Evolutionary and Ecological Perspectives

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A NEW SYNTHESIS: THE EVOLUTION AND ECOLOGY OF DISEASE

Evolutionary and ecological perspectives have transformed medical anthropology from a traditional focus on cultural aspects of health and healing and comparative study of medical systems to a broader perspective on human health in an environmental context. This transformation has been truly interdisciplinary. Medical ecologists, human biologists, and health practitioners have joined forces with epidemiologists, medical geographers, and medical historians to generate a new synthesis in the anthropological study of health. The scope of this review ranges from classic studies in medical ecology to current trends in Darwinian medicine, with focus on the history, methods, controversies, and debates associated with ecological and evolutionary perspectives in medical anthropology.

History

Field research in the mid-20th century on disease distribution and human adaptation in various habitats formed a solid foundation for foraging theoretical links among medicine, ecology, and evolution. In *The Ecology of Human Disease* (May, 1958), physician and geographer Jacques May applied spatial analysis to regional and cultural differences in malaria prevalence in Vietnam. Livingstone (1958) correlated hemoglobin frequencies with the histories of migration and ecological change in West Africa. Research on the microevolution of indigenous South American populations (Neel, 1971) generated profiles of genetic differences and disease resistance in relatively isolated foragers and cultivators. Research among high-altitude peoples by Baker and Little (1976) and colleagues revealed the physiological plasticity of humans and the limits to adaptability in rigorous environments. Field studies in subarctic regions (Steegmann, 1983) and in the Arctic (Laughlin, 1964) explored the subtle interplay of adaptive genetic, physiological, and behavioral responses to cold environments.

An early formulation of the connections between health practices and evolutionary theory was Alland's *Adaptation in cultural evolution: An approach to medical anthropology* (1970). This pioneering work helped to crystallize the emerging field of medical anthropology and provided models for studying the health repercussions of ethnomedical practices. In applying game theory and risk–benefit analyses to agricultural and dietary practices, Alland suggested that cultural evolution involved trial-and-error adaptive strategies.

The classification of medical ecology as a distinct subfield of medical anthropology was formulated in Fabrega's volume, *Disease and Social Behavior* (1974). Landy (1977, p. 12) noted that the ecological approach directly linked to evolutionary theory and held "great promise for anthropology." Anthropologists refined the concepts of ecosystem and evolutionary ecology throughout the 1980s, building on earlier formulations by Geertz (1963), Rappaport (1968), Steward (1955), and many others, and developing a new methodology for studying environmental variables in relation to subsistence, population size, and health (Moran, 1984). Regional field studies (cf. Schull & Rothhammer, 1990) and reviews of urban ecology and health in developing countries (cf. Schell, Smith, & Bilsborough, 1993) demonstrated the strengths of ecological models in research. With ecology and environment the central focus of several teaching texts (Moore et al., 1980; McElroy & Townsend, 2003; Townsend, 2000), the medical ecology paradigm has become well established.

Methods

Medical ecology is a theoretical orientation rather than a formal theory (Wellin, 1977), encompassing a broad systems approach in research. Hence the choice of research methods is eclectic, ranging from clinical measures (anthropometrics, fecal analysis for parasites, blood pressure readings) to standard ethnographic techniques (census and mapping, nutrition studies, geneaologies) to geographic information systems (GSI) analysis. Medical ecology is explicitly a field science, whether in rural or urban settings, with small-scale foraging societies or with migrants and squatter residents in large cities, and often involves multidisciplinary teams collaborating in data collection. Although traditionally the preferred field site has been one or a few isolated, indigenous communities, increasingly studies of human adaptation have shifted to regional analysis, systematic sampling, and incorporation of historical and economic variables (Moran, 2000, pp. xix–xx). The gold standard for studies of health in an environmental context included the collection of field data from a wide sample of households and communities, archival research on historic change, and ethnographic interviews to assess health behaviors and beliefs.

Evolutionary studies may involve the collection of samples in the field for later analysis, but research is also likely to take place in laboratories, using diagnostic equipment and computer analysis of genetic, demographic, and epidemiological data. Scholars of evolutionary medicine are often trained in physical anthropology and human biology, and some have medical degrees as well. Thus all the research methodologies of forensic anthropology, paleoanthropology, comparative anatomy, and clinical medicine can be put to use in testing hypotheses regarding the evolution of adaptive and maladaptive traits in various human populations.

ECOLOGY AND DISEASE

Medical ecology studies health and disease in an environmental context. Central to the model is the concept of ecosystem: a set of relationships among organisms within a given environment that provides both opportunities and constraints (Moran, 2000). The environment has three major components: biotic elements (sources of food, building materials, predators and vectors), abiotic (climate, solar energy, inorganic materials), and cultural elements (human systems). Each of these components play a central role in human well-being and survival.

Equilibrium and Change

Just as genetic variation and natural selection are key components of evolutionary medicine, models of equilibrium and change are central to medical ecology. Fluctuations among, or disruption of biotic, abiotic, and cultural subsystems are part of normal cycles and can be accommodated to a certain extent through a variety of adaptive mechanisms, both at the individual level and the population level. But when too severe an imbalance occurs, repercussions may include environmental degradation, loss of resources, population decline, changes in trophic (feeding) relations, and disease. This model suggests that the health of a population is a function of its ecosystem and of the adaptive mechanisms used by the population to maintain its place in the ecosystem (Moran, 2000). Yet adaptation does not always lead to optimal health; examples abound throughout history and prehistory of populations threatened by the long-term repercussions of their own subsistence, as well as of societal segments that do not benefit or flourish within the midst of profitable and productive economies.

When human activities (e.g., farming or building roads) disrupt the ecological niches of other fauna, subsistence changes may bring increased food security but also increased disease prevalence. On the one hand, the massive development projects of the last century have contributed to sharp increases in the incidence of previously endemic diseases. On the other hand, public health promotion of childhood immunization, nutritional supplements, improved water systems, and disease prevention have led slowly to the "epidemiological transition" of the 20th century, with lowered infant mortality and longer average life expectancy.

Infectious disease patterns vary by subsistence type and by region, but no society is free from disease. Medical ecologists are particularly concerned with "emerging" (and re-emerging) infectious diseases: HIV/AIDS, dengue fever, West Nile virus, antibioticresistant strains of tuberculosis, trypanosomiasis, schistosomiasis, Chagas' disease, and others. Malaria is among the most significant of the resurgent diseases. Once relatively contained by DDT, the anopheline vectors are now resistant to insecticides, and the parasites causing malaria have mutated into resistant strains. The current crisis in preventing malaria is due not only to biological change in disease agents, but also to poverty, malnutrition, and inadequate healthcare in the regions most sharply affected. This case demonstrates political ecology, an approach which includes economic and social factors in conceptual models (Brown, Inhorn, & Smith, 1996).

Reproductive Ecology

Human reproduction is affected by ecological factors such as seasonal variability in food, environmental carrying capacity, the production roles and spatial distribution in work of men and women, and diseases causing infertility or subfecundity (Townsend & McElroy, 1992). Studies of reproductive ecology have been carried out in isolated populations by Konner and Worthman (1980), Ellison (1990), and Binford and Chasko (1976). MacCormack (1994) was among the first anthropologists to focus on women as energy producers, with trade-offs between subsistence and reproductive roles. The idea of trade-offs, or reproductive compromises, is also fundamental in the work of Trevathan (1987), not only in a socio-cultural sense, but also in terms of the evolution of human fetal development and gestational parameters.

Controversies in Medical Ecology

Medical ecology has been criticized by cultural anthropologists and by critical medical anthropologists, who argue that adaptation theory, or "adaptationism," is politically conservative. Believing that adaptation theory explains poor health as evidence of “inferior genes,” some equate medical ecology to Social Darwinism. One positive outcome of this dialogue has been steps toward merging medical ecology and the political economy of health into a “political ecology of health.” This developing subfield holds promise for future research.

A second area of controversy is whether ecological models and methods, derived from studies of animal populations, can be applied accurately to human populations, given the far-reaching influence of culture. The concept of carrying capacity is particularly problematic, in the sense that it has been difficult to demonstrate that human regulation of family size or of sex ratios in offspring is directly related to environmental resources (Smith & Smith, 1994).

Despite these criticisms, medical ecology remains promising in the study of health in rigorous environments in which the limits of human plasticity and cultural ingenuity are tested. Traditionally these environments were those of climatic and barometric extremes. In recent years, extreme outposts such as Antarctic research facilities, submarines, and space stations have posed new challenges of crowding, isolation, and boredom. The application of medical ecology in these settings may prove productive in future research.

EVOLUTIONARY PERSPECTIVES ON DISEASE

Evolutionary perspectives encompass two dimensions: the evolution of disease organisms affecting human populations, and the impact of human biological and cultural evolution on the behaviors of these organisms, including interactions between vectors and hosts. Medical anthropologists also study evolutionary models of sickness behavior.

Evolution and Disease

Evolutionary medicine, also called Darwinian medicine, derives its intellectual and theoretical base from the theory of natural selection. Differences in mortality and reproductive success linked to genetic traits lead to the differential intergenerational transmission of those traits. Traits that emerge from random mutations and that prove beneficial in given environments are differentially transmitted and retained under selective mortality over many generations. Selective forces include climate, altitude, food availability, environmental hazards, and disease. \

Hypothetically, genetic variation providing resistance to infection, accommodation to nutritional deficiency, or acclimation to environmental constraints such as hypoxia are retained at varying rates in diverse populations due to differential survival and differential reproduction. That is to say, variants are correlated with increased Darwinian fitness. Stressors affecting the survival of children and the fecundity of young adults are most pertinent. While discrete genetic markers such as hemoglobin variants are easiest to correlate with morbidity, mortality, and fertility rates, behavioral traits may clearly correlate with fitness. Pregnancy management techniques, dietary patterns, birth systems, and infant care are non-genetic variables with immense importance in maternal and child survival rates in rigorous or pathogenic environments.

Differential fitness involves more than disease resistance, of course. The evolution of successful reproductive traits and strategies is a central interest in biocultural anthropology (Trevathan, 1987) and underlies much of "life history" theory (Hill & Hurtado, 1996). Parental care (especially maternal stimulation and bonding) has been studied in relation to normal and abnormal infant and child development in various environments, including historical conditions of extreme poverty in which child abandonment and infanticide were common (Hrdy, 1999).

The Evolution of Disease

In tracing the etiology of a disease or symptoms, evolutionary medicine distinguishes proximate and ultimate causation, following Mayr's 1961 dichotomy (Durham, 1991). The proximate cause of type II (non-insulin dependent) diabetes mellitus is the inefficient use of insulin by the body. Genetic predisposition to this type of diabetes, typically seen in older adults, appears maladaptive.
However, the ultimate causation in an evolutionary sense can be discovered in the pressures of prehistoric times. Given the unreliability and fluctuation in food supplies for foragers and cultivators, genes that increased the efficiency of energy extraction from food sources and increased storage of dietary energy would prove particularly critical for survival in times of food shortages or famine. However, contemporary populations who have inherited the trait, called a "thrifty genotype" (Neel, 1962), may find that this genetic pattern is no longer adaptive in situations of ample or excessive food supplies, especially carbohydrates.

Paradoxically, the concept of "adaptive trait" comes from analysis of homozygous inheritance of alleles leading to clinical problems such as sickle cell anemia, thalassemia, and G6PD deficiency (Greene & Danubio, 1997). In heterozygous inheritance, a modified genotype may change host characteristics so that a parasite cannot function normally, in many cases providing disease resistance or immunity. In homozygous form, the genotype may be deleterious to the host.

Evolutionary medicine provides clues for understanding chronic degenerative diseases (CDD) that affect elders in contemporary populations. The human species evolved over several million years in ecosystems unlike from the modified environments and subsistence patterns of the last 10,000 years. The human genome derived from a highly active, mobile lifestyle, an omnivorous, high-protein diet, a relatively short average life expectancy, and endemic parasitic infections. As Gerber and Crews (1999, p. 447) note, "alleles that have been retained in the gene pool are those associated with enhanced early survival, growth, development, and maturation to reproductive age, regardless of any lateacting detrimental effects they may have." Alleles that predispose individuals to physiological degeneration in mid-life, for example, through type II diabetes, gall bladder disease, autoimmune diseases, and hypertension, are examples of antagonistic *pleiotropy*, that is having opposite effects on fitness at different ages (Gerber & Crews, 1999, p. 446).

In addition to recasting the ailments of old age as evolutionary byproducts, Darwinian medicine also interprets health problems of youth, for example, neonatal jaundice, through an adaptive framework. Neonatal jaundice involves excessive bilirubin levels in the blood, indicating inadequate clearance of red blood cells and other proteins and slowed elimination of waste products through the intestinal tract. Elevated bilirubin can be toxic in the brain, leading to disability, hearing loss, or death (Brett & Niermeyer, 1999, p. 8). Since more than half of all newborns, especially breast-fed infants, develop jaundice in the first week of life without experiencing neurological complications, evolutionary medicine asks the logical question: Is this condition a disease? In the majority of infants, does it serve an adaptive function? Or was it adaptive in our evolutionary past? Brett and Niermeyer (1999, pp. 9, 14–15) suggest that bilirubin serves as an antioxidant in a stressful, relatively oxygen-rich environment. The infant's antioxidant enzyme defenses are immature in a situation of exposure to high levels of oxygen free-radicals in the lungs. Thus elevated levels of bilirubin may provide a selective advantage.

Similar analyses have been applied to infant colic, a mysterious condition of prolonged crying that seems to peak at two months and then gradually dissipates. In an evolutionary sense, crying represents an infant's communication to elicit feeding and care. Because care-givers and infants are often spatially separated in contemporary households, infant crying may be prolonged and fretful because of the difficulty of securing feeding and comfort.
Rather than treating the infant, the implications of this perspective is that parental care-giving patterns could be modified (Barr, 1999).

The Evolution of Healing Behaviors

Current interpretations of the origins of health-maintaining behaviors and of medical systems posit the evolution of "healmemes" in higher primates and in humans (Fabrega, 1997, p. 184; the term *meme* comes from Dawkins, 1982). A *healmeme* is a unit of information or instruction learned by an individual in dealing with pain, injury, or illness. This unit is stored in the brain and later communicated and transmitted to others. It is not a genetic trait, but if it has beneficial effects at the individual or group level, it will be retained. If not, it will be deselected.

More firmly rooted in genetic evolution, according to Fabrega (1997, p. 31), is the biological adaptation for sickness and healing, termed the SH adaptation. Elements of this adaptation include seeking relief for pain, communicating pain and distress through gestures and vocalization, and seeking or giving help to conspecifics. Nurturing and carrying helpless members of the group, sharing food and water, and direct healing actions (e.g., licking wounds, pressure to stop bleeding, resting to conserve energy) are other examples. Specific SH behaviors are not necessarily instinctive, especially in social animals. What is genetically programmed or "wired in" (Fabrega, 1997, p. 34) is the propensity to seek help and to give help when injury or illness occurs, or when problems arise such as parasite infestation (hence, grooming behaviors). Other aspects of the adaptation include "curiosity about sickness, some fascination with its manifestations, a compassionate appreciation of its burdens, and attempts to reverse its morbid effects" (Fabrega, 1997, p. 38). These components form the basis for the evolution of medical systems in human groups.

Applications of Evolutionary Theory to Cultural Variation

In recent decades, medical anthropologists have been searching for evidence of feedback loops between cultural variation, population dynamics, health, and genetics in the controversial field of Darwinian medicine. The theory of evolution itself, and the role of cultural factors in adaptive change, is being re-examined. For example, coevolution, "a theory of evolution by *cultural* selection" (Durham, 1991, p. 38), is believed to parallel organic, molecular evolution.

An example illustrating links between cultural variation and evolution is the unusual degree of diversity in Tibetan marriage systems, including polygyny, polyandry, polygynandry, and monogamy. This variation, in Durham's view (1991, pp. 59–70), is a solution to female and male infertility. It allows an infertile couple to bring an additional wife, husband, or *p'horjag* ("extra man") to the household so that heirs could be produced. It also allows considerable economic flexibility, a benefit in a high altitude ecosystem with low and seasonal productivity of scarce arable lands (Durham, 1991, p. 71). Parenthetically, similar flexibility in household structures and marriage forms were found traditionally in Arctic peoples for many of the same reasons.

Co-evolution theory does not imply that variation in marriage forms is genetically programmed. Rather, behavioral diversity parallels genetic diversity, and both lead to optimal flexibility in environmental uncertainty. The enhanced fertility of households contributes to reproductive success, while the marriage systems themselves are preserved due to their "replicative success" in achieving benefits to the household and the community (Durham, 1991, p. 78).

Controversies in Disease Evolution Studies

Physical and biocultural anthropologists have long argued over the issue of indigenous responses to viral and bacterial pathogens of historical import, for example, measles, smallpox, and malaria. Most indigenous populations experience high morbidity and mortality from diseases introduced by explorers and settlers during early contact. The reasons suggested for heightened susceptibility of native peoples range from inability to form antibodies (Black, 1975) to the synergism of malnutrition, stress, and disease exposure in conditions of contact (Cook, 1976). Other researchers have attributed high mortality during epidemics to the collapse of social structure, community provisioning, and care systems (Neel, 1970). Psychological reactions involving apathy and hopelessness contribute to dehydration, malnutrition, and increasingly lowered resistance to secondary infection.

Evolutionary medicine has proposed explanations for an array of modern ailments ranging from obesity to lower back pain, asthma, otitis media, depression, and addictions. Allergies, for example, are thought to be related to originally adaptive responses to parasitic infections (Nesse & Williams, 1994). Even more problematic are evolutionary explanations for current behavioral aberrations, such as homicidal assault, sexual abuse and incest, depression, and infanticide. Intellectually it may be satisfying to link contemporary ills to past conditions, but the extent of genetic determinism is problematic.

SUMMARY

Medical anthropologists trained in many specialties are developing models of evolution and ecology to explain and predict factors affecting the well-being of individual organisms, growth or decline of various populations, and the survival of the human species. As the human genome is mapped and analyzed by biologists and biocultural anthropologists, evidence of the connections between environmental adaptation and genetic change will become increasingly clear.

At present we have relatively few strong cases linking evolutionary change to historically documented ecological change.

A classic case involves cultural shifts to agriculture in West Africa some 4,000 years ago, leading to increased prevalence of particularly lethal forms of malaria. In this case, natural selection for alleles providing resistance to malaria (e.g., hemoglobin variants such as S, C, and E and enzyme deficiencies such as G6PD) provides a clear example of genetic adaptation to environmental perturbations (Greene & Danubio, 1997). Medical geographers and physical anthropologists continue to look for equally strong evidence for population resistance to plague, tuberculosis, smallpox, syphilis, and other diseases that have changed the course of human history. With suitable models of disease ecology and evolutionary mechanisms, medical anthropologists may contribute to future understanding and prevention of disease, disability, and environmental disequilibrium.

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