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PERSPECTIVE

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Bridging landscape ecology and urban science to respond to the rising threat of mosquito-borne diseases

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The prevalence of diseases borne by mosquitoes, particularly in the genus *Aedes*, is rising worldwide. This has been attributed, in part, to the dramatic rates of contemporary urbanization. While *Aedes*-borne disease risk varies within and between cities, few investigations use urban science-based approaches to examine how city structure and function contribute to vector or pathogen introduction and maintenance. Here, we integrate theories from complex adaptive systems, landscape ecology and urban geography to develop an urban systems framework for understanding *Aedes*-borne diseases. The framework establishes that cities comprise hierarchically structured patches of different land uses and characteristics. Properties of the patches (that is, composition) determine localized disease risk, while configuration and connectivity drive emergent patterns of pathogen spread. Complexity is added by incorporating individual and collective human social structures, considering how feedbacks among social actors and with the landscape drive risk and transmission. We discuss how these concepts apply to case studies of *Aedes*-borne disease from around the world. Ultimately, the framework strengthens existing theoretical and mixed qualitative–quantitative approaches, and advances considerations of how interventions including urban planning (for example, piped water provisioning) and emerging vector control strategies (for example, *Wolbachia*-infected mosquitoes) can be implemented to prevent and control the rising threat of *Aedes*-borne diseases.

Cities worldwide face mounting challenges, including rapid and unplanned growth, human migration and climate change impacts[1]. Coinciding with this is the widespread burden of mosquito-borne diseases[2,3]. Mosquito species of the genera *Aedes*, *Anopheles* and *Culex* spread diseases including dengue fever, malaria and West Nile virus. In particular, half of the global population lives in areas where *Aedes* species vectors are present, and that are environmentally suitable for *Aedes*-borne virus transmission[4,5]. In this Perspective, we emphasize the unique interactions between *Aedes* species mosquitoes, *Aedes*-borne viruses (for example, dengue, Zika and chikungunya viruses) and urban environments. *A. aegypti* and *A. albopictus* mosquitoes preferentially feed on humans as a source of blood meal and lay their eggs in water containers found throughout human-dominated landscapes[6]. With this biological connection to human hosts and the built environment, changes to the biophysical and human social conditions of cities affect *Aedes* species ecology and *Aedes*-borne virus transmission[7,8]. Given the resource-intensive nature of vector management and limited medical countermeasures, such as widely available vaccines, cities must optimize existing interventions (for example, the indoor spraying of adult mosquitoes) while efficiently scaling-up others (for example, urban improvement initiatives such as piped water provision, which minimizes larval habitat)[9–14]. Doing so, amid the dynamic conditions of growing cities, requires consideration of the ecology and epidemiology (hereafter, eco-epidemiology) of *Aedes*-borne diseases in the broader context of urban systems.

Researchers have generated substantial knowledge around why *Aedes*-borne diseases pose a threat to urban ecosystems broadly, as well as the distinct challenges that regions around the world face. Urban areas have less biodiversity compared with surrounding ecosystems, as well as high human population densities and microclimates that are well suited for mosquito and viral development; therefore, *Aedes* species exploit landscapes with few predator species, abundant hosts and environmental conditions conducive to population growth[15–19]. For resource-limited cities with high rates of informal development, population growth often exceeds infrastructure provisioning[20]. This leads to strained capacity to equitably provide public services and, for cities in tropical and sub-tropical regions with established *Aedes* species populations and circulating *Aedes*-borne viruses, ultimately increases disease risk[11,21,22]. For cities at the limits of *Aedes* species distributions, repeat mosquito introduction events through travel and trade, in addition to warming temperatures, accelerate population establishment (as documented for *A. aegypti* and *A. albopictus* in Argentina and *A. albopictus* and *A. japonicus* in the United States and Europe)[23–25]. Simultaneously, some cities in the United States and Europe are de-urbanizing and experiencing infrastructure disinvestment, thereby increasing larval habitat density[26,27]. Finally, human movement (across regional and global inter-urban networks) circulates viruses across the cities that people visit[28].

Research has also delved into varied patterns of mosquito abundance, transmission potential and disease vulnerability within cities. Heterogeneous ambient temperatures, resulting from a patchwork

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of vegetation and built infrastructure, affect vector and virus traits (for example, juvenile development and virus replication)[15,29,30]. Additionally, biophysical features such as storm drains collect rainwater and harbour *Aedes* species[31–34]. Investigations have uncovered interactions between piped water access, water storage and larval habitat and the role of super-producer households in dynamically determining block-level mosquito abundance[7,8,35]. Given the limited flight range of *Aedes* species (averaging = 50–250 m; maximum = ~1 km), researchers have also linked human movement (ranging from seasonal labour migration to inter-household visits) to *Aedes*-borne virus introduction and persistence in pockets of a city[28,36–38].

Applied *Aedes*-borne disease research is guided by eco-bio-social principles[39]. Yet, despite considering interconnected processes that contribute to risk, counterintuitive relationships continue to emerge from empirical data. Investigations have found that employment of the head of a household is a risk factor for dengue infections, when employment is generally associated with higher socio-economic status and lower arboviral risk[40–42]. Others have seen positive associations between household air conditioning and *A. aegypti* presence, and increased infection risk in neighbourhoods with lower than average nighttime temperatures[41,43]. Most elusive of all is a clear relationship between entomological indices, *Aedes*-borne virus transmission and disease incidence[44,45]. Some investigations report no association between *Aedes* species infestation and incidence, while others show positive associations[46–48]. In hypothesizing why on-the-ground data do not support anticipated findings, researchers contemplate risk factors omitted from investigations, nonlinear dynamics, scale incongruence or study design limitations[40,41,49]. Given these paradoxical results, we propose that *Aedes*-borne disease research would benefit from a framework wherein hard-to-explain patterns are expected of the system, with explicit consideration of urban complexities[50,51].

In this Perspective, we build an urban systems framework that complements and expands on existing empirical and theoretical approaches to *Aedes*-borne diseases. We bridge theories from the study of cities as complex adaptive systems (CAS), landscape ecology and urban geography to demonstrate how *Aedes*-borne diseases can be conceptualized as an emergent property of an urban system. We emphasize that nuanced examinations of cross-scale and dynamic urban processes will provide greater insight into *Aedes*-borne disease transmission, but require the co-production of knowledge with diverse human social actors (from community members to municipal institutions). This framework, developed alongside urban scientists, generates new lines of research and creates an essential pathway for mosquito-borne disease interventions to be integrated into initiatives that set cities on more healthy and sustainable trajectories[52–54].

Why we need an urban systems framework

Increasingly, research communities and health ministries are recognizing shared priorities between vector-borne disease and urban health initiatives and are calling for integrated vector management plans spanning departments of urban planning, water and sanitation[11,55]. However, in academic spheres, there is limited knowledge sharing across vector-borne disease and urban development disciplines, and in the public sector there is limited guidance on best practices for inter-sectoral decision-making. In the eco-epidemiological literature, urbanization is cited as a principal driver of *Aedes*-borne disease; however, urbanization itself is often quantified as the dichotomous conversion of rural to urban land cover or change in continuous variables such as population density[56]. There is a need for examinations of urbanization that integrate social science approaches and evaluate the role of the technical dimensions of a city (for example, technology and communications) in *Aedes*-borne outbreaks[52,57,58]. For public health interventions, it is well established that policy changes in cities have far-ranging, often unintended consequences[59]. Therefore, there is an imperative to enhance our knowledge of arboviral risk amid complex urban environments, particularly as localities implement costly vector control strategies (for example, *Wolbachia*-infected mosquito releases) or large-scale urban development interventions (for example, piped water provisioning).

In the urban sciences (here, the fields of urban geography, urban ecology, sustainability and urbanization science), cities are composed of countless individual-level processes interacting with broader social and technical structures and the biophysical environment[60–62]. Sub-fields study these complexities to inform environmental policy, disaster preparedness and land management[52,63–66]. Public health applications have explored human–environmental interactions associated with chronic diseases, contaminant exposures and health inequities[67–70]. However, few studies explore how urban structure and function contribute to vector or pathogen introduction and maintenance. Here, we build a framework for understanding *Aedes*-borne diseases in contemporary cities using three intersecting concepts: cities as CAS, hierarchical patch systems dynamics and relational geography.

Cities as complex adaptive systems. Disease incidence patterns are generated from co-occurring, interacting processes across multiple scales of the urban system[71]. Embedded in these interactions are attributes of CAS that explain how patterns emerge across higher scales, including self-organizing building blocks, interconnectedness and modularity, cross-scale interactions and dynamical processes[72–76].

Using the building blocks approach, a city comprises independent spatial cells that self-organize into patches, creating the fabric of the landscape[76]. Cells aggregate in different combinations, creating novel patches. Emergent systems' behaviours are generated through self-organization, whereby patches have properties that cannot be predicted from the properties of individual cells. Complexity increases not with the land area of the cells but with increasingly heterogeneous aggregation and divergent processes over time[73]. Human populations, too, are aggregated from building blocks, where individual social actors create socio-cultural groups (for example, households) and institutions[77,78].

Urban systems are characterized by their degree of interconnectedness and modularity. Complexity increases with interconnectedness, characterized by abundant and far-ranging linkages within the system[54,76]. In contrast, modularity describes the degree to which the components of a system separate and recombine[76]. While interconnectivity enables the flow of organisms and information across the spatial extent of the city and between social actors, it facilitates the spread of disturbances such as invasive species or cascading impacts of policy decisions[67]. Modularity decentralizes structure and function—for example, maintaining strong internal ties between nearby patches but weaker external connections between distant patches[79].

Processes in these patchy environments operate on a continuum of scales—from micro to macro scales[80]. Temporal processes, for example, separate into fast variables measured on short timescales and slow ones that are prolonged and tend to control fast variable dynamics[81,82]. Macro-scale processes (for example, climate) contextualize and set constraints on micro-scale dynamics. In contrast, micro-scale processes may be reinforced, generating positive feedbacks up to a given threshold[83,84]. Beyond this threshold, new processes and feedbacks are triggered, producing nonlinearities and emergent properties. Nonlinearities also emerge when macro-scale processes overwhelm micro ones[82]. Cross-scale interactions occur when interactions between macro- and micro-scale processes affect a response variable; for example, when broad-scale drivers affect the degree to which a local driver influences a response[83,85]. Additionally, macro- and micro-scale interactions may produce a response, with feedbacks that affect the cross-scale interaction itself[85]. Extreme heterogeneity in land use and social actors contributes to pronounced cross-scale interactions in urban settings[80].

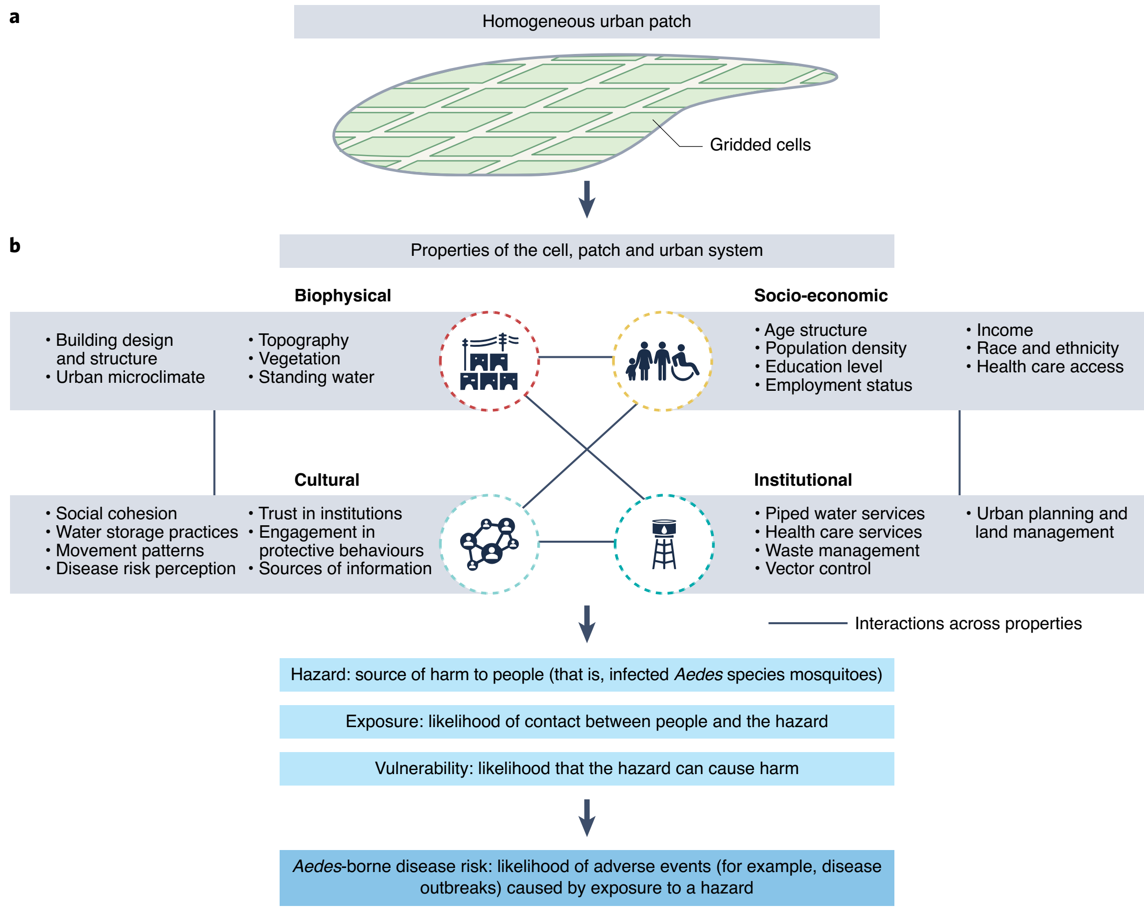


Fig. 1 | Interactive properties of the urban system determine *Aedes*-borne disease risk. a, Gridded cells form the building blocks of the urban landscape. These gridded cells aggregate to form homogeneous urban patches. **b**, Each spatial unit (whether a cell or patch) and the urban system itself has four sets of properties: biophysical, socio-economic, cultural and institutional. Biophysical properties include building design and structure (depicted in the circular icon); socio-economic properties include the age structure of family units; cultural properties include social cohesion or a sense of community belonging; and institutional properties include public services such as piped water access. These four properties interact to determine the hazard of infected *Aedes* species, human exposure to infected mosquitoes and disease vulnerability (the population's capacity to respond to disease). Hazard, exposure and vulnerability together determine the level of *Aedes*-borne disease risk for a given spatial unit.

Finally, cities are adaptive. All dimensions of the system change over time in response to external conditions, internal drivers and feedbacks. Embedded in this concept is that CAS have memory, in which past processes and events influence current and future conditions[75]. Examining this historical record—at the relevant scale—provides an essential baseline for understanding how given processes might behave in the future.

Hierarchical patch systems theory. To bridge cities as CAS with a spatially explicit understanding of disease, we use hierarchical patch dynamics from landscape ecology[86,87]. A landscape is made of patches that differ from their surroundings based on their composition. Importantly, patch size depends on the ecological process of interest, as the degree of spatial variation changes with scale[88]. Patches are spatially arranged in many ways and organized as nested spatial hierarchies. Information, materials and organisms flow in and out of patches over time, synergistically defining their levels of connectivity to determine the functioning of each patch and landscape as a whole[89]. Additionally, landscapes change over time (through transformations in spatial structure or via disturbance events), reciprocally effecting urban systems processes[84]. The patch systems framework has been applied to animal movement and green space management and is used in emerging urban ecology theory[86,90,91]. For cities, groupings of similar houses, city blocks or neighbourhoods are considered nested patches[86]. Therefore, the framework allows urban heterogeneities to be broken down and examined as the product of many nested structure–function relationships.

Relational perspectives on human social interactions. To examine urban social dynamics, we draw on relational geography—emphasizing that entities mature based on their relationship with other entities in processes of 'mutual becoming'[92]. Structuration theory from social geography describes how individual agency reinforces social structures through rules, laws and social norms[93,94]. Individuals are also responsive, using information to change their behaviour or alter the social structures that they are embedded within. This relational ontology helps us to understand how individuals mutually develop alongside other individuals, group-level social actors and the landscape. Rather than dichotomizing social and ecological processes, relational thinking acknowledges that processes are inextricably social and ecological at the same time[95]. When examining the dynamics between spatial organization and human activity, properties of a given patch may constrain or enable social actors' actions, tendencies (propensities for certain actions) and capacities (potential for future actions)—establishing path-dependent trajectories[96]. Therefore, areas of a city built during the same period with comparable social and biophysical features promote similar behaviour among people[97]. Reciprocally, individual- and group-level actors

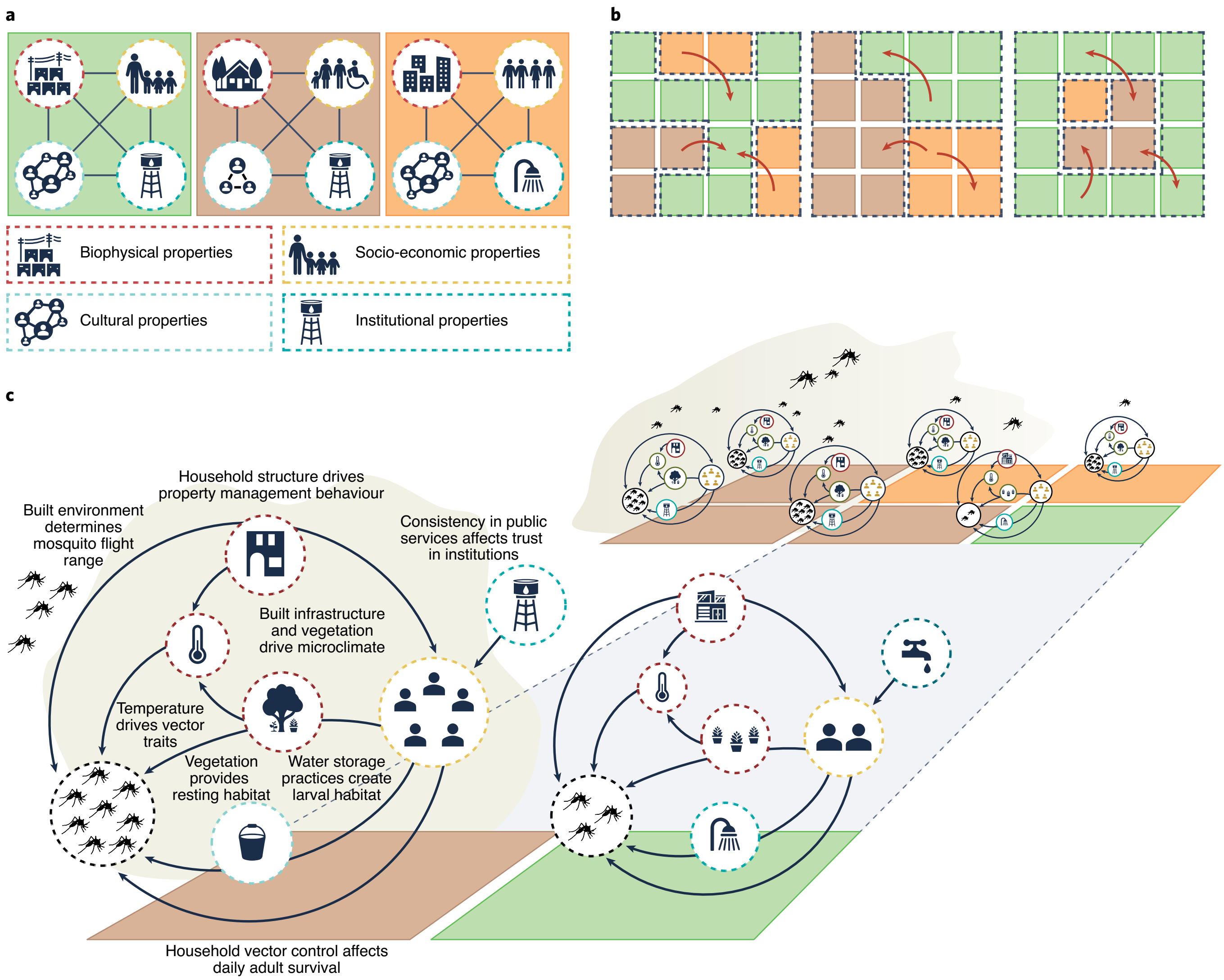


Fig. 2 | Landscape composition, configuration and connectivity determine risk and transmission. a, The composition of each gridded cell is defined by four interacting properties: biophysical, socio-economic, cultural and institutional. **b**, Gridded cells are arranged in different configurations to create homogeneous urban patches (as shown by the black dashed lines). Individuals move across urban patches (red arrows) with different patterns of flow, determining levels of connectivity between urban patches and driving transmission between connected patches. **c**, The composition of each gridded cell determines the localized level of *Aedes*-borne disease risk through biological, ecological and human behavioural processes, and the configuration of gridded cells determines the level of risk generated for aggregated areas (for example, neighbourhood blocks). Here, the brown gridded cell in the foreground shows interacting properties resulting in high *Aedes* species production. When the brown cells are configured together in space (in the background), this results in areas with high aggregate mosquito abundance.

influence the landscape at cell or patch levels. As these reciprocal processes accumulate, trajectories diverge, building heterogeneity and complexity over time. These theories are the foundation for our approach, aiding our understanding of dynamic systems processes, heterogeneities in risk and human–landscape interactions driving *Aedes*-borne disease.

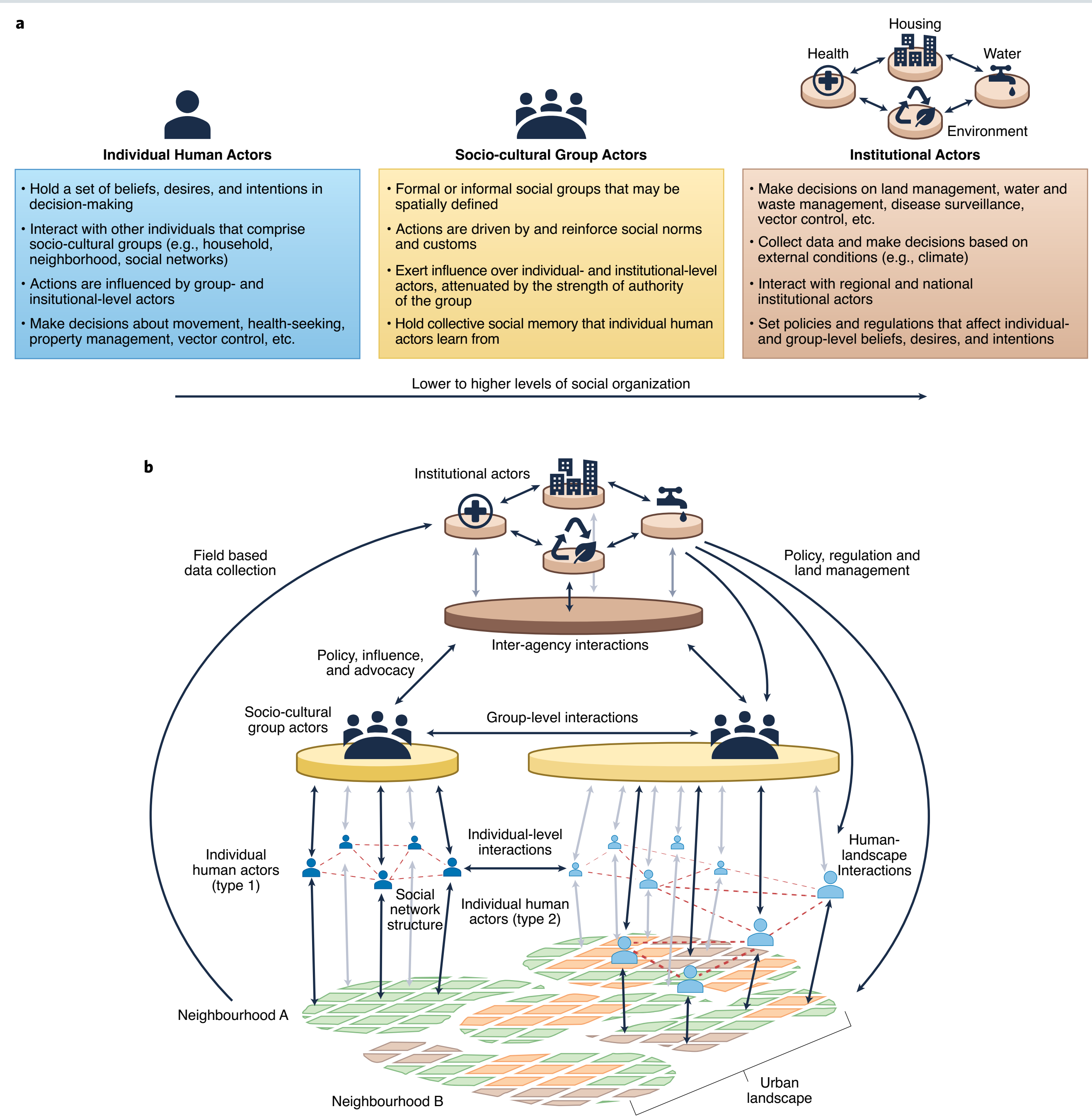
An urban systems approach to *Aedes*-borne disease

Landscapes of heterogeneous risk and transmission. To understand landscapes of *Aedes*-borne disease risk, we start with self-organizing gridded cells as building blocks, which aggregate to urban patches (Fig. 1a)[98]. The spatial extents of cells and patches vary based on the research question[89]. For example, an investigation examining threshold *Aedes* species population sizes necessary to maintain virus circulation may define gridded cells at a block scale and patches at a neighbourhood scale, given *Aedes* species' limited flight range[99,100]. However, if the question asks how *Aedes*-borne viruses circulate regionally based on seasonal human migration, cell-level processes may not be relevant and patches can be defined at the city scale[28,101]. This section considers how cells and patches are characterized, aggregated and interconnected to determine risk and transmission.

Landscape composition. In landscape ecology, composition denotes the spatial properties important for a landscape function[102]. Here, we describe the properties important for *Aedes*-borne disease risk. Risk is an integrated measure of the hazard (that is, mosquito abundance and infection), human exposure to infected mosquitoes, and vulnerability (the capacity to respond to disease) (Fig. 1b)[103]. We classify the spatial properties as biophysical, socio-economic, institutional and cultural using relational geography to understand how the characteristics of each cell are uniquely co-determined (Fig. 2a)[86].

Box 1 | Human social actors of the urban system

We build complexity onto the urban landscape by considering human actors at multiple levels of social organization and uncovering ways in which people are characterized, aggregated and interconnected (Box 1 Fig. a). Individual human actors are characterized by demographics, epidemiological roles (for example, infection status) and agency (for example, beliefs, desires and intentions)[250,251]. Group-level socio-cultural actors (for example, families, social networks and community boards) are made up of individuals who share characteristics but have their own properties as a collective[252,253]. Individual-based and group-level influences drive people to interact with their landscape based on values, beliefs and norms. Water storage in the household, for example, is a behaviour based on cognitive decision-making, attitudes and norms[254]. Previous work has connected the perceived quality of peri-domestic space with attitudes towards vector control activities[255]. For example, focus groups among community members in multiple Latin American countries have suggested that clean spaces in high-income neighbourhoods contribute to perceptions that regimented mosquito control is unnecessary while living in neglected areas makes mosquito control seem futile[121,256]. Here, neighbourhood-level social class reinforces perceptions and behavioural patterns. Institutional actors are at the highest level of social organization and include local governance structures such as housing authorities, as well as agencies managing water, waste and sanitation and health (depicted by the four interconnected icons). Their interconnectedness (depicted by arrows between



Box 1 | Human social actors of the urban system (continued)

the icons) comes from cross-agency interactions (for example, a shared political agenda or household water access coordinated by both housing and water authorities).

Over time, through relational processes, human social actors (including individual actors, socio-cultural group actors and institutions) mutually develop alongside one another and their landscape (Box 1 Fig. b). At the base of the figure is the urban landscape (shown as a mosaic of gridded cells) organized into administrative units (neighbourhoods). Neighbourhoods may have gridded cells with uniform composition (for example, neighbourhood A) or of varied composition containing sub-neighbourhood-level homogeneous urban patches (neighbourhood B). Sitting above the urban landscape are individual human actors who interact with the landscape directly through behaviours such as household property management. Individual actors may self-organize into social network structures that include people from one spatially defined neighbourhood (type 1 individuals) or multiple neighbourhoods (type 2 individuals). Group-level actors exert their influence on individuals through formal mechanisms (for example, ordinances) and informal mechanisms via norms and collective emotion[58]. They also exert influence on institutional actors through advocacy or lobbying, which influences governance decisions. The strength of their influence depends on characteristics of the group (for example, social class and numbers of years established). Finally, institutions such as health departments are made up of individual representative actors (for example, community health workers)[257,258]. Institutions collect field-based data at discrete times and locations (for example, resident complaints of mosquitoes) and monitor conditions over time (for example, vector surveillance). They receive information through interactions with socio-cultural actors (for example, businesses and lobbying groups) and stimulate changes to the landscape and lower-level actors via information, public services, policy and land management[259,260]. While individual and household-level effects are well documented in the *Aedes*-borne disease literature, there is a need for more nuanced understanding of the role of socio-cultural actors and institutions in driving processes.

Biophysical properties such as building design and microclimate affect temperature and humidity-dependent viral traits, mosquito biological and behavioural traits as well as vector–pathogen interactions[15,29,30,104–108]. Vegetation provides resting habitat and sugar meals for mosquitoes, highlighting fine-scale drivers of mosquito abundance and mosquito–human contact[109,110]. An area's biophysical properties are determined by underlying socio-economic factors[111–114]. Socio-economic properties also drive the quality of institutional services, such as water and waste management. Inconsistency in public services affects cultural properties, such as water storage behaviour and trust in institutions, thereby increasing disease hazard and vulnerability[35,115]. Finally, water and waste management services impact vulnerability, given the association between unsafe sanitation conditions and population health outcomes[116].

Cultural properties, including risk perception, protective behaviours and social cohesion, both determine and reinforce socio-economic, institutional and biophysical properties. Education, wealth and self-efficacy contribute to varied knowledge and attitudes regarding household water container management[35,117]. For neighbourhood-level risk, social cohesion or a sense of community belonging drive risk via dual effects on pathogen exposure and disease vulnerability[118]. On the one hand, neighbourhoods with high social cohesion may have high inter-household movement, with greater virus exposure[119]. On the other hand, social cohesion is protective, with communities better equipped to advocate for services with local goverance[120–122]. Determining which aspects of composition drive disease risk at a particular scale can inform scale-dependent management strategies.

Landscape configuration. While composition establishes localized levels of disease risk, configuration determines emergent patterns of risk at patch and landscape levels. Here, configuration describes the spatial layout and structure of the built environment (Fig. 2b)[123]. At city scales, configuration is driven by top-down restrictions on expansion and bottom-up urban growth processes. For example, configuration is limited by topographical constraints that have prohibitive construction costs (for example, sloped terrain), creating asymmetries in the land available for formal development[124,125]. Zoning regulations, green space protection and land tenure add additional restrictions to landscape configuration[126–128]. Patches of varying composition are arranged in unique ways, and patterns and processes emerge concerning the biophysical environment, demographics and human–landscape interactions, all with cascading impacts on *Aedes*-borne disease risk (Fig. 2c). Aggregated cells with varied building densities and impervious land cover have consequences for mosquito dispersal via physical obstruction, temperature and wind flow, with landscape genetics studies demonstrating that, over time, the built environment structures *Aedes* species populations[36,114,129–131]. Additionally, depending on cell-level configuration, human populations are spatially dispersed at different densities[132,133]. While human population density variation is known to drive differences in larval habitat density via water storage practices, empirical evidence regarding host density effects on vector processes (for example, host-seeking behaviour) requires further investigation[7,133,134].

Regarding human–landscape interactions, compact forms and high building densities may positively affect public transit and walking, affecting mosquito exposure and mixing rates between infected and susceptible individuals[135]. Additionally, as green infrastructure is promoted in vertically growing cities, vegetation may provide thermal refugia for vectors[30,136]. Configurational changes also affect disease hazards by creating novel habitat and shifting mosquito community structure[18,71,137]. For example, in Brazil, large urban centres such as São Paulo are surrounded by tropical rainforest, where sylvatic cycles of yellow fever virus are maintained between non-human primates and tree-dwelling mosquitoes[138,139]. Spillover into urban transmission cycles is heightened at urban–wildland interfaces, with *A. albopictus* colonizing the edge of forest fragments, and high densities of *A. aegypti* in built environments neighbouring forests[44,138,140].

Configuration is co-determined alongside socio-economic, cultural and institutional processes. Recent expansion of unplanned informal housing, for instance, may inspire future rural-to-urban migration. Additionally, adjacent high and low socio-economic status patches may further marginalize low socio-economic status patches[141,142]. Uncovering mechanisms by which landscape configuration affects *Aedes* species hazard and exposure is essential to understanding how urbanization alters the spatial epidemiology of *Aedes*-borne diseases[137].

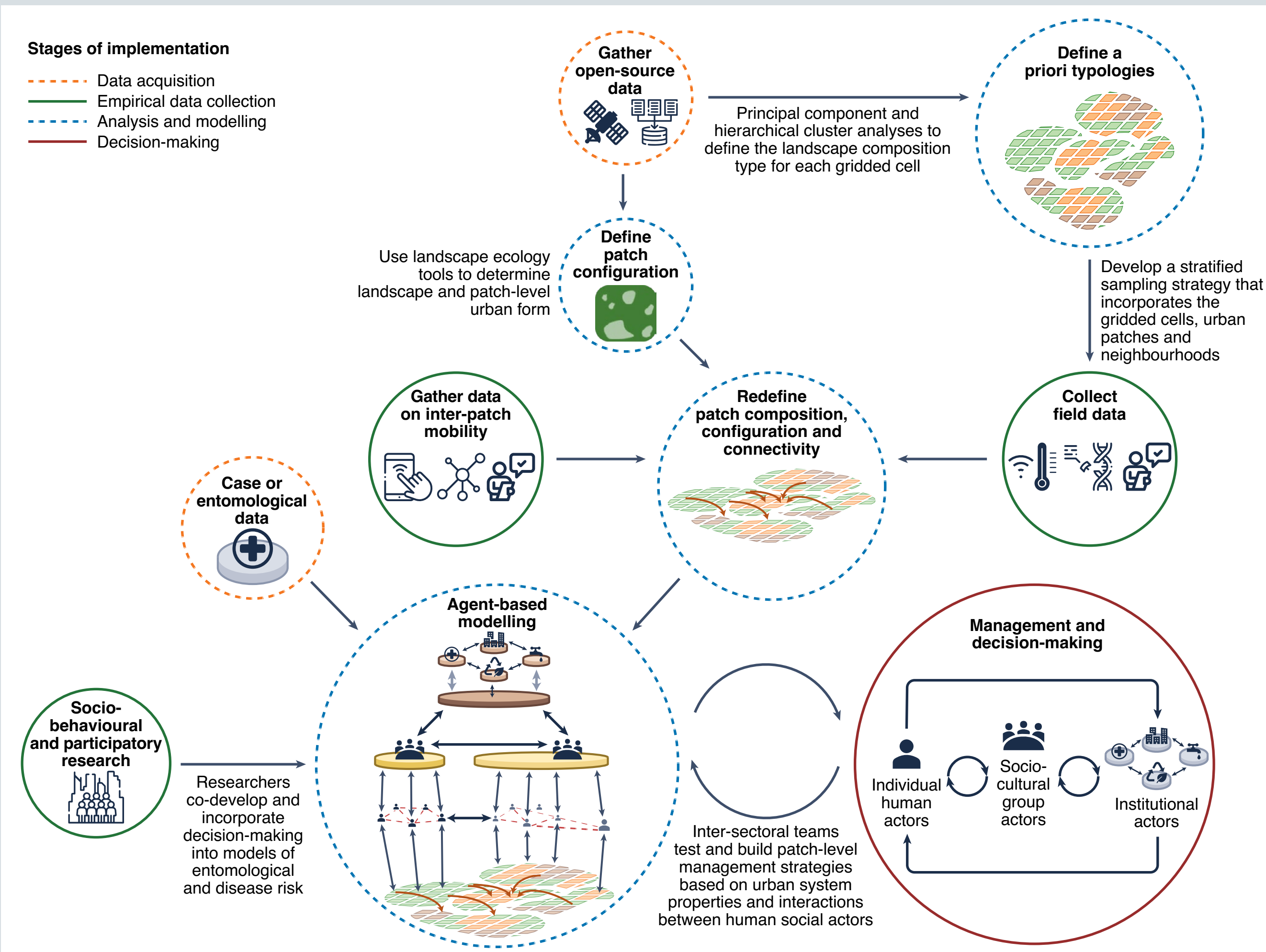
Landscape connectivity. Using metapopulation ecology, connectivity determines how pathogens and susceptible individuals are distributed across patches. While configuration remains relatively unexplored for *Aedes*-borne diseases, connectivity-driven pathogen spread is well established[21,111]. Transmission foci of dengue virus are connected by commuter patterns, long-distance transport and

Box 2 | Work flow: implementing the urban systems framework

Here, we build a work flow, showing how landscape analyses, socio-behavioural research and mixed qualitative–quantitative modelling can be used to implement an urban systems framework. Beginning with open-source datasets, remotely sensed information on elevation, building and population density, vegetation and road networks are a useful starting point when characterizing the biophysical and socio-economic properties of the urban system. Urban scientists often use principal components and hierarchical cluster analyses to characterize the variation across the urban landscape and define homogeneous landscape composition types (that is, typologies) for a city[181,261]. These a priori typologies can be defined for 100–250 m^2 gridded cells and may help researchers to develop stratified sampling strategies for *Aedes*-borne disease fieldwork (for example, entomological data collection, microclimate measurements, genetic data collection, social surveys and interviews), incorporating cities' biophysical and socio-economic variation, with research teams aiming to recruit a certain number of households per given typology[178]. Over time, field data can be used to generate information on cultural and institutional properties of the urban system and to validate or redefine gridded typology assignments.

With remote sensing data, tools such as FRAGSTATS or connectivity models can also be used to characterize patch-level configuration and urban form[262]. Distance-based configuration variables (for example, the distance to transportation hubs, crowd-gathering centres or hospitals) may also be relevant for disease risk[144,178]. Mobile phone data, mobility models and/or travel surveys may be used to determine within- and between-patch population movement (that is, connectivity)[263]. Additionally, at this stage, collaborations with urban geographers and historians may provide insight into areas of a city that were built at the same time and therefore share similar development trajectories and infrastructural vulnerabilities. With relevant empirical data, landscape composition, configuration and connectivity can be iteratively defined to reflect the hypothesized risk landscape for *Aedes*-borne disease.

Combined with high-resolution data on disease incidence or entomological indices, researchers may begin to explore the associations between gridded typologies and disease or entomological risk. For example Telle et al.[178] used logistic regressions to assess the association between a given gridded typology and the probability of a dengue index case (that is, one of the first 50 reported cases in a year) detected in a given administrative unit. More complex modelling approaches, including agent-based models (ABMs), can integrate socio-behavioural and participatory research into spatially explicit investigations of risk. Social and behavioural scientists may gather information on individual, group-level and institutional actors to understand social hierarchies, within-household decision-making and interactions with the urban landscape that drive *Aedes*-borne disease risk[253]. For example, ABMs exploring the effects of water storage on *Aedes* species populations may build sub-models that incorporate the



Box 2 | Work flow: implementing the urban systems framework (continued)

interactions between city-level water distribution systems and household-level management practices, in addition to studying the effects of household-level water management on larval recruitment rates. Focus groups with role-playing exercises can reveal individual-level behaviours and feedbacks triggered by certain interventions, and can provide insight into how slow versus fast variables drive decision-making[264]. Finally, ABMs can be used to develop complementary bottom-up and top-down interventions that consider cross-scale interactions, dynamic urban system properties and interactions between individual, socio-cultural group-level and institutional actors. With inter-sectoral teams, cities have the opportunity to build patch-level management strategies using interventions (for example, indoor residual spraying, larvicides, educational campaigns or infrastructure improvement) best suited to the needs and cultural conditions of each patch.

social networks[101,112–114]. Movement patterns are determined by landscape configuration, land use and the spatiality of social structures. However, there is the potential to examine which movement patterns and processes are relevant at different spatio-temporal scales. At the city scale, a settlement may have a central urban core that promotes movement from all surrounding patches into a central patch—exhibiting high interconnectedness[143]. However, zooming out to an entire metropolitan area may reveal separate and distinct movement patterns among different patches of the system—demonstrating modularity. At sub-city scales, residence-based healthcare facilities, schools and places of worship may promote modular movement patterns as opposed to in cities where individuals and families commute across town for these sites.

Finally, feedbacks between landscape connectivity and composition are described, with higher *Aedes* species larval indices near crowd-gathering locations (for example, schools and cinemas)[144]. This may be due to biophysical or cultural properties associated with crowd-gathering spaces (for example, container accumulation) that promote larval habitat. Further explicating links between landscape connectivity and composition and configuration may provide insight into positive feedback loops that create spatio-temporal hotspots of *Aedes*-borne disease.

Cross-scale and dynamic urban processes. Patch system approaches provide a framework for spatially structured processes; however, cross-scale and dynamical interactions also contribute to urban complexities. This is particularly true given the high degree of diversity of human social actors, compositional and configurational heterogeneity and the high rate of change in cities[80]. Social dynamics, for example, can be examined as cross-scale interactions between hierarchical levels of social organization—between individual human actors, socio-cultural group actors and institutional actors (Box 1). Additionally, in *Aedes*-borne disease research, scientists often ask what the most appropriate scale for associating mosquito abundance with human infection is[145,146]. Few studies acknowledge that spatial cross-scale interactions are inherent to this relationship and that the relevant scale varies based on urban context[147]. For instance, a neighbourhood's socio-economic and biophysical properties affect household-level mosquito exposure, as physical infrastructure determines *Aedes* species' flight range and penetration into buildings[148–151]. In low-income settings, houses may be built close together, with shared walls or incomplete construction[152]. This promotes human population mixing and outdoor–indoor and house-to-house mosquito movement, calling for block or neighbourhood scale analyses[153]. However, in higher-income areas with larger, separated dwelling units and less population mixing, it may be more relevant to study associations between mosquito abundance and infection risk at the household scale. Insight into the spatial scales at which socio-economic and biophysical properties constrain eco-epidemiological processes carries implications for the unit at which vector control should be implemented, with the potential for differences across neighbourhoods.

Alongside recognition of spatial cross-scale effects are clear indications that patch conditions are dynamic. However, defining relevant fast and slow variables, and understanding how they converge to drive disease outbreaks, requires further investigation[154–156]. Temporal heterogeneities arise from biological variation in viral mutation rates, serotype introductions and circulation, evolutionary adaptations and mosquito population dynamics, which have simultaneous long-term trends punctuated by changes of rapid ones[157]. Additionally, weather and climate effects vary over timescales, from diurnal to decadal and beyond. Social and behavioural phenomena, too, occur over a range of fast and slow scales, including hourly changes in socio-economic activities, information dissemination over news cycles and generational shifts in cultural values. Examining how information is stored and carried through time provides a pathway for understanding temporal cross-scale interactions[52].

Memory is a key temporal feature of *Aedes*-borne diseases, as previous events affect current and future processes. Biological memory is familiar to eco-epidemiologists. For example, dengue virus homotypic neutralizing antibodies may remain detectable decades after an initial serotype infection[158]. Additionally, ambient temperature has carry-over effects on vector traits as mosquito larvae develop into adults[159–162]. Memory also captures how individuals with previous infections may acquire more knowledge of the disease compared with naive individuals[163,164]. Other aspects of memory are less often integrated. Present day land use depends on a city's history, socio-cultural values and socio-economic processes[165–167]. The built environment also carries memory, as repeat extreme rainfall events deteriorate infrastructure, increasing the standing water available to ovipositing *Aedes* species[168].

Individual behaviours result from previous places of residence and adjust with changes in neighbourhood biophysical and cultural composition (due to human migration, government intervention and so on). Additionally, societal memory of piped water interruptions contributes to water storage practices well after reliable water distribution systems have been implemented[169]. The influence of previous events may not prompt permanent change, and a return to baseline may be quite sudden. Innovative methods of measuring cross-scale interactions and memory are essential to advancing *Aedes*-borne disease research, particularly as interventions consider interactions operating on a range of timescales[170].

Applying the urban systems approach

Global examples of the urban systems approach. While cities face similar challenges in controlling *Aedes*-borne diseases, they also have unique climates, histories and urbanization trends. Here, we highlight aspects of the urban systems framework that are already being used to study *Aedes*-borne disease within diverse urban settings—grounding our approach in relevant research practices. We emphasize the potential to expand on this work by asking research questions guided by relevant urban systems concepts across multiple spatial scales.

For example, in Machala, Ecuador—a port city in southern Ecuador (population 280,000)—vector control operations are managed out of two centrally located hubs in the city[171,172]. Lippi et al.[171] conducted a city-scale network analysis and determined that vector

Table 1 | Modelling approaches to *Aedes*-borne disease transmission in an urban systems framework

Model class	Key attributes	Urban systems concepts			Urban systems applications
		Complex adaptive systems	Hierarchical patch systems	Relational social interactions	
Hierarchical regression models	• Generalized linear mixed models and generalized additive mixed models • Spatially structured random effects account for heterogeneities across locations • Incorporate lagged, nonlinear structures and temporal dynamics • Bayesian frameworks incorporate variance components in a hierarchical manner and estimate predictive uncertainty	• Building blocks (that is, hierarchical structures) • Lagged effects • Nonlinear interactions • Cross-scale interactions	• Hierarchical landscape • Composition • Configuration • Connectivity	• Knowledge, attitudes and practices • Lagged social/historical factors	• Evaluate the lagged and nonlinear effects of weather and piped water availability on the relative risk of disease[161,229] • Assess cross-scale interactions driving *Aedes* species movement (influenced by the El Niño Southern Oscillation (slow variable and decadal scale) and weather (fast variable))[230,231] • Examine water storage practices based on current knowledge and attitudes, as well as historical institutional experiences[115]
Metapopulation models	• Populations are distributed over patches connected by human movement[232] • Parameterized connectivity between sub-populations • Homogeneous mixing within patches • Space between patches is modelled discretely • Dynamics are affected by demographic and environmental stochasticity, both for each local sub-population and the global population[233]	• Hierarchical structures • Emergent properties • Stochasticity • Feedbacks	• Hierarchical landscape • Composition • Connectivity	• Spatial autocorrelation (proxy for relational feedbacks)	• Assess whether interventions (for example, vector control) should be applied differentially to patches with high- or low-risk composition[234] • Assess the effects of intervention synchronicity for neighbourhood patches of different sizes and levels of connectivity[235] • Assess the likelihood of an outbreak based on levels of connectivity between a network of cities[236]
Cellular automata	• Each discrete cell is characterized by a state (that is, binary, categorical, quantiles or vector of attributes) • The current state depends on the previous state and the state of neighbouring cells, according to transition rules, which are either deterministic or stochastic • Nonlinearity of cellular automata leads to fractal patterns (that is, regular and ordered spatial patterns that generate similar geometries at different scales)[237] • Ideal for local conditions and emergent properties • Low amounts of data needed to parameterize	• Building blocks • Nonlinearity • Emergent properties • Stochasticity • Adaptive memory	• Hierarchical landscape (grids and patches) • Composition • Configuration • Connectivity	• Spatial autocorrelation (proxy for relational feedbacks)	• Simulate urban expansion with different land use types combined with an urban patch-growing algorithm[237,238] • Simulate urban expansion with water management systems for each new cell (combined cellular automata and systems dynamics model)[239] • Spatio-temporal spread of dengue across cells with diffusion-based human mobility[240] • Evaluate outbreak persistence using human population size, vector-to-host ratio and biting rate across different cells[241]
Agent-based models	• Ideal for complex processes, feedbacks and interactions • Individual-based traits and behaviour/decision rules • Space is modelled discretely or continuously • Stochastic • Large amounts of empirical data required to accurately parameterize	• Building blocks • Nonlinearity • Emergent properties • Stochasticity • Adaptive memory	• Hierarchical landscape • Composition • Configuration • Connectivity	• Sensing • Adaptation • Beliefs, desires and intentions • Associations with hierarchical social groups	• Simulate urban water supply and effect on *Aedes* species populations, with changes due to population growth and weather[242] • Effects of interventions (for example, trade policies, vaccination and spraying) on *Aedes* species and *Aedes*-borne disease incidence[9,243] • Simulate spatial growth patterns of informal settlements, with changes in population density that affect *Aedes*-borne disease[244]

(Continued)

Table 1 | Modelling approaches to *Aedes*-borne disease transmission in an urban systems framework (continued)

Model class	Key attributes	Urban systems concepts			Urban systems applications
		Complex adaptive systems	Hierarchical patch systems	Relational social interactions	
Neural networks	• Data-driven approach to classify or predict an outcome layer based on one or more input layers[206] • Uses a feature detector (an array of weights) to determine whether a feature is present or not—a process known as convolution • Image segmentation and classification (that is, convolution and pooling algorithms to identify key regions in an image)[245] • Granular data are beneficial (they allow for local predictions and result in larger training datasets (more observations) than higher-scale aggregations)[206]		• Composition • Configuration	• Detect collective emotion	• Classify street images to extract urban features that predict rates of disease[246] • Use drone images to crowd count and estimate site activity at different times of the day[247] • Analyse high-resolution satellite images to detect/predict changes in urban form[208,209] • Analyse Twitter messages to characterize collective emotion over the course of an outbreak[248,249]

control allocation could be optimized if the hub locations aligned with the city's road infrastructure. This work demonstrates how understanding of the modularity of road infrastructure can be used to distribute resources to high-priority neighbourhoods as quickly as possible. Landscape structure was also of importance in Yogyakarta, Indonesia (population 375,000), although under different circumstances[173]. There, researchers used landscape genetics to examine city-scale *Aedes* species population gene flow[174]. They found that *A. aegypti* from an inner-city district clustered with a single outer-city district, indicating interbreeding[174]. Other outer-city districts showed greater genetic isolation from inner-city mosquitoes, regardless of geographic distance. These results prompt questioning as to how patch composition, configuration and connectivity may drive this structuring[114,175,176]. Characterizing the spatial structure of *Aedes* species populations is particularly important for cities like Yogyakarta, where *Wolbachia*-infected mosquito releases are an emerging control strategy[177]. Multi-scale investigations will aid in expanding these initiatives to additional cities, exploring questions such as 'Which socio-economic, cultural and institutional properties are associated with social acceptance of *Wolbachia*-infected mosquito releases?' and 'Which characteristics of the built environment facilitate *Wolbachia* establishment within *Aedes* species populations in the shortest period of time?'

There has been substantial effort to characterize the extreme heterogeneity observed in socio-economic status, population density and built infrastructure within cities. Telle et al.[178] used principal component analysis on socio-economic and population density variables to create eight homogeneous typologies for 10,676 gridded cells (250 m^2) in New Delhi, India (population ~30.3 million). In association with geolocated dengue cases, they found the highest incidence in low-income, high-density typologies[179]. Such methods offer a way for landscape composition to be operationalized and tested in association with *Aedes*-borne disease incidence. In the urban sciences, typology analyses provide a starting point for characterizing spatial variation using remotely sensed and publicly available data when ground-based data are challenging to access[180,181]. Field surveys, interviews and molecular data can then validate or refine typology assignments based on cultural and institutional properties or functional, biological processes. In Box 2, we present a work flow, demonstrating how typology analyses, landscape metrics and population mobility can be integrated to begin implementing an urban systems framework.

While composition may provide an indication of high transmission areas, viruses themselves exhibit fine-scale spatial structuring driven by immunological dynamics. Bangkok, Thailand (population 10.5 million) is endemic for four dengue virus serotypes, allowing researchers to explore antigenic evolution (mutations in genes that code for the viral surface proteins recognized by host antibodies)[182]. Using serological data, Salje et al.[183] found that immunological memory for dengue virus serotypes develops at sub-neighbourhood levels. Using micro-phylogeography, their team defined dengue virus transmission chains using sequence and serotype data[184]. They found that 60% of cases <200 m apart were from the same transmission chain, indicating sequential transmission between households in a neighbourhood. Further research may explore how sub-neighbourhood composition (for example, social cohesion and population density) determines the probability of nearby cases, or how configuration and connectivity determine the time to introduction between neighbourhoods with established transmission and naive ones.

Other urban science topics are less explored and can expand our insight of *Aedes*-borne disease in the context of contemporary urbanization. Across West and Central Africa, settlements are growing in rural areas far from main cities in micro-urbanization processes[185]. These settlements are sparsely distributed with low housing density. Eco-epidemiologists can ask questions including 'What drives the introduction and persistence of *Aedes*-borne diseases within networks of micro-urban settlements?' In China, rural areas surrounding major cities are often either partially urbanized or entirely subsumed by urban sprawl[38,186]. These villages are geographically part of cities, but the infrastructure and residents retain traditional characteristics. Inter-disciplinary questions may explore patch-level properties (for example, biophysical or cultural properties) of urban villages that contribute to varied rates of transmission compared with the city average. Additionally, throughout eastern Asia, cities are becoming increasingly more vertical[187]. For example, 79% of Singapore's residents live in high-rise apartments[188]. Researchers may then ask 'How do high-rise buildings drive differences in water management behaviour compared with other types of dwellings?' This type of building structure also affects vector surveillance strategies that depend on door-to-door inspector visits. Researchers must explore novel sampling methods that accurately detect changes in *Aedes* species populations on a meaningful spatial scale[189]. Finally, across many cities, governments contend with challenges in equally distributing public services. In New Delhi, India, 40% of households have a 24-h water supply, while more than 25% of households have water for <4 h per day[190]. Therefore, it is essential to consider the role of institutional actors and to ask 'Does water distribution drive differences in water management practices for different neighbourhoods?', 'How do water supply, distribution and management practices vary temporally?' and 'Does this affect local-level variation in *Aedes* species abundance?'

Modelling the eco-epidemiology of *Aedes*-borne diseases. Building datasets that adequately capture the above urban systems processes requires substantial time and resources. However, in this section, we begin by demonstrating that there are low-stakes ways of incorporating CAS, patch systems dynamics and cross-scale interactions into eco-epidemiological analyses. Hierarchical regression models—particularly those using Bayesian approaches—accommodate urban system complexities including lagged effects, nonlinear interactions and multi-scaled data with variable sample sizes (Table 1)[191]. Evaluation of cross-scale interactions, however, is noticeably absent[85,192]. In the landscape ecology literature, Soranno et al.[85] quantified cross-scale interactions between local and regional land use drivers of lake phosphorus using interaction terms between variables at different hierarchies as a straightforward way of examining local, regional and cross-scale dynamics. Quantile regressions have also been proposed to identify scale thresholds[193]. In the relationship between an outcome and predictor variable at multiple regression quantiles, scale thresholds are indicated at scales where one predictor variable is no longer essential and another takes over. However, if thresholds are not critical, the predictor would have the same effect size at any quantile. Quantile regressions have been used to study nonlinear climate and income effects on dengue risk. However, cross-scale applications have not been pursued, leaving room for methodological development[194–196].

Dynamical models focus on mechanistic formulations of transmission, including space–time dependencies of demographic and environmental processes. Metapopulation models divide a population into spatially structured patches. Patches are assumed to be independent, invoking relational geography ideas of patches having unique trajectories. Additionally, the rate at which susceptible individuals are infected varies based on patch composition[133,197]. While between-patch connectivity is intrinsically considered with metapopulation models, researchers are including more sophisticated movement parameters by programming asymmetric mobility and differential time spent in patches[198,199]. Feedbacks can also be incorporated whereby patch-level infection limits population mobility[200]. Configuration may also be considered as *Aedes* species populations are more likely to diffuse across nearby patches, although this requires further development within metapopulation frameworks[201,202]. In particular, we see theoretical models as essential to advancing our understanding of the relationships between patch composition, configuration and connectivity.

Cellular automata and agent-based models (ABMs) are commonly used in eco-epidemiological and urban sciences research (to model urban expansion scenarios)[203,204]. Both model classes incorporate nonlinearity, stochasticity and adaptive capacities through specified rules (that is, transition rules for cellular automata and decision rules for ABMs). While many eco-epidemiological models have memoryless Markov properties in which future states of a process depend only on the present state, cellular automata and ABMs incorporate at least short-term adaptive memory. ABMs can uniquely incorporate individual-level behaviours rooted in beliefs, desires and intentions. They can include feedbacks between agents with specific socio-behavioural profiles and higher-order social structures, which can in turn be used to guide interventions and decision-making (Box 1)[205].

A challenge with ABMs is acquiring sufficient data to parameterize the model, create decision rules and understand local transmission dynamics well enough to make evidence-based assumptions. In contrast, machine learning methods do not require local-level assumptions and are entirely data driven[206]. Machine learning facilitates the inclusion of large numbers of correlated variables and modelling complex interactions between these variables[207]. They fit models without presupposing functional forms (for example, linear), providing more flexibility than hypothesis-driven models. They are increasingly used in landscape ecology and urban planning and are capable of learning and predicting different urban growth patterns[208,209]. However, a more complete representation of current urban conditions and future scenarios requires engaging with social actors of the system.

Participatory and transdisciplinary research. Increasingly, researchers are using participatory methods to understand how human actors experience and influence their landscape, networks and risk. Approaches require diverse contributors, with research and non-research experts (for example, policy practitioners, community leaders and so on) contributing as equal team members[121,210–212]. Together, there are opportunities to create innovative datasets, develop decision support tools and identify viable actionable solutions[213,214]. Yet, these outputs require negotiating the scope, intent and ethics of participation, particularly when using emerging technologies and engaging marginalized communities[214–216].

Public health is increasingly relying on community informatics, where data are gathered from the public via digital platforms. Users can report vector encounters or cases through mobile apps or websites in real time and engage with other participants[217–220]. These approaches have data limitations but allow for collections across broader geographic areas than is possible with small research teams. They also benefit from informing and empowering community members[221]. Additional urban science methods, including participatory drone mapping, virtual reality interviews and scenario mapping, can all inform *Aedes*-borne disease work[222–224]. Researchers can compare community-created maps with entomological risk maps to contrast academic definitions of risk versus risk experienced by community members[225]. Evans et al.[57] used participatory mapping, entomological data and Bayesian models to investigate relationships between entomological risk and community reported risk. While field data and spatial models showed similar mosquito abundance across sites, socio-economically mediated human–environmental interactions led to differences in mosquito avoidance behaviours and risk perception. This mixed qualitative–quantitative example is a starting point for future participatory simulation modelling. ABMs in particular allow researchers and participants to co-develop model environments, incorporate agent rules and interpret results. Participatory modelling is essential for *Aedes*-borne disease interventions, particularly given scale mismatches between administrative decision-making and disease risk. Emerging evidence points to the disconnect between the bottom-up, interactive nature of urban processes and the top-down role of governance, as services are allocated in management units created for operational or cost-saving purposes[80]. Engaging communities in *Aedes*-borne disease interventions channels local knowledge on current conditions towards best practices, particularly at finer scales, which are overlooked by city-wide management plans.

Ameliorating scale mismatches requires engagement and clear communication between stakeholders of different backgrounds. Working alongside local communities facilitates this, leading to innovative approaches that involve cross-scale collaboration to solve a problem. Health ministries are increasingly endorsing multi-stakeholder, transdisciplinary and inter-sectoral collaborations to reduce *Aedes*-borne disease risk. However, there is little guidance on doing so[226–228]. At the very least, these approaches require a shared language and objectives, and aligned vision among collaborators. With this framework, we establish that there are not only common goals but clear theoretical and methodological cross-overs between *Aedes*-borne disease eco-epidemiology and the urban sciences that must be matured and made accessible to researchers and practitioners at all levels.

Conclusion

In this Perspective, we bridge concepts from the urban sciences with hierarchical patch systems theories foundational to ecology. With an urban systems framework, we facilitate new ways of studying *Aedes*-borne diseases within complex cities. We draw from ever-growing knowledge on the science of cities, synthesizing CAS, hierarchical patch systems and relational geography to consider how individual and collective social structures interact with the biophysical landscape to generate arboviral disease risk. With insight into the scales at which socio-ecological-technical processes constrain eco-epidemiological ones, cities have an opportunity to work with communities to co-create vector control management units that consider local context. The framework's broad nature and roots in ecological tenets allow existing eco-epidemiological methods to be integrated with greater interpretability and reproducibility for diverse cities worldwide, as well as for other emerging infectious diseases. Application of the framework is enhanced through transdisciplinary, inter-sectoral teams including government officials, social scientists and community members. Ultimately, the framework will improve existing conceptual and quantitative approaches and advance strategic interventions ranging from urban planning (for example, piped water services) to emerging vector control strategies (for example, *Wolbachia*-infected mosquitoes) for complex urban systems around the world. An urban systems research agenda requires building on this foundation, advancing innovative methods and developing pipelines to move evidence into action.

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