

The ecological dimensions of vector-borne disease research and control

Dimensões ecológicas do controle e gerenciamento de doenças transmitidas por vetores

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Abstract

Alarming trends in the resurgence of vector-borne diseases are anticipated to continue unless more effective action is taken to address the variety of underlying causes. Social factors, anthropogenic environmental modifications and/or ecological changes appear to be the primary drivers. The ecological dimension of vector-borne disease research and management is a pervasive element because this issue is essentially an ecological problem with biophysical, social, and economic dimensions. However there is often a lack of clarity about the ecological dimension, the field of ecology (e.g. role, limitations), and related concepts pertinent to ecosystem approaches to health. An ecological perspective can provide foresight into the appropriateness of interventions, provide answers to unexpected vector control responses, and contribute to effective management solutions in an ever-changing environment. The aim of this paper is to explore the ecological dimension of vector-borne diseases and to provide further clarity about the role of “ecological thinking” in the development and implementation of vector control activities (i.e. ecosystem approaches to vector-borne diseases).

Dengue; Chagas Disease; Communicable Diseases; Ecological Studies; Ecosystem

Introduction

Vector-borne diseases pose a significant public health problem today, with a number of “old” diseases resurging in recent decades alongside newly emerging infectious diseases ¹. Some of these were effectively controlled just 50 years ago but these previous hard-won gains are now threatened or have already been lost ^{2,3}. Dengue is perhaps the most striking example. From 1950-1959 less than 1,000 cases were reported worldwide ⁴. Now an estimated 50-100 million cases occur annually ⁵. At least 20 other vector-borne diseases have also emerged during this time, having increased in incidence and/or expanding their geographical range ⁵.

Coinciding with this increase in vector-borne diseases have been dramatic ecological changes. Marked increases in the rate and extent of environmental degradation over the last century, largely attributable to human activity, have fueled growing concern and acceptance of the interdependence of man and the environment ^{6,7}. The association of anthropogenic environmental change and infectious diseases in particular has recently begun to attract attention and prominence in relation to policy (e.g. Millenium Ecosystem Assessment, 2005). The growing interest in ecosystem approaches to health is a response to an increasing recognition of “*the inextricable links between humans and their biophysical, social, and economic environments, and that*

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these links are reflected in a population's state of health"⁸ (p. 1).

The alarming trends in vector-borne disease emergence are anticipated to continue unless more effective action is taken to address the variety of underlying causes – of which social factors, anthropogenic environmental modifications and/or ecological changes appear to be the primary drivers⁹. The systemic nature of these changes and complexity of interactions among factors make simple, targeted or “silver-bullet” solutions ineffective, except for in the short term. As a result, ecosystem-based approaches are now advocated to provide sustainable solutions, as they previously have been the areas of natural resource management and agricultural pest management¹⁰. However, public health research and policy have yet to incorporate the ecological dimension into management and control strategies to any significant degree. This may in large part be due to the complex and abstract nature of the ecosystem concept as well as the lack of an operationally explicit description of what constitutes “the ecosystem approach”. The aim of this paper is to partially address this need by exploring the relevance of ecological science to vector-borne diseases, explaining “ecological thinking” and attempting to describe its role in the development and implementation of vector control activities (i.e. an ecosystem approach to vector-borne diseases).

History of ecology in vector-borne disease research and control

The importance of the ecological context in the management of vector-borne diseases was likely realized immediately following the discovery of arthropods as vectors of disease in 1877. As early as 1935 Klinger¹¹ (p. 244) pointed to the “*need to have a thorough knowledge of breeding places and habits and to apply the most suitable methods to the situation*”. Since about this time a large body of ecologically relevant knowledge has accumulated for these diseases. Basic ecological science has grown in parallel, but neither area has consistently benefited from the knowledge generated by the other¹².

Akin to the initial focus of ecological science in the late 19th and early to mid 20th centuries, early vector-borne disease research concentrated on explaining the natural history, taxonomy, biology and distribution of organisms (i.e. vectors and pathogens). This quickly resulted in a great deal of ecological knowledge that was immediately applied to develop vector management strategies. This includes a number of notable

early successes, such as the first systematic effort to control mosquito vectors in 1901 by William Gorgas, the eradication of a number of important diseases in the United States from 1910-1948 (e.g. yellow fever, dengue and malaria), and the successful eradication of the dengue vector *Aedes aegypti* and, as a result, dengue throughout much of the Americas from 1950-1970^{13,14}.

Ecology-based vector control methods received a boost beginning in the 1960s when the use of persistent chemical pesticides like DDT came into question due to their potentially negative environmental health and ecological impacts. The importance of using biological and ecological approaches, including undertaking ecosystem studies, thus began to be advocated¹⁵. In fact, the ecological impacts of DDT and other chemicals became the environmental *cause célèbre* of this period and arguably helped usher in the modern “environmental awakening”¹⁶. To this day, ecology is often equated solely with research and policy that deals with the natural environment and its protection. That is, with humans as being outside of nature and external stressors. This is contrary to the perspective, discussed further below, that humans and nature are intertwined and interdependent. Nonetheless, these concerns and the extensive environmental protection legislation that emerged led vector ecology research and policy toward more environmentally sound methodologies. These methods went beyond chemical control to include environmental management and biological and social control methods.

Subsequently, another set of environmental challenges to vector control has emerged stemming from the profound ecological changes, particularly (but not limited to) the tropics where most vector-borne diseases originate and by far the largest number of people suffer or are at risk. A phase shift has taken place during the past few decades in which most regional ecosystems in the world have transformed from what largely was natural landscape and non-intensively cultivated cropland to primarily human dominated landscape¹⁷. Rapid and widespread urbanization, agricultural intensification and exploitation of natural resources now make it difficult to draw boundaries between urban and rural as well as rural and natural landscape – thus between what is human and what is nature. Exceptions include the boundaries of national parks or other protected areas, assuming they are aggressively and effectively enforced. Nonetheless, people often flock in great numbers to many of these areas or aggregate outside the boundaries, so that the effects of dramatically increased human densities are not necessarily limited to urban areas. As a

result of this shift, marked by the recent discovery that humans now or will soon be responsible for essentially “consuming” over 50% of the earth’s net ecological productivity¹⁸, science is increasingly emphasizing an integrated, human-nature model for understanding ecosystems and their dynamics (e.g., Michener et al.¹⁹).

This has resulted in a growing shift in ecological research towards concern with not only the degradation of the natural environment but an acceptance and recognition by a growing number of ecological scientists and researchers who focus on the “human-built” environment of our inseparable role as part of all ecosystems²⁰. This is evidenced by the new journal *Urban Ecosystems* (Springer) for example. None of this should be taken to suggest that (predominantly) natural ecosystems, landscapes and natural populations do not remain a significant aspect of ecology research or vector-borne diseases. However, vector ecology and control now face a dramatically different set of challenges as the disease transmission arena today is fundamentally different from what it was just a few decades ago. As is the case for all “complex adaptive systems”, ecosystems are continuously evolving as non-equilibrium systems within the environment – in which host-vector-pathogen complexes are inextricably embedded^{21,22}.

In sum, despite some set-backs, such as the over-reliance on chemical pesticide solutions

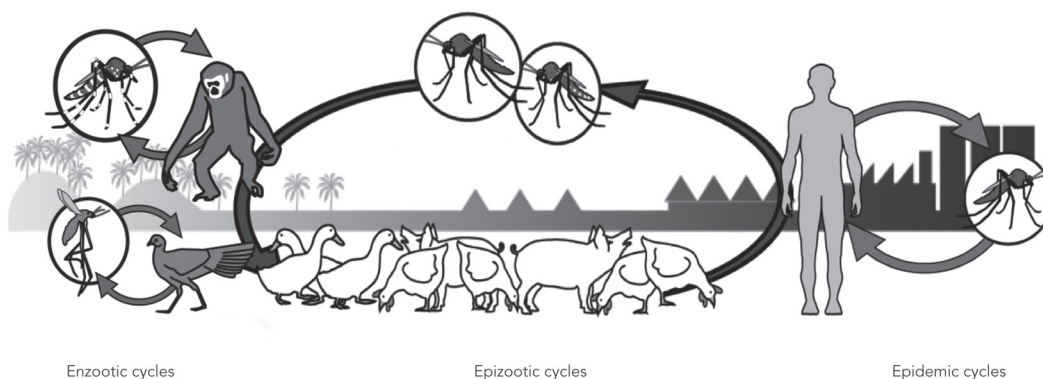
that is characteristic of the post-WWII era of technological “quick fixes”, vector borne disease management has been evolving towards a more integrated, holistic, ecology-based science. This is reflected in the emergence of “integrated control” in the 1960s, followed by “integrated pest management” in the 1970s and “integrated vector control” and “community-based participatory” approaches emerging in the 1980s^{12,23}. What is by far the most holistic and disciplinarily inclusive approach yet, “the ecosystem approach” began in the 1990s⁸. It is noteworthy that in all of these approaches the idea and policy impetus behind them generally has been out in front of the science (the conventional hypothesis-driven experimental evidence) and the capacity of academic and public health institutions to readily grasp and implement them.

The ecology of dengue and Chagas disease

Vector-borne disease transmission cycles typically involve a set of important pathogen(s), arthropod vector(s), vertebrate host(s), and occur within a variety of particular environments (Figure 1). Dengue and Chagas are examples discussed here and occupy different ends of a wide spectrum of vector borne disease ecologies.

Figure 1

Vector-borne disease transmission cycles.



Note: vector-borne diseases occur in a staggering number of environments and include an incredible diversity of pathogens, hosts, and vectors. However, these diseases can generally be described within three broad categories of environments and transmission cycles: natural (e.g. forests), modified (e.g. rural, agricultural), and human (urban). This schematic is not intended as representative of a particular disease but as a general model that is adaptable according to the pathogen, vector(s), host(s), and environment(s) in which they occur.

Thus they provide an illustrative comparison of how the ecosystem approach may be applied to vector borne diseases. The pathogens (a virus versus protozoan) and vectors (mosquitoes and triatomines) could not be more different in their life histories. The hosts of dengue have only been found to include humans and nonhuman primates whereas Chagas disease is capable of infecting over 200 species of mammals ^{24,25,26}. The habitats for these diseases are also quite different. Dengue has primarily been a disease of urban areas, while Chagas predominates in rural settings. Chagas transmission has also occasionally been found on the fringes of peri-urban areas, and the pathogen and vector do occur in some large urban areas, but natural transmission involving humans is rarely documented ^{27,28}. Dengue is also found in peri-urban and rural areas, and apparently is increasingly being transmitted between these and urban areas ^{4,29}.

Vector-borne diseases in general are especially ecologically sensitive since environmental conditions can have dramatic effects on the vectors, pathogens, and potential hosts involved in transmission ¹⁰. The diversity of environmental factors and contexts associated with vector-borne disease emergence is illustrated in Table 1 ^{1,6,30}. In simple ecological terms, the association between environment and disease epidemiology is a consequence of vectors and non-human reservoir hosts, as is the case for all species, having specific

habitat requirements. As habitats change, whether due to natural or human processes involving a range of possible causal mechanisms and factors, so too does disease epidemiology.

How habitat changes and how this affects the biology of a pathogen is varied and complex, within as well as among vector-borne diseases. One way to simplify this complexity using an ecosystem perspective is to view the emergence and/or resurgence of vector-borne disease in terms of regional environmental changes ^{31,32}. An ecosystem considered on a regional scale (i.e., a major river basin, upland area or any geographically distinct area) necessarily includes human built/modified and natural zones and "infrastructure". On this spatial scale (and considering an approximately decadal time scale), changes in land use and resource production (urbanization, agricultural expansion and intensification, and natural habitat alteration) driven by human population and economic expansion are among the most obvious changes associated with vector-borne disease emergence. At least 25 vector-borne diseases have been associated with changes in urbanization, deforestation, and agricultural practices ^{2,31,32}. In Amazonian regions of Brazil alone there have been at least nine emerging arboviruses (including dengue) that have been associated with recent environmental changes ³³.

Environmental factors (and their driving variables) and ecological factors are sometimes

Table 1

Environmental drivers and causal factors associated with infectious disease emergence.

Institute of Medicine *	Factors in the emergence of infectious diseases **
Microbial adaptation and change	Ecological changes
Human vulnerability	Human demographic changes and behavior
Climate and weather	Travel and commerce
Changing ecosystems	Technology and industry
Economic development and land use	Microbial adaptation and change
Human demographics and behavior	Breakdown in public health measures
Technology and industry	
International travel and commerce	Millennium Ecosystem Assessment ***
Breakdown of public health measures	Demographic
Poverty and social inequality	Economic
War and famine	Sociopolitical
Lack of political will	Cultural and religious
Intent to harm	Science and technology
Physical, biological, chemical	

* Smolinski et al. ¹;

** Chareonsook et al. ²⁹;

*** Hassan et al. ⁶.

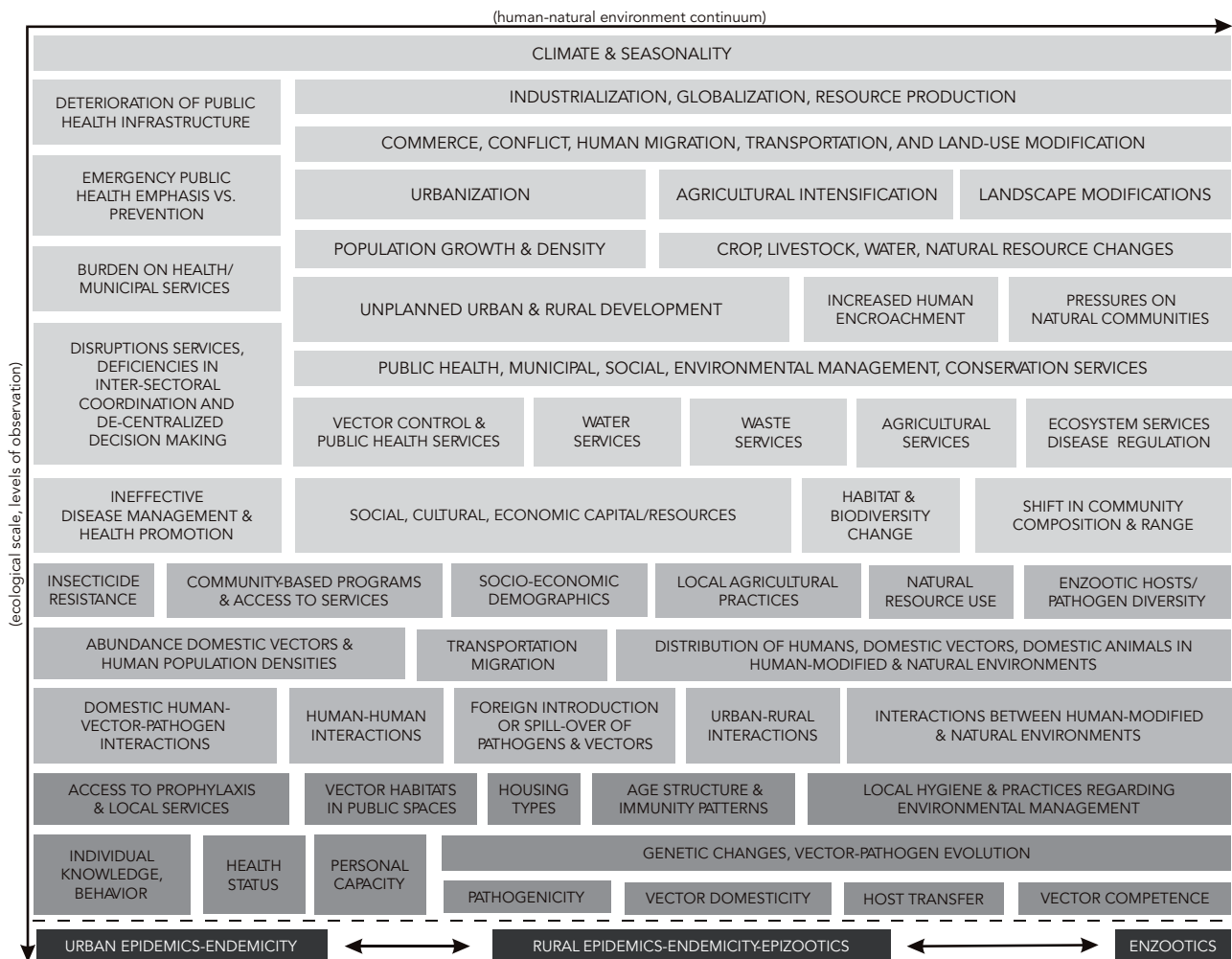
referenced interchangeably; however, there is a subtle and important difference between the two. “Ecological” refers not only to those factors or processes directly related to interactions of humans/vectors/pathogens with their natural or human-modified environments. It also includes those changes affecting interactions and processes (e.g., pathogen spillover and viral evolution) within and/or between humans, vectors, and pathogens that influence pathogen transmission.

Moreover, as the above case of the Brazilian Amazon illustrates, the changing “environment”

includes demographic and social patterns (e.g. migration), public health and basic infrastructure, along with political and economic circumstances. It is this entire system of interactions involving human and natural constituents and processes, causal relations including driving forces, modulating factors, and effects (including disease emergence) that collectively constitute an ecosystem. A spectrum of these elements is presented in Figure 2, from which this ecological perspective and the interconnectedness of these diverse interactions is evident.

Figure 2

Spectrum of ecological interactions associated with vector-borne disease transmission.



Note: from left to right: a continuum of factors/drivers spanning from human to natural environments. From top to bottom: factors/drivers oriented according to ecological scale and/or level of observation.

Ecology, systems thinking and vector-borne disease management

Unfortunately, there is often a lack of clarity among non-ecologists about what constitutes ecology, its potential role, limitations and concepts pertinent to ecosystem approaches to health and vector-borne disease management. As a scientific discipline ecology is an area of scholarly research that has generated principles, concepts, methods and tools to understand the natural world. Academically, the field of ecology has been largely dominated by research on the natural (i.e. non-human) environment and non-human study systems. However, it has been adapted to human environments and health³⁴. Yet a serious shortcoming of ecological science has been the lack of models that incorporate the behavior of people, as part of “the system”.

Systems ecology, one of many sub-disciplines of ecology, explicitly applies the systems approach to natural as well as human built environments. The systems approach not only draws on a body of theory and methods (though not a discipline per se) but is often described as a “way of thinking”. Thus, systems ecology largely involves the use of methods (drawn from outside and within biology) for studying natural or hybrid human-natural systems (e.g., urban or agricultural) that consider the system as a “whole”³⁵. Most researchers are quite familiar with the systems approach and its central idea that “the whole is greater than the sum of the parts.” However, it is often less clear how to define the system and regrettably there are no simple rules.

Boundaries and interacting components

Fortunately, ecosystems have been found to have general properties and characteristics with which it is helpful to be familiar in order to understand how they and their parts behave dynamically, including host-vector-pathogen complexes. As a start, all systems, conceptually speaking, have boundaries. These may be visible, such as when the edges of an urban area are distinguishable by a sharp change in human infrastructure and density. Or, they may involve a more gradual transition, requiring the boundaries to be decided upon operationally. In either case, imposing boundaries and placing limits on the number of relevant elements considered focuses management resources/activities and provides a preliminary exploration of the potential scales involved (see below). Differentiating between the variables (i.e. health determinants) that are within or outside of the system is particularly useful in separating those which are actionable versus

those which may be monitored as potential confounders³⁶.

A systems perspective is also conceptually critical for considering the interactions among the set of relevant elements influencing the transmission of vector-borne diseases, including those involving management activities. An understanding of these interactions makes possible the effective targeting of management actions. Moreover an understanding of the multiplicity of interactions allows for flexibility in the types of appropriate actions that may be applied. This perspective also promotes an understanding of the dynamic changes that may occur within a system as a result of ecological changes and/or vector management activities.

Scale

The concept of scale is typically applied in reference to physical dimensions of space and time but broadly definable as “*the spatial, temporal, quantitative, or analytical dimensions used to measure and study any phenomena*”³⁷ (p. 11). In research and management activities, more frequent reference is made to levels: the points of observations (i.e. measurements) performed at a particular scale.

Geographical and temporal scales are intimately tied to an accurate understanding of the distribution of vectors, incidence of disease, and scope of management activities. Social and policy relevant scales also need to be considered because of the importance of human dimensions and the applied nature of these activities. Vector management and inter-sectoral activities often utilize jurisdictional scales that include local, municipal, state/provincial, national, and multilateral levels³⁷. In addition, many community-based programs employ social scales and research at individual, family/household, and neighborhood/community levels. However, in ecology the most common scale is based on ecological organization and related research is performed at discrete levels including ecosystem, landscape, community, population and genetic levels. These levels are less explicitly addressed in ecosystem approaches to human health and may or may not correlate with geographical, social, and policy relevant scales.

The wide variety of levels and scales embedded in the ecological problem of vector-borne diseases certainly poses a challenge for both research and management activities. The central challenge lies in understanding the appropriate scales in which disease transmission, environmental influences, and/or anthropogenic changes may be best understood and most efficiently

mitigated. Oftentimes management activities may be more appropriate or have greater impact at specific scales. Scaling up vector control programs, without regard to ecological differences between areas, can be just as ineffective as top-down programs with the opposite demands. Furthermore many environmental drivers and causal factors may function at different levels or scales, and act independently of and/or in concert with the system. For example, the impact of independent actions at local levels may result in broader city-wide, regional, or global trends. Conversely, global factors such as climate change may act broadly and/or have varying impacts at local levels^{38,39}.

Ecosystem organization

Ecosystems can be analyzed according to the organization of system elements and interactions, relative to defined scales, and this has proven useful in understanding natural ecosystems and the idea of nested hierarchies^{36,40,41}. This type of organization occurs as a result of asymmetric system interactions between levels and provides a structured approach for exploring the significance of these interactions and their dynamics. Many interactions, patterns, and processes will tend to aggregate at certain levels. At the heart of hierarchy theory is that those elements present at higher levels typically impose constraints on lower levels; conversely, the combined elements at lower levels dictate what is physically possible at upper levels. Upper-level elements often occur over a larger spatial area and temporal range. Those at lower levels tend to operate over smaller areas and shorter periods of time⁴⁰.

These ideas have a variety of conceptually liberal implications to vector-borne disease management, irrespective of the dimension in which it is approached (i.e. biophysical, social, economic). As an example, some vector management activities (e.g. community-based strategies, improved housing) at local levels may be constrained by upper level phenomena (e.g. economic commitment, climate change). In addition, potentially broadly effective upper level interactions and processes (e.g. inter-sectoral coordination) may be negated by lower level phenomena (e.g. insecticide resistance, behavioral changes, individual commitment). Furthermore, some phenomena (e.g. climate change, city-wide vector eradication) may be of great significance but operate at spatial and temporal scales that require sustained commitment by funding sources with limited patience. In complex ecosystems this theory may demand a fairly comprehensive understanding to provide reasonable direction.

Fortunately, in vector-borne disease transmission and management activities a great deal is already known about specific situations and the number of significant elements/interactions/processes that are actionable may be quite limited and worth exploring.

The linkage of ecosystem characteristics and vector population density

The objective of vector control initiatives (e.g. integrated, biological, community-based, health promotion and ecosystem based approaches) is to reduce vector populations to low enough levels to interrupt transmission. It makes sense to ultimately direct ecosystem management efforts towards the ecological regulation of vector populations whether it be from biophysical, social or economic perspectives⁴². Thus understanding the connection between ecosystem properties and vector population dynamics (i.e., what regulates their size and distribution) is fundamental.

Ecologists distinguish two modes of regulation in animal populations: density-independent and density-dependent regulation. In the former, factors (e.g. temperature, humidity, and rainfall and other abiotic factors) affect population size and operate independently of how many individuals there are in a population. In the case of the latter the regulating factors involved (e.g. competition, predation, parasitism and other biotic factors) tend to increase in their effect with population density. The observation that vector populations can rebound to levels higher than those prior to intervention, because the mode of intervention had ecosystem level impacts such as eliminating biotic factors that naturally control the vector population, suggests density-dependent regulation is operating in those cases⁴².

In human modified environments there may be a diminished capacity of the ecosystem to regulate vector abundance naturally; however, density-dependent regulation of Chagas and dengue vectors is believed to occur. Laboratory studies have suggested that the feeding behavior of domestic Chagas vectors at lower densities may result in more efficient Chagas transmission. While this finding may not readily occur it raises an interesting point because reductions in adult vector abundances may not always be reflected in a proportional decrease in disease. Density-dependent regulation is also at least partly evident in *Ae. aegypti* populations based upon their feeding success⁴². The implication is that vector management strategies aimed at stages other than the adult (e.g. larval breeding source reduction) may be more effective, and others have

noted that there are at least “*theoretical reasons that suggest that killing the adults is not the most efficient way of reducing vector populations and minimizing dengue epidemics*”⁴³ (p. 97).

Density-independent factors such as seasonality and climate variability are especially significant in regulating vector populations⁴². Seasonal rainfall regulates the types and number of sites for container breeding mosquitoes, and recruitment rates are tied to seasonality because *Ae. aegypti* eggs can survive between rainfall seasons. A density-independent factor such as temperature can affect dengue transmission rates by altering the extrinsic incubation period in mosquitoes⁴⁴. Seasonality is also observed in Chagas vector populations and transmission. In combination with density-dependent regulation, these characteristics have led to the belief that insecticide control of these vectors could be improved if seasonally timed^{42,45}. Unfortunately, many of these factors are often not directly actionable with the exception of the timing of management activities and finding creative solutions to mitigate their impact.

The importance of density-dependent and density-independent factors is also evident in the spatial distribution of vector populations. The relationship between abundance and distribution are often inseparable because the dispersal of vectors frequently depends upon the local density⁴⁶. In a study from rural Argentina, the authors found that the number of *Triatoma* vectors that spatially dispersed were proportional to the abundance of vectors and that “*high-density sites were apparently producing more dispersers*”⁴⁷ (p. 8). Sylvan Chagas vectors also likely disperse further when their primary hosts are reduced or the density of vectors to these hosts is proportionally high, and these populations pose a significant challenge since they are difficult to control and provide a source for transient or permanent infestation of peri-domestic habitats^{47,48}. It seems intuitive that greater abundances of *Ae. aegypti* vectors may also follow similar trends in the relationship between abundance and dispersal. However, it is also likely that in drier seasons (or areas) that *Ae. aegypti* may disperse further in search of suitable oviposition sites, at which time populations may not be at their greatest⁴⁹.

The persistence of a vector species within a particular ecosystem or landscape is often understood as a balance between the extinction and recolonization of populations between heterogeneous patches of habitat⁵⁰. This is physically apparent in the mosaic appearance of a landscape, the common exception being agricultural monocrops, and reflects the discontinuous distribution of habitat, including that of vector species.

A vector's capacity to disperse between patches may result in spatiotemporal “hot spots” of vector abundance and be predicated by physical barriers, distance, vector behavior, and/or other population regulatory factors. Otherwise a suitable habitat may not always be occupied, or may be at low numbers, but it nonetheless can be an important site as a “stepping stone.” These characteristics are important because the abundance and dispersal of vectors may quickly negate control efforts. Thus basing intervention strategies on an understanding of these “patch-dynamics” including intra-patch dispersal is key to the long-term success of vector control operations. In some areas this is already understood well enough to suggest the spatial extent that control efforts need to cover⁵¹.

Discontinuous vector populations and the efficiency of population dispersal can result in genetically differentiated populations within the same ecosystem. A high degree of genetic variability and selective pressure on these populations can result in the possible emergence, spread, and persistence of insecticide resistant genes or vector behavioral changes that facilitate transmission. Dengue vector populations display a great deal of heterogeneity in their population dynamics, especially during drier seasons. Further demonstrating their spatially fragmented structure, they can exhibit a high degree of genetic variability even in urban areas⁵². The spread and possible persistence of insecticide resistant genes are a function of metapopulation spatial structures and temporal dynamics in these populations. Domestic vectors of Chagas differ in these regards by exhibiting low genetic variability and comparatively low dispersal rates. These characteristics and their susceptibility to insecticides at all life stages (except eggs) likely contribute to the effectiveness of insecticide against domestic Chagas vectors. Sylvan populations of Chagas vectors pose a more significant challenge because they are difficult to control with insecticides⁴⁷.

We have only touched on how the problems and principles linked to population regulation in ecology bear on vector borne disease. However, it should be clear from the broad perspective offered by ecosystem thinking that the patterns and processes associated with vector populations are dynamic, and the outcome of a combination of factors reflect the population biology of the species, as well as the size, spatial distribution, and heterogeneity of habitat patches. The landscape structure, community composition and diversity (not only epidemiologically important vectors, hosts, and pathogens) – that is, the collective affect of biodiversity – characterize the ecosystem

and its spatiotemporal dynamics, resilience, and resistance to invasion, stressors, and vector management related activities⁵³.

Conclusion

The need for a more integrated, transdisciplinary, systems-based approach to understanding and controlling disease transmission has become increasingly obvious due to the wide range of social and biophysical factors involved. The integrative ecological paradigm gaining increased acceptance in science that views humans and nature as part of a single “complex adaptive system” provides a hopeful basis for better understanding, developing, and implementing sustainable disease control strategies^{41,54}. The impetus for adopting a similar approach in regard to vector-borne disease problems currently exists and has been accompanied by increasing calls for a better understanding of the ecology of these diseases^{7,10,55}.

Holistic frameworks for understanding health and disease have been proposed and are evidenced in recent discussions and funding opportunities including those termed EcoHealth, (eco)nomical-(bio)physical-(social), ecosystem, socio-ecological, and others^{8,56,57,58,59,60,61}. The ecological dimension can also be viewed similarly: as a system of interactions within and between hosts, vectors, pathogens, and the environments associated with disease transmission. From this perspective even human-human interactions and behavior associated with disease transmission, although not traditionally the topic of ecological research, can be viewed as ecological in nature. Regardless of the specific framework or interpretation, the ecological dimension remains a pervasive element because vector-borne diseases are essentially ecological problems that span biophysical, social, and economic environments.

Ecosystem concepts and methodologies have long been utilized in understanding the complex interactions associated with natural ecosystems; however, as these environments have become increasingly dominated by humans, a growing need to understand the human dimension of these systems has arisen. This need is also mirrored among vector-borne disease problems as these diseases have continued to emerge from natural ecosystems and become entrenched in human-dominated environments⁵. The integration of knowledge from other disciplines (e.g. sociology, anthropology, economics) with the capacity to address the human dimension are greatly needed in order to better understand coupled

human-natural systems, particularly in urban environments^{62,63,64,65,66}. The basic concepts presented in this review (e.g. scale, heterogeneity, boundaries, organization, etc.) were chosen because they are central ecological themes that are pervasive in natural, human, disease, and/or integrated systems.

More commonly, the ecological dimension is associated with traditional topics of ecological research that are applicable to vector-borne disease research and management needs. A variety of current needs were highlighted in a recent Institute of Medicine report which cited: an improved understanding of anthropogenic change and the emergence of disease; more accurate risk assessments that merge ecological and epidemiological information; responses to insecticide resistance; and novel methods to manage vector-borne diseases⁵⁵. These needs are wide-ranging, both in topic and scale, and many are important in developing more accurate system based understandings of vector-borne disease transmission. These needs also span the continuum of ecology sub-disciplines and levels of ecological organization (besides the ecosystem/system level) including landscape, community, population, and genetic levels.

In the last decades, significant advances have been made in integrating concepts and tools from the field of ecology, particularly in regard to landscape ecology, remote sensing, spatial analyses and vector-borne diseases^{67,68,69}. Central to landscape ecology is the study of spatial heterogeneity and studies of vector-borne diseases from this perspective have included the spatial distribution of vectors across or within landscapes (particularly urban areas), spatial and temporal analyses that reveal relevant scales for surveillance and improved understanding of transmission dynamics, predictive models of disease and vector distributions, and the potential impact of environmental and anthropogenic change^{69,70,71,72,73,74,75}. The use of landscape ecology concepts and spatial analysis tools are increasingly being integrated with vector-borne disease epidemiological efforts, which have been reviewed elsewhere and include: malaria, Lyme disease, Tsetse-borne trypanosomiasis, arboviral diseases, leishmaniasis, Chagas, and others⁶⁸. As a result, more accurate risk assessments (at least at course levels) have been achieved for some diseases, especially for those with vectors and/or vertebrate hosts in which their distribution can be associated with specific geographical characteristics and features (e.g. climate, vegetation, urbanization, socio-economic demographics)^{68,73}.

Vector-borne disease research efforts have also benefited from greater interdisciplinary col-

laboration between the fields of epidemiology and community ecology, which is concerned primarily with the study of assemblages of organisms and their interactions with each other and the environment. Others have noted the importance of these types of endeavors stating: ecological community structure is a key factor in understanding the public health risk of communicable disease emergence, mode of transmission, and control options^{57,76}. The models and analyses associated with these efforts are important in understanding the impact of change, biodiversity loss, and impact of invasive species. These efforts show promise in the development of predictive models and understanding responses to change for vector-borne diseases such as lyme disease and others, especially for zoonotic and multiple host/vector systems^{76,77}. However, these types of analyses also require obtaining a wealth of data that may not be practical for many applied purposes.

At the population level of ecological research, efforts are typically focused on understanding the dynamics of a particular species and their interactions with the environment. This is an important area for vector-borne disease research because there is a need to advance an understanding of the factors regulating vector populations and accurate vector abundances, which can be used in predicting risk. For diseases such as dengue improved methods in estimating vector densities have been a priority, especially efficient methods that can be used in surveillance over large areas, identification of at risk populations, and targeting control strategies^{78,79,80,81}. These topics are beyond the current discussion but provide an additional example of the need for further integration of ecological and epidemiological related research.

A common thread in the integration of ecological studies and vector-borne disease research and management has been the use of geographical information systems (GIS), relational databases, predictive modeling, and spatial analyses. These types of tools are extremely valuable in exploring the dynamic interactions between humans, vectors, pathogens, and changing physical, social, and economic environments. The use of these enabling technologies and integrative methodologies are important in providing additional capacity to address many of the ecological

challenges reviewed here and have significant potential in facilitating the integration of data from different fields.

Pragmatic approaches that can be used in efficiently acquiring, monitoring, and synthesizing information regarding system interactions associated with vector-borne disease transmission risk, which can then be used to guide and adapt effective management activities, has remained largely elusive to date but ecosystem approaches to these problems are certainly progressing towards this goal. Fortunately, there is a wealth of information that has and is being obtained that can be used in these efforts and applied to local contexts. The use of the integrative tools discussed here, interdisciplinary knowledge, and the dynamics at various ecological levels of organization are important in assessing current strategies and the appropriate scales for surveillance and control.

We argue that the ecological dimension is a unifying element of vector-borne diseases that is capable of providing research direction and a holistic perspective important for all participants/stakeholders involved. Unfortunately, the ecological dimension often appears initially forbiddingly complex, requiring a thorough understanding including all relevant linkages, regardless of discipline, in which the methodologies for defining and assessing a system of interest may remain unclear. However, it is important to differentiate between gaps in ecological understanding that may be filled by basic research and the needs of applied public health and management activities.

For applied vector-borne disease management activities and specific environments, populations, and locations there may often only be a limited number of significant factors regulating disease transmission, and appropriate and/or actionable responses. A progressive step forward for these types of applied activities is the collection of spatially and temporally explicit data that are more easily incorporated into system based analyses and decision making support systems. Ultimately, the true strength of these types of approaches will likely not to be in an extremely detailed understanding of ecosystem complexity but will be derived from a diversity of perspectives and flexibility in finding creative and pragmatic solutions.

Resumo

A tendência alarmante em direção ao ressurgimento de doenças transmitidas por vetores continuará, a menos que ações eficazes sejam tomadas para controlar suas causas primárias. Fatores sociais, mudanças ambientais causadas pelo homem e/ou mudanças ecológicas são, aparentemente, a base do problema. A dimensão ecológica da pesquisa e do gerenciamento dessas doenças é um elemento difuso e constante, já que consiste, essencialmente, em um problema de caráter ecológico com dimensões biofísica, social e econômica. No entanto, há pouca discussão sobre a dimensão ecológica, sobre o campo da ecologia (p.ex.: seu papel e suas limitações) e sobre os conceitos relacionados à abordagem ecossistêmica na saúde. Uma perspectiva ecológica poderá permitir uma análise antecipada da eficácia de intervenções, oferecer respostas para resultados inesperados provenientes de ações para controle de vetores e contribuir para o planejamento de medidas eficazes de gerenciamento em um ambiente em constante mudança. O objetivo deste trabalho é explorar a dimensão ecológica de doenças transmitidas por vetores e esclarecer o papel do "pensamento ecológico" no desenvolvimento e implantação de ações de controle vetorial, ou seja, abordagem ecossistêmica para o controle de doenças transmitidas por vetores.

Dengue; Doença de Chagas; Doenças Transmissíveis; Estudos Ecológicos; Ecossistema

Contributors

The development of this manuscript was an integrative effort of ideas, backgrounds, and expertise. B. A. Wilcox contributed his knowledge of disease ecology and the history of ecological theory and concepts, and their application. B. R. Ellis has a background in vector-borne infectious diseases and was responsible for drafting the document with the support of B. A. Wilcox who provided editing and revisions.

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