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De-urbanization and Zoonotic Disease Risk

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In recent decades, human populations worldwide have undergone a fundamental shift from predominately rural to urban living. Today, more than half of all people live in urban areas, and this figure will swell to roughly two-thirds by 2050 (United Nations 2014). These sweeping demographic changes demand the attention of disease ecologists because anthropogenic activities are global drivers of emerging infectious diseases affecting both wildlife and humans (Murray and Daszak 2013; Gottdenker et al. 2014). For example, human population density within a species' range is positively related to zoonotic pathogen richness in mammals, which in turn influences disease emergence (Olival et al. 2017). Urbanized, human-dominated landscapes in particular have strong influences on disease patterns in wildlife, domestic animal, and human populations (Hassell et al. 2017). While the effects of urbanization on infectious disease systems are important and increasingly recognized as an emerging research priority, we argue here that it is also essential for disease ecologists and One Health practitioners to consider the opposite, but surprisingly common, process: de-urbanization.

De-urbanization Trends and Zoonotic Disease Implications

Driven by diverse economic, social, and cultural factors, de-urbanization is characterized by shrinking urban populations and can result in abandonment and urban decay (Gulachenski et al. 2016; Lima and Eischeid 2017). Against a background trend of a growing global human population, a number of countries and cities are shrinking. More than 50 countries are expected to undergo population decrease by 2050, and ten are projected to have total population declines of > 15% in this timeframe (United Nations 2017). Developed nations will be particularly affected by shrinking population size. In one of the most notable and widely reported examples, Japan's total population may plummet by nearly 40 million, or approximately one-third, by 2065 (IPSS 2017). Given that the majority of the world's population resides in urban areas (United Nations 2014), shrinking countries will likely encompass depopulating cities within them. Significant city population declines can also occur in countries experiencing overall population growth, such as the USA. For example, prominent American cities, including Baltimore, Cleveland, Detroit, Pittsburgh, and St. Louis, have shrunk relative to population sizes in the mid-twentieth century, sometimes by large proportions (> 25%) (Hollander et al. 2009).

Population decline and consequent urban shrinkage could allow for increased ecosystem services and positive environmental outcomes, for instance through greening strategies (Haase et al. 2014; Lima and Eischeid 2017), yet the general ecological consequences of de-urbanization are not well understood. In particular, there are important outstanding questions regarding the influence of de-urbanization on infectious disease (Gulachenski et al. 2016; Rael et al. 2016). For example, how is zoonotic disease risk affected by human depopulation of urban centers and the resultant disuse and dilapidation of infrastructure? What

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disease mitigation strategies will be most effective in abandoned and decaying habitats?

There are specific reasons to be concerned about the potential effects of unmanaged de-urbanization on zoonotic disease risk (Fig. 1). First, wildlife in urban and peri-urban habitats are known to harbor pathogens that threaten human health, including *Bartonella* spp., *Salmonella enterica*, *Rickettsia rickettsia*, and a diversity of viruses (Himsworth et al. 2013; Firth et al. 2014; Ayral et al. 2015; Rainwater et al. 2017). One analysis showed that mammalian hosts of emerging infectious diseases were approximately 15 times more likely to use human-modified environments than other co-occurring mammal species (McFarlane et al. 2012). Thus, whether because of a greater propensity to serve as pathogen reservoirs or because of increased contact rates with people, urban-associated wildlife can drive human disease. Furthermore, human commensal species may also represent important sources of antimicrobial resistance genes that complicate disease treatment (Williams et al. 2018). Second, pathogen

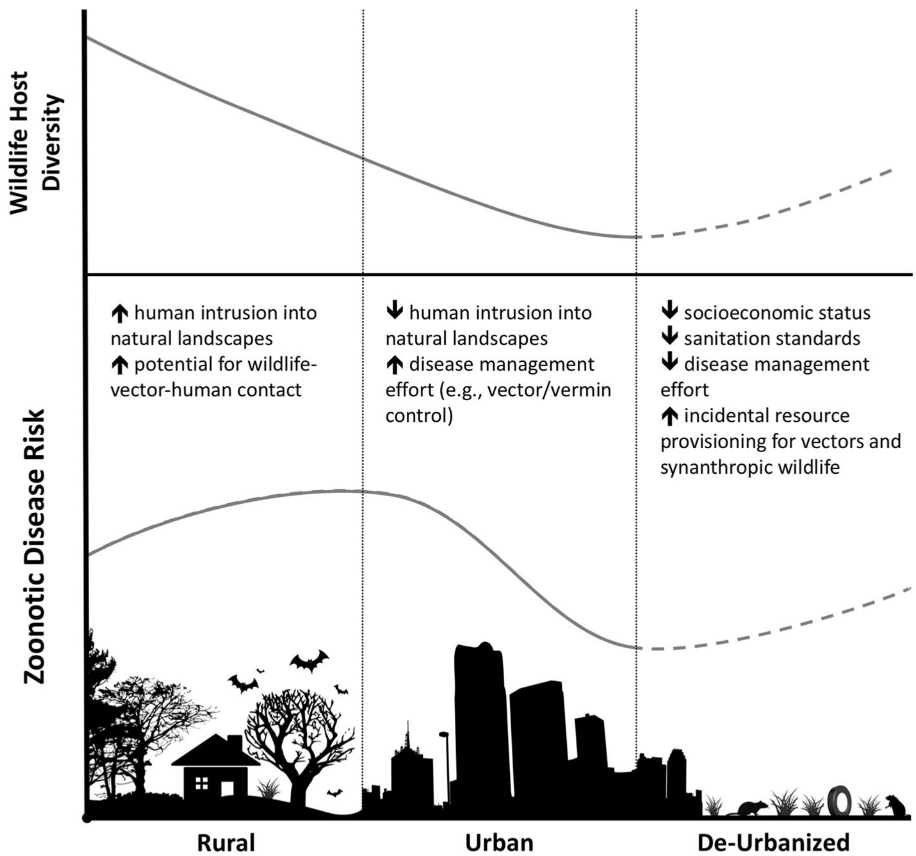

Figure 1. Hypothesized wildlife host diversity and zoonotic disease risk (gray lines) for a region through time as it undergoes land conversion from rural to urban and, finally, de-urbanized habitat. We highlight wildlife host diversity (top panel) as the fundamental source of the hazard relevant to zoonotic disease emergence—the zoonotic pathogen pool to which people may be exposed (Hosseini et al. 2017). Hazards are modified by risk factors to produce realized risk. We therefore list specific factors affecting zoonotic disease risk (bottom panel) within each land use type; the up and down arrows indicate relative level of a factor (i.e., high or low) within that land use. Treating risk as the probability of an adverse event within a population (Hosseini et al. 2017), our hypothesized zoonotic disease risk curve shows that the highest risk may be expected at the rural–urban transition where relatively dense human populations can be subject to contact with wildlife and vectors serving as pathogen reservoirs. Risk is likely to be lower in more highly modified and well-maintained urban environments that have lower wildlife host diversity, a reduced pathogen pool, and higher public health intervention effort. Zoonotic disease risk may increase (dashed line) in de-urbanized landscapes characterized by vacant habitats that bolster vertebrate reservoir host populations (e.g., rodents) and incidental resource provisioning (e.g., tires) that benefits vector populations. Although we suggest that de-urbanization will generally increase both wildlife host diversity and zoonotic disease risk, we show these relationships with dashed lines to represent the site-specific nature of biodiversity trends and uncertainty in the published literature as to whether greater host biodiversity will increase or decrease disease hazard and risk (Wood et al. 2014; Geoghegan and Holmes 2017; Hosseini et al. 2017).

spillover and human disease risk can be influenced by changes in host density, community composition, and/or the pathogen pool within disused and decaying urban landscapes (Gulachenski et al. 2016; Rael et al. 2016). Using the disease risk framework of Hosseini et al. (2017), these represent modifications to the underlying hazard, or source of harm, of the zoonotic disease system (Fig. 1). Finally, and critically, specific socioecological conditions associated with de-urbanization and urban abandonment, including higher poverty levels, the lack of appropriate infrastructure and housing maintenance, and the absence of vector or vermin control, are risk factors that could increase the likelihood of spillover from animal reservoirs (Himsworth et al. 2013; Ayral et al. 2015; Hosseini et al. 2017). We recognize that the importance of de-urbanization for disease dynamics may be limited in tropical regions where the broad trend is toward increasing urbanization. However, there is notable risk of zoonotic disease emergence throughout temperate portions of the Americas, Europe, and Asia (Allen et al. 2017), some of the very places where de-urbanization has been most often documented (Lima and Eischeid 2017).

In fact, cases already exist where the environmental conditions accompanying de-urbanization have resulted in increased human disease risk. For instance, a period of economic depression leading to home and recreational pool abandonment in Bakersfield, California, was linked to a > 200% increase in human West Nile virus cases, likely because neglected pools provided favorable breeding habitats for the virus' mosquito vector (Reisen et al. 2008). As this example illustrates, resource provisioning by humans, whether intentional or accidental, is thought to be a major driver of disease dynamics in urban wildlife (Bradley and Altizer 2007). Therefore, focusing on resource fluctuations resulting from de-urbanization may be particularly important for vector-borne diseases because of their effects on vector abundance. Another case study found that mosquitoes were more abundant in low income neighborhoods as a result of greater prevalence of unmaintained waste items, like used tires, that serve as breeding habitat (LaDeau et al. 2013). Similar conditions could result from de-urbanization and urban abandonment, and these examples together suggest that effective management of vector-borne disease in de-urbanizing regions will depend on careful monitoring of vector resource availability (Fig. 1; Rael et al. 2016).

Neglected anthropogenic habitats may also support reservoir host populations that harbor directly transmitted pathogens. For example, rodents, which represent important urban reservoir hosts, are known to prefer habitats with unkempt vegetation, organic debris, and litter (Battersby et al. 2002; Traweger et al. 2006; Johnson et al. 2016; Santos et al. 2017). Open, vacant land use types, which can result from de-urbanization, are particularly attractive to these species (Battersby et al. 2002; Johnson et al. 2016). Even in well-developed nations, a lack of rigorous sanitation can create housing conditions that bolster reservoir populations and result in deadly spillover events, as evidenced by recent cases of leptospirosis in New York City (Santora and Remnick 2017). Control of nuisance reservoir populations in de-urbanizing landscapes will require a combination of active management strategies coupled with public education and outreach (Lambropoulos et al. 1999; Costa et al. 2017).

Research Agenda to Investigate De-urbanization and Zoonotic Disease

Developing a comprehensive understanding of zoonotic disease risk across the rapidly changing continuum of urbanized and de-urbanized habitats will be critical to future public health efforts around the world. Here, we suggest some key topic areas for investigation as well as guiding principles to most effectively conduct research within de-urbanized regions. We believe studies at the nexus of de-urbanization and zoonotic disease will be most useful if they address any or all of the following key research areas. First, given that wildlife host species harbor the pathogens that represent the fundamental zoonotic disease hazard (Hosseini et al. 2017), consistent, long-term monitoring of wildlife in de-urbanizing areas will provide valuable insight regarding host species diversity, density, and community composition dynamics. Specifically, there is a need to establish whether host species diversity in de-urbanizing regions will change as a result of greater habitat and resource availability and, if so, over what timeframe (Fig. 1). Sampling of wildlife in and immediately surrounding human habitations will further establish which species are most likely to contact people and are therefore of greatest public health concern. In addition to studying wildlife diversity at the species-level, evaluation of genetic diversity within host or vector populations could also reveal important effects of de-urbanization (i.e., related to population connectivity, founder effects, etc.), with consequences for reservoir infection status and disease management (Lambrechts 2011; Ostfeld and Keesing 2012; Richardson et al. 2017; Angley et al. 2018). Second, a central piece of the zoonotic disease puzzle would be addressed through monitoring of pathogen prevalence, load, and diversity within the wildlife host communities occupying de-urbanized areas. Characterization of the pathogen pool within these hosts, considering a range of pathogen types, will provide critical data on the relative competence of different host taxa and the total disease hazard to which human populations may be exposed. Third, the core biological properties we highlight for investigation should be supplemented with data on habitat characteristics (e.g., building type and configuration, garbage volume) and basic abiotic variables like microclimatic temperature and humidity that can structure host communities (Rothenburger et al. 2017). Fourth, and finally, human behavioral research (quantitative and qualitative) is needed to better link demographic and socioeconomic shifts with changes in the likelihood of zoonotic pathogen exposure. Assessing population-level temporal changes in knowledge, attitudes, and practices related to pathogen exposure in human communities experiencing de-urbanization will be key to the development of interventions that effectively mitigate disease risk (Gould et al. 2008; Paige et al. 2015).

Successful implementation of this research agenda requires adherence to some major guiding principles of study design. First, there is a need for involvement of multi-disciplinary research teams. Scientists focused on infectious diseases in de-urbanizing areas will clearly benefit from collaboration with researchers of urban wildlife ecology, who offer expertise on host species occupying urban and de-urbanizing habitats as well as those most likely to colonize from surrounding areas as de-urbanization proceeds (Bradley and Altizer 2007; Hassell et al. 2017). Depending on the specific topics being investigated, teams might also include anthropologists and behavioral research scientists, epidemiologists, and public health experts. These interdisciplinary partnerships will facilitate the integration of wildlife and pathogen diversity data with information on human zoonotic disease cases from public health organizations and subnational disease surveillance efforts, thereby allowing for the explicit linkage of ecological conditions in de-urbanizing areas with health impacts on the local community. Second, studies should adopt comparative designs that also consider rural and urban sites when possible and historical ecological data for temporal context where available. Interestingly, careful consideration of study design highlights the fact that de-urbanizing environments may represent ideal "natural" experiments in which to test basic disease ecology theories. For instance, given potential changes in host community composition as abandoned urban lands undergo succession, these habitats could provide data relevant to the widespread debate on the biodiversity-disease dilution effect, which posits a negative relationship between host community species diversity and human disease risk (LoGiudice et al. 2003; Wood et al. 2014; Gulachenski et al. 2016; Levi et al. 2016; Wood et al. 2016). Many studies on this topic leverage land use gradients to compare disease characteristics of relatively intact biological communities occupying low-disturbance habitats with altered communities in degraded habitats (Wood and Lafferty 2013). However, de-urbanizing regions may provide the unique opportunity to monitor disease-related metrics in real time as host communities reassemble following colonization by previously excluded species. Before-after control-impact (BACI) studies evaluating host and pathogen diversity in regions with stable levels of urbanization versus those undergoing de-urbanization would be particularly valuable.

In conclusion, although the general consequences of de-urbanization for zoonotic disease risk are yet to be elucidated, a targeted research agenda should be enacted to investigate the ecological and public health linkages, especially as de-urbanization becomes more prevalent worldwide. It is also important to note that substantial social and environmental justice concerns could arise in de-urbanizing areas (Gulachenski et al. 2016), requiring the input of those working in these fields. If de-urbanization and urban decay tend to generate environmental conditions more favorable for disease outbreaks, existing socioeconomic disparities in disease risk and morbidity are likely to be further exacerbated in depopulated areas (Battersby et al. 2002; Meyer et al. 2007; LaDeau et al. 2013; Ayral et al. 2015). For example, economic status is an important predictor of the prevalence of some mosquito-borne diseases, with those in lower income categories suffering greater disease incidence (Harrigan et al. 2010; Rothenburger et al. 2017). Thus, already vulnerable communities in poor urban centers may be especially impacted by the additional and synergistic effect of an increased disease burden resulting from de-urbanization. Understanding zoonotic disease patterns and processes that will arise in de-urbanizing landscapes is a worthy and achievable goal, as it will lead to more effective public health interventions in environments increasingly subject to cycles of intense human modification and abandonment.

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