidity across impervious surfaces and residential infrastructure can also influence dispersal activity (Vazquez-Prokopec *et al.* 2004). The divisions that urban infrastructure may create in vector populations could lead to more complex metapopulation transmission dynamics, such as source-sink metapopulations (Hanski & Hanski 1999) in which vector fitness is high in some blocks/patches but not others. Vector genetics are important determinants of life history traits and vector competence among individual populations within a species (Zouache *et al.* 2014). Population structure is likely influenced by land use and socio-economic heterogeneity in urban environments, but data are needed to identify relevant spatial scales and quantify their importance in urban landscapes.

The motivation behind development of the vectorial capacity model was to guide control strategies (Garrett-Jones 1964; Smith *et al.* 2012). The equation for V predicts high sensitivity to adult survival and many studies demonstrate how this conclusion is highly dependent on a suite of assumptions that may be unrealistic in real field settings where mortality rates and population mixing are not constant, vector-host interactions are environmentally dependent and vector-pathogen interactions vary with genetic structure (Bellan 2010; Smith *et al.* 2014). Perhaps less well-recognized is the importance of the socio-economic environment of modern cities that can affect entomological parameters and efficacy of vector control (Bartlett-Healy *et al.* 2011; Fonseca *et al.* 2013; Barbu *et al.* 2014; Buttenheim *et al.* 2014). Social factors interact with the biophysical environment to create a complex and often hard to predict, socio-ecological context within which vector-borne diseases circulate.

The predictive capacity needed to manage transmission is often limited to broad spatial and temporal scales, yet human disease incidence within a region is often patchy (Reiter *et al.* 2003; Liu *et al.* 2009; Sugumaran, Larson & DeGroote 2009; Foley *et al.* 2013). New data and models are needed to better understand how UHI and habitat suitability regulate both vector-pathogen and vector-host interactions. Infrastructure, transportation grids, and human behavior create an urban habitat mosaic that is fundamentally different from many of the model systems or laboratory experiments used to generate inference on transmission risk. Data are required to better understand how physiological constraints associated with urban temperature and regimes influence the individual parameters that define transmission potential (Chown & Duffy 2015). Modeling disease metrics for even the most well-studied mosquito vectored system, human malaria, still relies on too few data points from a limited

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suite of species, including some that are not relevant to transmission of *Plasmodium* parasites (Mordecai *et al.* 2013). Empirical work is needed to better understand the range of conditions experienced by vectors in the field and evaluate the integrative impacts of urban habitat and microclimate conditions on vectorial capacity. Finally, while the many studies reviewed here provide valuable insights into the processes that define vectorial capacity, few address the complexity of interacting socio-ecological factors that ultimately determine transmission risk in urban habitats. In addition to a call for more data to parameterize models to reflect realistic field conditions, we also highlight the need for models that can accommodate the influence of socio-economic drivers to better predict transmission risk at spatio-temporal scales relevant to management strategies.

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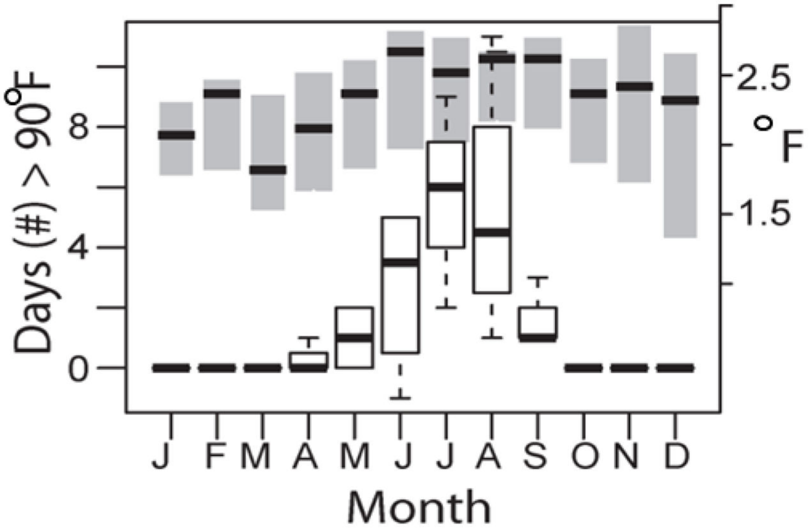

Figure 1. An urban heat island

Differences in climate metrics for 2011–2013 between urban and suburban sites in Baltimore, Maryland. Boxplots show the additional number of days with maximum daily temperature ≥ 90°F (left axis) at the urban versus suburban site. Right axis shows increase in mean monthly temperature at the urban site (shaded bars). Standard boxplot designations used; dark band denotes median values. Data from CDC.NOAA.gov, collected from NOAA stations located at Baltimore-Washington International Airport and Maryland Science Center.

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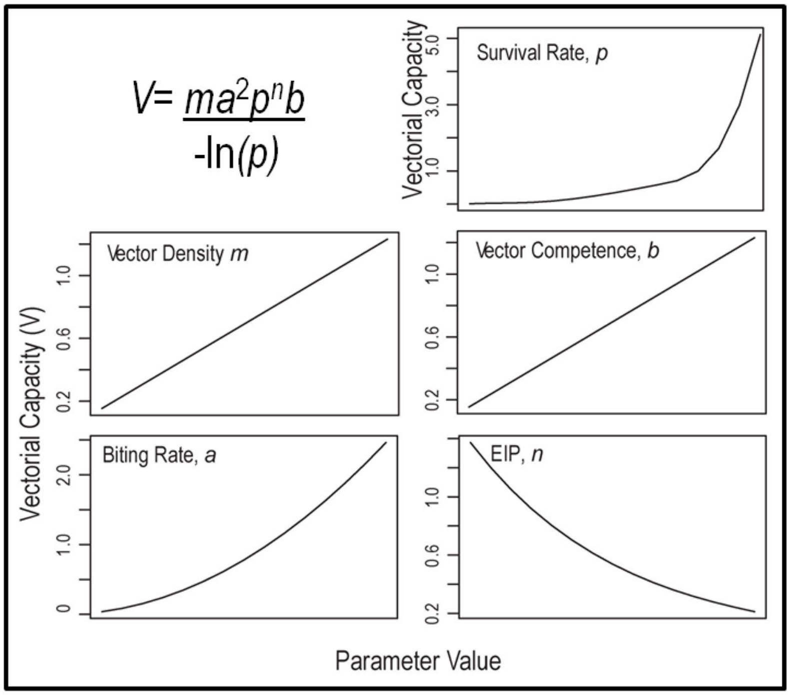

Figure 2. A metric for understanding vector-borne disease transmission and risk

Vectorial capacity (*V*) describes transmission potential by integrating the potential for a competent vector to bite an infected host and then survive long enough to become infectious. The trend lines in each panel (above) show how increasing each of the five biologically-relevant vector parameters influences transmission potential (*V*). The value of each of the vector parameters may be influenced by local conditions within the urban environment. EIP is the extrinsic incubation period of a pathogen inside the vector.

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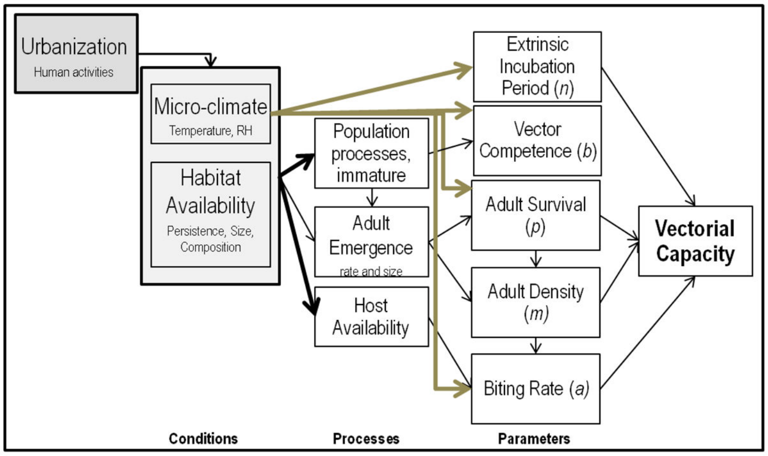

Figure 3. A conceptual depiction of urban influence on vectorial capacity

Urbanization involves replacing natural land cover with built surfaces and infrastructure, which directly alters micro-climate and habitat availability for vector and host species. These environmental characteristics influence vector population processes, with consequences for each of the parameters defining vectorial capacity (Fig. 2). Lighter arrows highlight parameters of *V* that are directly influenced by changes in urban temperatures. Thicker arrows denote pathways with >2 published studies (in mosquito vectors) showing consistent directional effect.