The Human Environment Interface: Applying Ecosystem Concepts to Health

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Abstract One Health approaches have tended to focus on closer collaboration among veterinarians and medical professionals, but remain unclear about how ecological approaches could be applied or how they might benefit public health and disease control. In this chapter, we review ecological concepts, and discuss their relevance to health, with an emphasis on emerging infectious diseases (EIDs). Despite the fact that most EIDs originate in wildlife, few studies account for the population, community, or ecosystem ecology of the host, reservoir, or vector. The dimensions of ecological approaches to public health that we propose in this chapter are, in essence, networks of population dynamics, community structure, and ecosystem matrices incorporating concepts of complexity, resilience, and biogeochemical processes.

Contents

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1 Introduction

Definitions of One Health have varied among different authors and institutions, but a defining central tenet is that a One Health approach brings a holistic understanding of health. This broader view includes human medicine, veterinary medicine, and an understanding of the ecological context of health (which we call 'Ecohealth'). To date, One Health approaches have tended to focus on closer collaboration among veterinarians and medical professionals, but remain unclear about how ecological approaches could be applied or how they might benefit public health and disease control. In this chapter, we review ecological concepts, and discuss their relevance to health, with an emphasis on infectious diseases, notably emerging infectious diseases (EIDs). Nearly two-thirds of EIDs are zoonotic, and a majority of those (72 %) originate in wildlife (Anderson et al. 2004; Cleaveland et al. 2001; Daszak 2000). Diseases are considered 'emerging' if they are identified as occurring in a new geographic area, expanding their incidence rapidly, displaying novel genetic code, or moving into humans for the first time. The most important are pandemics, those that become established in humans and spread internationally. Pandemics tend to be zoonotic, foodborne, or antimicrobial resistant pathogens, and their emergence and spread is overwhelmingly a result of changes in human demography (e.g. travel, population growth), behavior (e.g. drug use), economic activity (e.g. agricultural intensification), or anthropogenic changes to the environment (e.g. land-use change, climate change) (Weiss and McMichael 2004; Jones et al. 2008). The interactions among these underlying drivers and the dynamics of pathogens in wildlife, livestock, and people are a key focus of studies of the ecology of infectious diseases.

2 Ecology

Ecology emerged from natural history and rose to prominence as a scientific discipline in the late nineteenth century as the 'study of the interactions of organisms with their environment' (Haeckel 1869). While originally a descriptive science, the theories of adaptation, evolution, and speciation rapidly became central to the field, and led to increasingly analytical approaches (Lawton 1999). Over the past few decades, ecologists have analyzed data from field observations, laboratory studies, and large-scale field experiments to describe the structure and dynamics of populations, their interactions within communities, and the

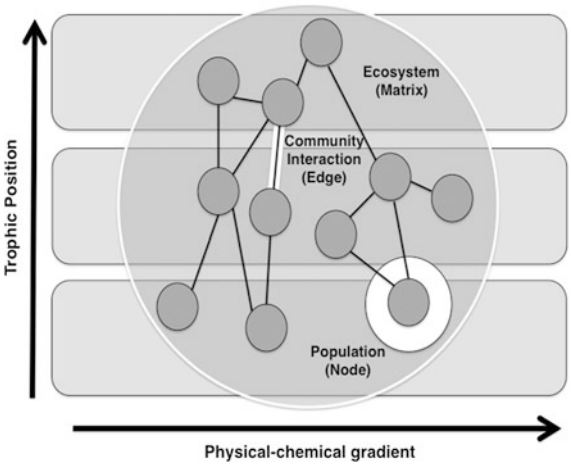

Fig. 1 Diagram illustrating the ecosystem components described in the text: a node is a population of organisms; edges are links between nodes in a community; and the overall environment including abiotic components is the ecosystem matrix. Nodes are structured vertically into trophic levels and horizontally along an environmental gradient

complexity of ecosystems. In this chapter, we build on the work of Wilcox and Jessop (2010) and Last (1998), adding an ecosystem network perspective to describe how ecological approaches can be focused on infectious diseases.

We focus on three components: population, community, and ecosystem ecology. **Population ecology** is the study of the population dynamics of a species with relevant metrics of density, natality, mortality, immigration, and emigration (Hall 1988; Murray 1999). Population dynamics are generated through competition, predation, parasitism, and the distribution of species. **Community ecology** describes the clustering of populations of species into communities and the processes that dictate composition and diversity. Pertinent community metrics are similarity, continuity, species, and genetic diversity. **Ecosystem ecology** is the study of biotic and abiotic components of ecological systems, their biophysical interactions, and the flow of energy and materials (Lindeman 1942; Odum 1969; Cook 1977). The metrics for ecosystems include state, rates, and productivity. Ecosystems provide the framework for organization of species and resource compartments, and modulate rates and dynamics of functions, processes, and services.

In modern ecological approaches, a **network perspective** can be used to describe interactions among ecosystem components, with populations referred to as **nodes**, links between nodes in a community as **edges**, and the overall environment and abiotic components as an ecosystem **matrix** (Fig. 1). This framework complements a shift in ecosystem thinking from structures and hierarchies, to networks and webs. While the concepts in this chapter are presented in the context of wildlife and emerging infectious diseases, they are generalizable to diverse ecosystem interactions.

Traditional views of ecosystems were focused on the concept of directional succession, whereby ecosystems developed along a predictable pathway to a climax system (e.g. mature deciduous forest) (Clements 1916; Gleason 1939). In reality, ecosystems are dynamic and complex aggregations of communities continually adapting to internal and external influences. Rarely are they stable or at

equilibrium, as described by static representations of food chains, trophic guilds, and species dominance. Moreover, they demonstrate non-equilibrium dynamics in a mosaic of patches shifting among stable states when disturbed. The complex structure of ecosystems has long frustrated efforts to forecast and predict their behavior, yielding models of resilience, complexity, and chaos.

3 Ecosystems: Abundance, Structure, and Flow

Historically, public health has focused on the dynamics and structure of human populations—only a single node within the context of global ecosystems. Holistically, human health can best be considered in the context of other organisms within a network of populations, communities, and ecosystem interactions. Infectious diseases within a One Health context require an additional dimension, namely the natural environment as the habitat of the disease agents themselves, examples of which include water borne diseases.

3.1 Population Dynamics

3.1.1 Background

Population ecology focuses on the dynamics of an individual species in a defined area, where the Malthusian growth model is a central theory. However, wildlife populations are not static, nor is their growth linear. Moreover, they display complex cycles and populations evolve from interactions, including competition, predation, herbivory, and mutualism, while demonstrating stochastic dynamics and lagged responses to disturbance.

Because knowledge of wildlife populations still is incomplete, there are many species for which historic data are lacking or routine monitoring not yet possible. Furthermore, coverage varies across geographic regions, taxonomic groups, size, abundance, and economic or social values.

3.1.2 Relevance to Human Health

Despite the fact that most EIDs originate in wildlife, few studies account for the population dynamics of the host, reservoir, or vector, in contrast to studies of human populations and demographics. This uncertainty concerning wildlife health presents a threat both to domestic animals and human populations. At a minimum, those infectious disease agents closely linked to human health should be identified and subjected to intense study, e.g., those that incubate and spread disease or provide ecological services such as disease regulation and/or vaccine discovery.

Identifying these key species helps set priorities for routine surveillance, as well as uncovering as yet unknown species that present a threat or cure.

Fluctuations in host and vector abundance engender a variable risk distribution for disease transmission. Some species are unique in their proximity to human physiology (e.g. primates and wild pigs) or in their expansive ranges (e.g. birds and bats), posing unique threat as integrators, spreaders, and laboratories for recombination and mutation of disease pathogens (Daszak 2000).

3.1.3 Limitations

Wildlife population ecology can be employed to improve global health models, but within limitation. Populations are difficult to define and species-based definitions are generally inadequate. Those that are naturally or artificially isolated often exhibit distinct behaviors and present differential risks (Levins 1968). Populations are a continuum, where factors such as age, sex, and size can influence risk of disease transmission, especially where distribution of the agent is not uniform. Thus, it is simplistic at best to consider population dynamics in isolation from the community structure and ecosystem matrix.

3.2 Community Structure

3.2.1 Background

Community ecology describes an assemblage of nodes and their interactions, or edges. The contributions of individual populations can be characterized by employing network metrics, an example of which would be a high degree of connectivity that identifies critical, keystone nodes influencing the structure of the system. It should be noted that communities can demonstrate both equilibrium and non-equilibrium dynamics.

Characterizing biodiversity is fundamental to community ecology. It is also one of the more widely reported and popular concepts. Biodiversity varies across spatial scales and describes both intraspecific or genetic diversity of a node, as well as diversity of nodes described in terms of richness, abundance, and evenness (Bisby 1995; Jost 2007; Whittaker 1972).

3.2.2 Structure

Food webs represent a central concept in ecology, being employed to model community structure as complex hierarchies of nodes (Lindeman 1942; Elton 2001; Forbes 1887; Hairston et al. 1960). Inter-node interactions (edges) among consumers and resources form the backbone of food-web networks and the nodes

can be structured into trophic levels, or functional groups, such as top predators (Borrvall and Ebenman 2006; Finke and Denno 2005), mesopredators (Elmhagen and Rushton 2007), herbivores, and primary producers. Edges are generally unidirectional, but can flip during the life history of an organism when lower trophic levels prey on juveniles of higher trophic levels.

Single trophic food webs are the simplest (Tilman 1982), but few real-world examples exhibit those dynamics, with multi-trophic perspectives more realistic, albeit complex (Cohen 1978; DeAngelis 1992; Polis and Winemiller 1996). Predator–prey relationships are dominant in representations of the structure of trophic hierarchies, along with the influences of co-evolution, mutualism, autotrophy, herbivory, competition, genetics, and speciation.

Food webs are structured from top and bottom. Top-down control of food webs can occur via predation and resource consumption by consumers, influencing community size structure. At the same time, bottom-up mechanisms operate via abundance, availability, and edibility of primary producers (autotrophs) and secondary producers (herbivores).

3.2.3 Change

Structural dynamics of a system, i.e., arrangement of nodes and edges, can influence the magnitude and variability of community response to disturbance. Endogenous (internal) pressure from one node can reorganize the entire system. Food webs are often portrayed with linear connections among trophic levels; however, responses to exogenous (external) disturbance can expose complex nonlinear dynamics and feedback loops. Unlike characterizations such as a balance of nature or tree of life, it is apparent from food-web manipulations that ecological networks are complex systems encompassing hierarchies, webs, nested systems, cycles, and flows (Carpenter and Kitchell 1996; Scheffer and Carpenter 2003).

3.2.4 Relevance to Human Health

When ecology is incorporated into public health endeavors, the scope is frequently limited to distribution and abundance of individual nodes. Studying the population dynamics of disease hosts and vectors clearly is important if zoonotic disease emergence is to be understood, but populations need to be studied in the context of edges defining their interactions with other nodes. Indeed, a community approach to disease emergence can reveal important nodes and interactions that differ from those identified in population analyses. For example, some nodes, such as keystone species, may be disproportionally important to the system due to strong connectivity or high centrality. Superspreaders are highly connected and rapidly disseminate disease through a network. Identifying and monitoring the keystone species, superspreaders, and nodes that regulate host and vector abundance is important in disease prevention and control.

Trophic cascades regulate host abundance when changes at one trophic level cascade through the food web. For example, when a predator population collapses, regulation of the disease is reduced if the disease host or vector is thereby released from control by predation. Removing predators directly relieves pressure on prey abundance and may also alter physiological stress, behavior (Bakker et al. 2005), and morphology (Werner and Peacor 2003) of their prey. Clearly, both host and predator require monitoring in such circumstances.

Inter-species competition affects abundance, evolution, diversity, and pathogenicity of a disease agent. These processes can be tightly coupled to their pathogen hosts and, in turn, the community dynamics of the system. Hence, the invasion of an exotic species, triggered by wildlife trade, transportation, or climate change for example, could cause food webs to reorganize thereby altering the probability of disease emergence.

On one hand, the introduction of a species like the tiger mosquito (*Aedes albopictus*), which is an aggressive disease vector, can alter the conditional (binary) probability of contracting certain vector-borne diseases. On the other hand, invasions by suboptimal hosts can 'dilute' disease risk. Invasions can also introduce boom and bust dynamics, destabilizing systems and tipping native populations into irreversible alternate states. Invasive species also diverge genetically from their original populations through isolation and founder effects, contributing to "waves" of disease occurrence.

Spatiotemporal variance in food webs is particularly acute for migratory populations, where resource consumption changes with habitat and the effect on nodes in one system can be transferred to another. In effect, migration provides a unique opportunity for populations and communities to exchange pathogens. In these scenarios, mapping distributed food webs could help identify pathways for disease transmission.

3.2.5 Limitations

Food web and community network analyses introduce a high degree of complexity to mathematical and statistical models of systems. Furthermore, it is difficult to determine accurately the trophic position of individual nodes in food web models. While advances in stable isotope analysis, fatty acids, and ecological stoichiometry help determine trophic position relative to other nodes in the community, as well as composition of diet; isotopic measurements often have location-specific limitations, whereby values are relative to local autotrophic production in the system as influenced by external subsidies. Thus, it is difficult to draw meaningful comparisons among food webs. What is required is a method that generalizes models and captures topological position and functional importance of networks without a food web-specific bias (Olff et al. 2009). By using food-web manipulations, it has been possible to demonstrate biogeochemical processes play an important role in structuring communities (Carpenter and Kitchell 1996; Scheffer and Carpenter

2003). So, although community ecology considers both nodes and the edges that connect them, these systems must ultimately be studied in the context of their environment or ecosystem matrix.

3.3 The Ecosystem Matrix

3.3.1 Background

Ecosystem ecology encompasses biophysical mechanisms regulating ecosystem metabolism across both biotic and abiotic compartments, this includes ecological function, physiological processes, populations and communities, resource availability, nutrient cycling, and connections among systems. The connections, flows, and cycles affecting the life history of an organism are highlighted, including materials of composition and their life cycle. Traversing networks that incorporate abiotic pathways may help map these connections, a useful example of which is the carbon cycle, with biotic and abiotic compartments through which carbon can flow, sequester, or transform.

The ecosystem matrix is a spatiotemporal mosaic that provides background structure for ecosystem networks. It is a complex system with unpredictable dynamics, including bidirectional relationships among organisms that extract, modify, and release resources into their surroundings. The physical–chemical conditions that surround an organism regulate metabolism as they consume resources and generate waste (Begon et al. 1996). Ultimately, resource flows influence system dynamics of populations and communities.

3.3.2 Biogeochemistry

Biogeochemistry describes the flow of matter, such as nutrients and toxins, through an ecosystem matrix, including processes such as decomposition and decay. It spans biotic and abiotic compartments through biologically mediated chemical cycling of nutrients. Microorganisms play a critical role in the availability of resources by decomposing waste and processing mineral components, essentially driving nutrient cycles in ecosystems. Temperature, salinity, pH, and redox generate gradients regulating distribution of organisms and their metabolism, in effect the availability of resources (Schlesinger 1991).

Availability of resources, notably nutrients, is related to population dynamics, e.g., the life cycle of organisms, and community structure, such as food webs. Phosphorus, for example, is a commonly limiting nutrient in freshwater lakes that constrains productivity. While phosphorus can be introduced through external subsidies, the ecological community can influence availability of the resource

internally, thereby altering community composition. Certain zooplankton, for example, sequester phosphorous for their reproductive needs to the extent that they limit growth and abundance of competing species. These competitive interactions will ultimately affect water quality and physical characteristics, such as transparency and temperature profiles (Elser et al. 1998).

Physical–chemical conditions of the matrix drive enzymatic processes and affect habitat suitability and niche structure in ecosystems. Olff et al. (2009) proposed an additional horizontal ecological-stoichiometry axis to supplement the vertical trophic axis in food webs (Fig. 1). These frameworks build upon research in marine systems (Azam et al. 1983) and terrestrial systems (Bardgett 2005; Wardle 2002) that emphasize a 'dual foundation' for food webs based on both organotrophs and autotrophs.

3.3.3 Landscape

The landscape provides the physical structure for the ecosystem matrix, including habitat niches for organisms. Physical connectivity (e.g., wildlife corridors) can dictate the distribution and dispersal of organisms. As chemicals transition among media such as water, the atmosphere, and land they are modified in ways that alter their availability. Landscapes support a mosaic of abiotic conditions that determine the phase space of abiotic resources, including chemical state and suitability for uptake.

3.3.4 Ecosystem Engineering

Ecosystem engineering is the process whereby organisms influence the biophysical feedback mechanisms that structure their habitat. This can fundamentally alter ecosystem function from local to global scales (e.g., beaver dams to forest respiration). Ecosystem engineers influence the matrix in which they live, rendering it more or less habitable for themselves and their competitors (Jones et al. 1994; Wright and Jones 2006). In Australia, for example, a rabbit fence was built to confine expansion of invasive rabbits, altering patterns of herbivory that, in turn, affected evapotranspiration and regional precipitation. Ultimately, this altered the microclimate and suitability of the environment for multiple organisms and processes (Lyons et al. 1993). Feedback loops and cycles add complexity and nonlinearity to the system. They can lead to emergence of alternate stable states, with abrupt tipping points, where shifts to alternate regimes modify function and introduce chaos (Scheffer and Carpenter 2003; Carpenter et al. 2008; Huisman and Weissing 1999; Van de Koppel et al. 2001, 2005; Rietkerk 2004).

3.3.5 Relevance to Human Health

Ecosystem processes influence human health directly via interaction with toxins and nutrients, and indirectly via regulation of disease cycles and intensity. Bioaccumulation of toxins throughout food webs poses a health threat, an example of which is dichlorodiphenyltrichloroethane (DDT), effective in controlling disease vectors but endangering animal and human health by its bioconcentration. Ecosystems provide services such as sequestering toxins in wetlands and sediments, but these processes often are fragile and their disruption results in system-wide impacts. Nutrient enrichment, or eutrophication, of lakes has been directly correlated with prevalence of aquatic disease agents (Johnson and Carpenter 2008). Regulation of disease is an indirect ecosystem service. However, perturbations of ecological systems can alter the regulatory process and unleash novel pathogens, demonstrated vividly by Lyme disease and the dilution effect (Ostfeld and Keesing 2000).

4 Integrated Ecological Health Threats

In today's world, the biosphere is undergoing unprecedented anthropogenic ecosystem engineering, ranging from land conversion to ecological simplification and extensive biogeochemical change. The impact of these alterations spans ecosystem nodes, edges, and pathways with profound ramifications for ecosystem services and resilience. As the modified ecosystems and regimes emerge, their potential to impact human health must be understood.

Investigators have developed hotspot maps to characterize risk of disease emergence (Jones et al. 2008) and threats to biodiversity (Mittermeier et al. 1999). However, coupled socio-ecological models of risk have yet to be developed. As a network evolves, dynamic risk mandates continuous adaptive iterations to monitor emerging threats. The major drivers are direct anthropogenic land-use change, e.g., deforestation, agricultural expansion, habitat destruction, and complex indirect feedback from anthropogenic impact affecting biogeochemical cycles, e.g., nutrient cycles and climate change.

The phase space for ecosystems evolves as communities are restructured. Emerging systems are unstable and exhibit complex non-equilibrium dynamics and alternate states. Getting ahead of an epidemic curve (Fig. 2) requires more than simply aggregating concepts of populations, communities, or ecosystems (Schoener 1986). The changing network properties of the system must be monitored, along with indicators of resilience and leading indicators of collapse, if how a major disturbance is propagated or dampened through the system is to be understood. Failing to comprehend the emerging topology of coupled socio-ecological systems presents a challenge of Knightian uncertainty, where risk is immeasurable, and panarchy, where cause and effect are disproportionate. In these instances, disturbances can become amplified through emerging network dynamics.

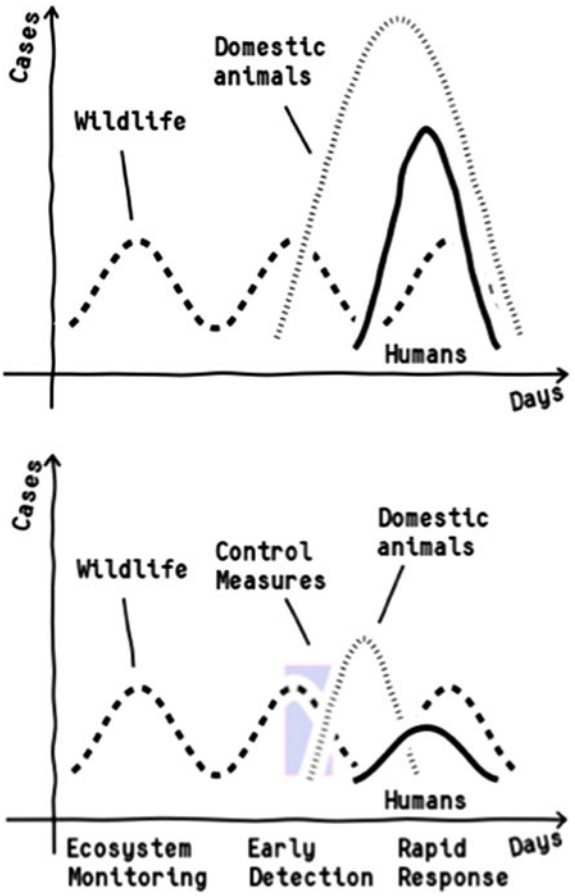

Fig. 2 An epidemic curve where the *upper* panel illustrates emerging infectious diseases fluctuating in wildlife populations through time before spilling over to domestic animals then humans. The *lower* panel demonstrates "getting ahead of the epidemic curve" whereby timely surveillance and control measures mitigate the impact of a disease outbreak through time

4.1 Land Use, Land Conversion, and Ecological Simplification

Changes like habitat destruction and land-use/land-cover change affect the physical structure of the environmental matrix and have profound impacts on ecosystems. They jeopardize critical services, e.g., disease regulation and other, as yet unknown, ecosystem services. For example, minor disturbances from deforestation in the Peruvian Amazon exposed frontier effects, whereby cases of infectious disease peaked with human encroachment, but re-stabilized as humans and pathogens adapted (Olson 2010). It is difficult to anticipate consequences of ecosystem encroachment since the dynamics are highly variable and outcomes unpredictable. However, in this case the system exhibited altered contact and transmission rates, as well as improved habitat for malaria vectors.

Genetic diversity dictates adaptability. We should anticipate widespread physiological, morphological, and behavioral adaptations with land-use change, and inevitable consequences for disease emergence. Geography and landscapes have long been known to play a critical role in disease, indeed the earliest disease maps by Finke and Humboldt date from the Early Victorian Period (Tylianakis et al. 2007). Hence, we can anticipate that landscape changes will fundamentally alter existing ecosystem networks. Changes at the landscape level, such as isolation due to habitat fragmentation, counter the trend of more highly connected systems. However, an increase in isolated systems may lead to increased genetic drift and introduce new vulnerabilities from founder effects and genetic bottlenecks. These refugia and biological corridors become hotspots for disease transmission as organisms are crowded out of the human landscape and stressed by reduced resource availability.

4.2 Biogeochemical Impacts

The Green revolution brought widespread alterations to global biogeochemistry. Accompanying changes in agricultural practice altered the agrarian landscape—an important habitat in terms of both surface area and productivity. In this context, biogeochemistry is particularly relevant to health, given anthropogenic modification of global processes. Following World War II, the industrial efficiencies of bomb factories were adapted to production of agricultural fertilizers. As a consequence, ecological stoichiometry was radically altered. In geological time, this is a short-term experiment and it is not yet clear what the long-term implications will be for global-scale ecosystem processes. Indeed, the fertilizers manufactured are typically nutrients that limit productivity. Hence it is inevitable that these will impact abundance and distribution of organisms, including disease hosts and vectors.

5 Ecological Influences on Disease: Abundance, Contact, Distribution, and Evolution

In 2004, researchers convened by the Wildlife Conservation Society (WCS) coined the term “One World–One Health,” at a time of increasing global interest in connections between emerging infectious diseases and environmental stewardship. What has become the One Health movement calls for interdisciplinary and cross-sectoral approaches to disease prevention, surveillance, monitoring, control, and mitigation, as well as environmental conservation. The goal of improving lives, with integrated health approaches, has been embraced by veterinary, medical, public health, agricultural, and environmental health organizations in the One

Health Initiative. This movement has helped integrate ideas from environmental, veterinary, and agricultural science with public health, and has been successful in bringing broader attention to socio-economic influences on human and animal health.

Ecohealth emerged in the 1990s from an interest in connecting ecosystems and health through the original work of the International Development Research Council (IDRC) (Lebel 2003). The Ecohealth community has since grown to include researchers from a broad range of disciplines, all of whom share an interest in the intersection of ecology and health.

Humans must be included in Ecohealth models and wildlife in One Health models. Otherwise, our understanding of disease risk cannot be complete. Conceptual and mathematical models from the social sciences and public health can usefully be combined with those developed for agriculture and ecology. Thus, the coupled socio-ecological models will allow characterization of emerging systems, with the challenge of capturing non-linear complex behaviors.

In conclusion, the dimensions of ecological approaches to public health that we propose in this chapter are, in essence, networks of population dynamics, community structure, and ecosystem matrices incorporating concepts of complexity, resilience, and biogeochemical processes.

6 Case Studies

6.1 Wolf and Moose Dynamics on Isle Royal

Disease emergence can strongly impact the abundance and diversity of wildlife populations. The dynamics of wolf and moose populations on Isle Royale is a classic case study. The single predator–prey dynamic is unique in its simplicity and is one of the longest studied. The system has never achieved equilibrium and cannot be explained either by top-down control of moose abundance by wolf predation or bottom-up control of wolf abundance by moose availability (Vucetich et al. 2011). Moreover, the system exhibits both influences, with episodic disturbances from disease and climate. The introduction of parvovirus by a domestic dog caused the wolf population to crash in 1980. Subsequently, the moose population exploded which impacted balsam fir, their winter food. Consequently, in 1996 the moose population crashed during a harsh winter. Moose are mega-herbivores (Owen-Smith 1988) that grow sufficiently large to escape predation from wolves, so wolves are only able to prey on the young and infirm. The moose are vulnerable to ticks, which contributes to poor body condition and makes them more vulnerable to wolf predation. Ultimately, the dynamics of an invasive disease agent influenced community structure, as did predation, resource availability, parasitism, abiotic conditions, and genetic diversity. These events challenged the certainty of

predictive models of population dynamics and community structure. This case study illustrates the difficulty of modeling EIDs in relation to ecosystem dynamics.

6.2 Ecology of Cholera

Correlation of the incidence and intensity of cholera, primarily a waterborne disease, with environmental parameters, e.g., temperature, salinity, nutrients, conductivity, and other factors, including rainfall, extreme weather events, and with access or lack of access of the populace to safe water and sanitation has been studied by many investigators over the past 20 years.

The observation of Colwell and Huq (1994) that the causative agent of cholera, *Vibrio cholerae*, is a commensal of zooplankton, predominantly copepods, led to examination of the annual incidence of cholera in Bangladesh. Controlling factors were determined to be water temperature and salinity, but also relationship to the annual cycle of plankton (Colwell 1996). The annual bimodal peaks of cholera in Bangladesh (Spring and Fall) correlated with plankton blooms in the spring and fall, with copepods proving to be a vector for *V. cholerae* (de Magny et al. 2008). Further studies, employing satellite remote sensing to monitor chlorophyll, sea surface temperature, and sea surface height in the Bay of Bengal, provided useful models of the relationship of cholera and climate (Lobitz et al. 2000). Refinement of the models and detailed analyses of the river system of the Ganges delta led to further and more detailed characterization of the drivers of the spring and fall cholera outbreaks, namely rainfall, river height and flow, and salinity (Jutla et al. 2010).

Cholera, and very likely other waterborne diseases, can be tracked to their environmental source (Jutla et al. 2010). Thus, ecology of the *V. cholerae* proved to be key in understanding incidence of the disease (Colwell et al. 1977; Lipp et al. 2002). Based on ecology and evolution of *V. cholerae*, predicting cholera incidence in various regions of the world is promising. In fact, preliminary results demonstrate effectiveness of regional hydroclimatology combined with satellite data for cholera prediction models for coastal regions in South Asia and Sub-Saharan Africa, providing lead time to strengthen intervention efforts before the seasonal outbreaks of cholera occur in these endemic regions.

6.3 Nipah Virus Emergence

The role of wildlife and livestock in the transmission of infectious agents to humans has been recognized for decades (Karesh et al. 2012). Zoonoses such as rabies remain endemic in wildlife and continue to spillover to people as they have done for probably centuries. However, the importance of wildlife from which

pathogens are transmitted has become critical in the era of EIDs. The majority of EIDs are zoonotic and originate in wildlife (Jones et al. 2008). Pathogens such as Nipah virus (NiV), SARS coronavirus, and Ebola virus originate in wildlife species from tropical or subtropical regions, where human population density is high, and rapid changes to the environment drive increasing risk of spillover. The role of ecology in understanding patterns of zoonotic disease emergence is significant and ecologists need to be integrated into One Health efforts.

Traditional epidemiological investigations of emerging zoonoses focus on the network of human cases affected by an EID, tracing back to origins and examining risk behavior. Unfortunately, studies tend to view the role of wildlife as a risk factor for spillover and rarely involve detailed studies of wildlife population dynamics. For example, fruit bats were identified as the reservoir of Nipah virus (NiV) in Malaysia and are, therefore, a risk factor for its emergence elsewhere. In Malaysia, NiV first emerged in pig farms close to fruit bat habitats. It was hypothesized that the intensive nature of the farms were the trigger for its emergence (Chua et al. 2000). An alternative hypothesis was that bats brought the virus into the country from nearby Sumatra following forest fires there during a severe El Nino event (Chua et al. 2002). A collaborative group including wildlife biologists, veterinarians, virologists, mathematical modelers, physicians, and epidemiologists collected and analyzed data on the hunting of bats, pig population dynamics at the index farm, large-scale movement of fruit bats and the capacity of the virus to survive in urine, saliva, and fruit juices (Pulliam et al. 2011). This work was able to demonstrate that the continued presence of bats in the index farm region, and the particular dynamics of intensive production allowed the virus to invade the pig farm, produce a partially immune population of pigs, then re-invade to create a long-term exposure of pig workers, and the large-scale outbreak observed (Pulliam et al. 2011).

Early epidemiological studies of the emergence of NiV in Bangladesh identified drinking of date palm sap as a risk factors, and suggested that this might be due to contamination of the collecting pots by fruit bats (Luby et al. 2006). Subsequent investigations involved wildlife biologists who used infrared cameras to confirm contamination in the field (Khan et al. 2011), and conducted longitudinal surveillance of bat populations to examine whether seasonal patterns exist that could be used to estimate risk. These studies demonstrate the value of analyzing wildlife reservoir ecology in tandem with epidemiological and specific disease investigations. Such an approach will become increasingly important, given the disproportionate rise in EIDs originating from wildlife over the last few decades (Jones et al. 2008).

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