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Regulating Services: A Focus on Disease Regulation

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Over the past few decades there has been an explosion of interest in the ecology of infectious diseases and their roles in ecosystem function. Many studies have focused on the dynamics of pathogens within human, other animal, and plant populations and their role in causing mass mortality events and population declines. Other researchers have focused on diseases that are increasing in incidence or geographic or host range—"emerging" infectious diseases—of humans, wildlife, and plants.

However, relatively few researchers have approached disease ecology in the context of ecosystem services, where diseases, parasites, or pathogens perform functions potentially useful to humans. In this chapter, we review the literature on three aspects of parasites and pathogens in the field of ecosystem services. The first is probably the most well known: their role in morbidity and mortality to their hosts, through which they disrupt the host's ability to provide an ecosystem service, i.e., disrupting the survival or life-history success of ecosystem service providers. The second is the role of pathogens as regulating service providers by suppressing populations of pest species, resisting invasion, and acting as biocontrol agents. The third aspect is poorly understood but a subject of growing interest: rather than parasites performing the service per se, it is the role of species, communities, and biodiversity in regulating the risk of infectious diseases to people, i.e., performing a regulating service, that reduces disease risk. The thrust of our chapter is to review the state of the field, and we have paid particular attention to highlighting those areas where future research is likely to be most fruitful and to identifying strategies to take the field forward. We have therefore added a fourth section that discusses efforts and strategies to estimate the value of pathogens and the cost of their impact on natural capital and ecosystem services.

GLOSSARY

density dependent. A density-dependent process varies with the population density of the species concerned. For instance, below a certain host population size, parasitic infections may not occur (there are not enough hosts for the parasite to be transmitted between them), whereas above a certain host population size, parasitic infections may become prevalent. The probability of any individual host getting infected depends on the density of surrounding hosts.

emerging infectious disease. A disease that has recently and significantly increased in impact, in the number of cases it causes, or in its geographic range; a disease that is caused by a newly evolved pathogen or has recently been transmitted from one species to another to result in an outbreak in the new host species.

parasite. An organism that resides within or on, and is nutritionally dependent on, another organism. In this article, we include all forms of infectious microbes, including viruses, prokaryotes (e.g., bacteria), and eukaryotic parasites (e.g., roundworms).

pathogen. An infectious agent or parasite that causes illness in its host, usually defined as clinical illness, i.e., causing significant pathology or damaging physiological change.

1. INFECTIOUS DISEASES AS DISRUPTERS OF ECOSYSTEM SERVICES

Infectious diseases have been reported to be the cause of morbidity and mortality in a range of key ecosystem service providers (ESPs) (table 1). In these cases, pathogens act as "mediators" of the loss of ecosystem services and effectively perform an "ecosystem disservice." The impact of pathogens is greatest when they cause population declines of keystone species or ecosystem engineers. For example, the death of one-third of the Serengeti lion population caused by canine distemper (a disease introduced via domestic dogs) had a disproportionate impact on the ecosystem. Pathogens sometimes spread rapidly through highly susceptible host populations, which include host populations that have not evolved in the presence of the pathogen. Introduced pathogens may also impact abundant species at lower trophic levels and have similarly dramatic effects on ecosystem services.

Human attempts to control or manage diseases can also have unanticipated ancillary impacts (either positive or negative) on ecosystem services. The introduction of rinderpest into Somalia in 1889 with imported domestic cattle led to a pan-African outbreak and widespread loss of livelihood as it caused the death of millions of domestic and wild ungulates and ecosystem collapse over large areas. But it also provides an example of positive ancillary impacts: the widespread removal of cattle in many regions also removed a major host for tsetse flies (*Glossina* spp., vectors for trypanosomiases including African sleeping sickness). This opened areas for productive human activities that would otherwise have been endemic zones for disease. Examples of human response with negative ancillary impacts are often found when the presence of dangerous pathogens in wildlife reservoirs leads to calls for culling, reducing, or eliminating wildlife and, thus, the positive services the wildlife might provide. For example, the presence of rabies virus in vampire bats (which feed on people as well as cattle and other livestock in Latin America) has led to indiscriminate culling of wild bats and to population declines of bat species that control agricultural pests and pollinate fruiting trees. Similarly, the controversial culling of badgers in the United Kingdom to reduce the risk of transmission of bovine TB (which they carry) to cattle reduces the population of a keystone species, which is also a subject of much cultural and ethical value. Ironically, culling in this case may increase disease incidence in surrounding areas as a result of increased movement by badgers following culling. Thus, both the direct effects of disease on wildlife populations and the impacts of human attempts to control the spread of the disease within the wildlife population or to new hosts can create ecosystem services or disservices. The complexity of disease and host interactions is a running theme of this chapter and makes the ecosystem service role of pathogens difficult to assess and anthropogenic impacts difficult to measure. For example, the introduction of West Nile virus into the United States in 1999 has led to increased use of insecticides, larvicides, and other control activities with unknown, and likely complex, impacts on ecosystem services.

2. DISEASES AS PROVIDERS OF REGULATING ECOSYSTEM SERVICES

A number of studies have demonstrated the ability of some communities to resist invasion—a regulating service that can be a function of diversity or species composition. Can this be extrapolated to infectious diseases within a host? Here, the presence of a pathogen or community of pathogen species could act to resist invasion of an introduced related pathogen. There is a growing literature on competitive or facilitative interactions in parasite coinfections, and evidence indicates that pathogen and parasite interactions play significant roles in host–parasite ecology, prevalence of infections, and impacts on hosts. The role of parasites in invasion resistance has been hypothesized for the poultry bacterium *Salmonella gallinarum*, which has been largely lost from domestic chickens following the routine prophylactic use of antibiotics to combat other ubiquitous poultry pathogens. The most common *Salmonella* sp. in domestic chickens in developed countries is now *Salmonella enteritidis*, a mouse microbe that appears to have jumped host in the absence of the chicken endemic *S. gallinarum*. Both pathogens share the same epithelial cell receptors, and it is hypothesized that the presence of the former prevented the latter from emerging—a population-scale ecosystem service. At a regional scale, it has been hypothesized that the presence of endemic flaviviruses in Central and South America may act to dampen the impact of West Nile virus (another flavivirus) in the region through cross-immunity or evolutionarily acquired resistance.

Pathogens also provide an ecosystem service by naturally suppressing pest species and through their use in the development of biotechnological tools to deal with pests or other pathogens. The most important example of the latter may be seen when pathogens have been used in or proposed as biological control agents. This has been reviewed widely in the literature, and notable examples include the use of *Myxoma* virus and rabbit calicivirus disease to control introduced rabbit

Table 1. Diseases as disrupters of ecosystem services

Disease	*Pathogen*	*Host*	*Ecosystem service*	*Impact on ESP*
Colony collapse disorder	Israeli acute paralysis virus (IAPV) in consort with other pathogens or factors	Honeybees	Pollination	Large-scale loss of populations across United States
Tasmanian devil facial tumor disease	Infectious clonal tumor	Tasmanian devil	Pest control, scavenging	Large-scale population declines
West Nile virus encephalitis	West Nile virus	Vertebrates	Seed dispersal, insect pest control, scavenging	Large-scale population declines
Amphibian chytridiomycosis	Fungus *Batrachochytrium dendrobatidis*	Amphibia	Pest control, water quality control (larvae feeding on algae), genetic resources of biomedical potential (e.g., gastric brooding frogs, dendrobatid frogs)	Large-scale declines globally, species extinctions (up to a quarter of the genus *Atelopus*)
Chestnut blight	Fungus *Cryphonectria parasitica*	American chestnut	Primary productivity, disturbance regulation	Effective extinction of codominant species in United States
Pilchard herpesvirus disease	Pilchard herpesvirus	Pilchard	Secondary productivity	Large-scale mortality events
Ebola virus disease	Ebola virus	Nonhuman primates	Ecotourism, harvesting for food	Large-scale mortality of gorillas and other nonhuman primates in Africa
Avian influenza	H5N1 avian influenza	Waterbirds, poultry	Food	High mortality rates in outbreaks in Asia, Africa, and Europe
Rabies	Rabies virus	Range of wild carnivores, bats, people, other vertebrates	Pest removal, pollination and others	Wild animals culled in response to disease risk, some species inadvertently removed when targeting reservoirs

populations, *Bacillus thuringiensis* genes to control insect pests of agricultural crops, and *Bacillus* spp. toxins to kill mosquito larvae. The challenge for this, and other efforts in biocontrol, is to achieve the desired goal (often suppression of populations of one species or group of species) without substantial impacts on nontarget species.

Pathogens also perform this function naturally, through density-dependent reduction of host population growth. Where anthropogenic activities increase the population density of pest species, pathogens that are transmitted in a density-dependent manner tend to infect more hosts, cause more morbidity and mortality, and ultimately reduce the population growth of the host.

When pathogens emerge from wildlife into people, we respond as a species with high-tech strategies such as vaccines and drugs. Many of these vaccines and drugs are based on lab tests developed from other recently isolated pathogens; e.g., the serological tests for Nipah virus were originally based on antibodies to a related virus, Hendra virus; likewise, tests for H5N1 avian influenza originally relied to a large extent on genetic information and research on other strains of influenza. Thus, once a pathogen has emerged, other related pathogens perform an ecosystem service in supplying genes and reagents to be used in biotechnology. The rapid growth of biotechnological tools over the past few decades suggests that this is likely to be an important aspect of pathogen ecosystem services that is currently underestimated.

Pathogens as Providers of a Supporting Service: Maintenance of Biodiversity

Pathogens may act as ecosystem service providers by natural suppression of their hosts, which may be community dominants, pest species, or introduced species. The role of pathogens in maintaining the diversity of communities is becoming increasingly evident and indicates that pathogens are providers of a supporting ecosystem service: maintenance of biodiversity. Pathogens may suppress community dominants and thereby provide frequency-dependent selection between species, especially when pathogens are density dependent. More recently, it has been suggested that the absence of pathogens from their native ranges has facilitated the invasion of introduced species of both plants and animals. Similarly if pathogens are fundamentally involved in driving the evolution of sex, then they have played (and continue to play) a vast role in driving increased rates of evolution of biodiversity.

3. ECOSYSTEM REGULATION OF INFECTIOUS DISEASES

We can examine the role of parasites in ecosystem services from an alternative perspective, that is, not as the organisms performing the service per se but from ecosystem services that species, communities, and biodiversity perform in regulating the risk of infectious diseases to people. There is increasingly compelling evidence for this, particularly where anthropogenic disturbance has been linked to increases in either disease or disease risk, including Lyme disease, Leishmaniasis, malaria vector biting rates, and monkeypox. Several mechanisms have been proposed to explain the increased disease risk in disturbed areas, including better habitat for disease vectors, increased human incursion into natural areas, and changes in the host community, all of which lead to increased contact between reservoir hosts and humans.

It has been hypothesized that biodiverse and intact ecosystems have lower prevalence of disease-causing pathogens than do anthropogenically disturbed, species depauperate ecosystems because the more diverse communities contain, on average, less competent hosts for pathogens. This idea builds on an old disease control strategy known as zooprophylaxis in which an incompetent host (e.g., cattle for malaria) was used to deflect mosquito blood meals from competent hosts (in this case humans) that would otherwise have infected vectors feeding on them. In a natural ecosystem context, it has recently been expanded for Lyme disease, where it was hypothesized that the prevalence of *Borrelia burgdorferi* (the causative agent of Lyme) would be lower in intact forest than fragmented forest patches. The mechanism proposed for the observed pattern was a higher diversity of mammals in larger forest patches that would be, on average, less competent hosts than the few species (e.g., white-footed mice, *Peromyscus leucopus*, and eastern chipmunks, *Tamias striatus*) remaining in small forest patches. Substantial modeling work has supported this mechanism in principle, although so far, no published multisite field study has provided evidence that a mechanistic link exists between the biodiversity at a site and Lyme disease risk. A key issue is whether diversity, per se, or species composition plays the more important role in regulating pathogen prevalence.

Thus, substantial work remains to determine the mechanisms by which biodiversity and intact ecosystems regulate disease risk. Both positive and negative impacts of biodiversity on pathogen prevalence are to be expected. For example, some pathogens have complex life cycles and multiple hosts or require specific microclimates that are only present in intact communities.

Thus, loss of biodiversity may reduce the risk of these diseases affecting humans, as one or the other of their hosts disappears. In contrast, for other pathogens, the vectors or amplification hosts are human commensals (i.e., species that live near humans, like house mice), and anthropogenic disturbance thus facilitates pathogen transmission. Finally, regions of high biodiversity may be the most important source of new pathogens of humans and livestock. Many potentially zoonotic pathogens exist in biodiverse ecosystems, and the intrusion of humans into natural habitats and contact with wildlife (e.g., by hunting for bush meat) may be the most important mechanism facilitating disease emergence. One could view conservation programs that preserve high biodiversity in a region (and therefore high biodiversity of pathogens) as providing a risk of future disease emergence. However, a more accurate view is that encroachment (e.g., through road building and deforestation) into these areas provides the risk of emergence, and therefore, preserving areas of high biodiversity against development performs an ecosystem service by reducing the likelihood of human contact. This is discussed further in section 4, below.

Ecosystem Management of Disease Risk

Our review demonstrates that the successful management of disease through an ecosystem approach requires a detailed understanding of the ecology of pathogen transmission, the diversity of pathogens in the host community, and the impact of anthropogenic disturbance on host and vector communities. Successful management may entail setting aside habitat where pathogens are present and minimizing human and domestic animal intrusion. Alternatively, management may require suppression of particular host or vector species through habitat alterations. However, challenges exist with the latter strategy because benefits obtained through habitat conversion (e.g., draining wetlands for mosquito control) may be less than any cost of lost ecosystem services (water filtration, flood control). Management may involve promoting land use practices that preserve large fragments of intact forest rather than reducing forest patches to sizes that may promote the dominance of disease reservoirs. This may be a valid strategy for Lyme disease, which may be more prevalent in small forest patches because of increased density of one of its key rodent reservoirs, the white-footed mouse. Similarly, maintenance of intact ecosystems may reduce the invasion of introduced mosquitoes and the emergence of a range of diseases. However, benefits of increased disease control would have to be compared to other advantages of converting habitats or reducing patch sizes of managed habitats.

Other strategies to reduce disease risk might include social behavioral modifications. These include domestication of hunted animals to reduce high-risk contact with disease reservoirs, the introduction of domesticated food animal production to a region to reduce bush meat hunting, or anthropogenic removal of disease reservoirs. However, these can also have significant negative impacts. The first may result in the spillover of unknown pathogens into human populations [e.g., Severe Acute Respiratory Syndrome (SARS) coronavirus, which was harbored by domesticated civets and other species in wildlife markets in China]. The second approach may result in the spillover of wildlife pathogens into high-density livestock populations and ultimately into people (e.g., Nipah virus in Malaysia, which was transmitted from bats to pigs to people). The third can reduce populations of keystone species dramatically if not properly regulated (e.g., wolves in the United States) and may have the counterintuitive effect of increasing pathogen prevalence and disease risk in some situations.

4. VALUING THE ECONOMIC IMPACT OF PATHOGENS AND THEIR ECOSYSTEM SERVICES

Early publications on ecosystem services tended to focus on valuing biodiversity and intact ecosystems through the services they provide. There are very few studies that estimate the value of the positive benefits of pathogens, parasites, and diseases. The value of pathogens has largely been estimated through their negative impact on human health (i.e., morbidity and mortality) and on economic activities (e.g., trade and travel), and that is what we concentrate on in this section. The costs of disease outbreaks may be dramatically heightened by the high cost of technologically advanced health care (e.g., the cost of intensive care for acute infections of pathogenic viruses) and by the cost of quarantine and vaccination programs to prevent further spread (e.g., the high cost of the SARS outbreak was largely caused by measures taken to avoid further spread). The annual cost of *E. coli* 0157 in the United States has been estimated at US$405 million (in 2003 dollars), and the economic burden of Lyme disease treatment in the United States may reach $500 million per annum. Costs are incurred even in the absence of medical cases when the public perceive a high likelihood of infection or outbreak. For example, a single rabid kitten found in a pet store in New Hampshire in 1994 led to treatment with expensive postexposure prophylaxis (currently ~$1000/patient) for 665 people who had visited the store, even those who had not made contact with the kitten. These medical costs may be dwarfed by the costs of pathogens to livestock production and agriculture, both of which are intrinsically linked to ecosystem services. Even the costs of proactive (prophylactic) efforts to deal with pathogens can be substantial because they underlie much of the global effort in plant and animal breeding, the continual development of efficient housing and feeding regimes for livestock, and chemical treatment of crops and food products. For example, in the largest ever program to eradicate a plant disease, the U.S. government spent $200 million in citrus canker eradication in the mid-1990s, clear-cutting 1.8 million infected trees. Preharvest pest and disease damage combined to the eight most important crops accounts for 42% of attainable production, or US$300 billion globally, although it is not known how much of these are disease related versus insect pest related. Simple analyses of the cost of livestock diseases that do not account for the complexities mentioned above still produce extremely high values. For example, the 2001 food-and-mouth disease outbreak cost between $8 and $18 billion to the U.K. economy through lost production, lost travel, and lost trade.

Perhaps the greatest economic impact of infectious diseases occurs where they directly affect trade and commerce on a global scale. For example, the emergence of SARS in 2003 in China, and its subsequent spread throughout Southeast Asia, then globally, likely resulted in the loss of between $30 and $100 billion dollars to the global economy. This impact was largely because of the reduction in travel to the region, subsequent loss of trade, and ripple effects as the economies of other countries that traded with those most severely hit were themselves affected. The economic impact of H5N1 avian influenza, should it become a self-sustaining human pandemic, is estimated to be between $100 and $800 billion globally, and between $71.3 and $166.5 billion in the United States alone. Projections of future trends in globalized travel and trade suggest a steady increase in the percentage of global GDP per capita spent on these activities and a concomitant increase in the risk of future pandemic emergence. This suggests that the future cost of pathogens is likely to rise through this impact.

It is likely that the economic cost of pathogens that affect wildlife, wild plants, or other components of ecosystems will be even higher than the global economic burden of diseases to human health. However, few studies have analyzed this. One recent study suggested that diseases introduced into the United States cost around US$41 billion per annum by affecting humans, livestock, and crop plants. However, these estimates were made before the introduction of West Nile virus into the United States (which has likely increased the cost significantly), and they have not been extrapolated globally. They also do not value the complexities of ecosystem services, wherein diseases may remove a flagship forest species (e.g., loss of dogwood trees caused by dogwood anthracnose) or involve a direct risk to human health (e.g., presence of Lyme disease or West Nile virus in a region) and reduce the desirability of a region for hiking or as a place to live. Any of the recent efforts to include diseases in valuation of biological capital or ecosystem services are therefore likely to be gross underestimates. Given the rapidly increasing knowledge on the wide array of wildlife pathogens that continue to be discovered and the global nature of the problems associated with disease emergence, the true cost of diseases to ecosystem services is likely to be orders of magnitude higher than the recent estimates. Clearly, this is an area where future research will be extremely illuminating.

Valuation of the cost of pathogens in wildlife or wild plant communities can be relatively straightforward, especially where these communities are cropped or harvested by people for direct economic gain. From the ecosystem service perspective, diseases directly reduce natural capital (raw materials, food production, etc.) but also reduce the economic margins of industries that use renewable natural resources (e.g., forest harvesting, fishing). Studies that have quantified the impacts of diseases in this respect usually consider single outbreaks or single pathogens. For example, a pilchard herpesvirus emerged in Australia during the 1990s, producing repeated outbreaks, and was thought to have been introduced with South American pilchards used to fatten tuna in fish farms. This disease is estimated to have cost AU$12 million over 3 years in 1997 dollars. Chronic wasting disease of wild deer, elk, and other species in the United States and Canada is a prion disease similar to "mad cow" disease, bovine spongiform encephalopathy, which emerged in the United Kingdom in the 1980s when changes in the rendering process meant that less intensively processed cattle protein was fed back to cattle. Chronic wasting disease cost around $10 million to the state of Wisconsin and $19 million to the state of Colorado in 2002, largely because of the loss of hunting license revenue and increased surveillance and control activities. The introduction of African horse sickness into Spain in the 1990s resulted in the slaughter of 146 horses and other control measures costing an estimated $20 million at the time.

The difficulties in assessing the economic cost of pathogens are increased when the complexity of human responses to their diseases is included. For example, the control of reservoir hosts (e.g., bats for rabies, badgers for TB) has an uncalculated and likely diverse impact on the value of ecosystem services (see above). Likewise, control programs that target the (usually arthropod) vectors of human diseases can result in removal of related vectors along with other species and a cascade of ecosystem impact. For example, DDT, although effective in controlling disease vectors (mosquitoes and other insects), was bioaccumulated in the food chain and led to dramatic declines of top bird predators in the United States, Europe, and other regions. Other vector-control programs, such as the draining of wetlands, may be equally expensive if their true (or full) cost is assessed.

The accurate valuation of the cost of wildlife diseases that affect hosts without direct marketable value is also difficult and has not been attempted for most cases. If we consider the growing recognition of emerging infectious diseases as a cause of wildlife biodiversity loss, efforts to assess the cost of some of the most significant of these (e.g., amphibian declines caused by disease, and the loss of potential medical drugs) would be useful. We can hypothesize that the global spatial distribution of the risk of disease emergence to ecosystem services is likely to markedly change previous assessments. Recent work on trends in disease emergence in humans shows that the risk of emergence is greatest where the pathogen diversity is highest (i.e., the tropics), where wildlife host biodiversity (and therefore the overall number of pathogen species able to emerge) is greatest. The tropics are also an area of high ecosystem service value. Thus, the cost of anthropogenic activities in these regions that facilitate disease emergence is heightened when diseases are taken into consideration. Testing this hypothesis may provide important insights in economics, public health, ecology, and wildlife health.

These preliminary thoughts on valuation of pathogen impacts on natural capital and ecosystem services provide some interesting conclusions for balancing the cost-effectiveness of human activities. First, they support previous calls for wildlife disease emergence impact statements; second, they suggest that activities with a high risk of disease spread or emergence (e.g., global trade in animal products, bush meat hunting) have a higher economic cost than previously proposed; third, they highlight the complexity of pathogens and parasites within ecosystems such that any single human activity can have multiple outcomes when diseases are incorporated into the analysis. These all suggest that accurate analyses will be difficult but ultimately extremely worthwhile.

The examples given above all highlight the large number of studies that value the cost of diseases on humans, livestock, and (albeit less well understood) on ecosystems. There is a dearth of information on the value of the benefits of parasites to ecosystems. One potentially important "value" of an ecosystem service related to parasites is in the finding that higher biodiversity of wildlife tends to produce a higher risk of emerging diseases because of the higher diversity of pathogens that these wildlife harbor. It might be argued, therefore, that intact ecosystems provide a regulating service by preventing the emergence of these diseases. The emergence of almost all emerging infectious diseases (EIDs) is driven by a series of anthropogenic factors, including demographic changes (e.g., increases in human population density leading to the emergence of dengue hemorrhagic fever); socioeconomic changes (e.g., increased injection drug use leading to HIV/AIDS spread or global trade leading to the pandemic emergence of West Nile virus and SARS); or anthropogenic environmental changes (e.g., changes in forest cover leading to the emergence of Lyme disease). Where land use changes involving degradation of intact habitat cause disease emergence, the intact ecosystem could be considered to hold latent ecosystem service value in preventing the emergence of these diseases. For example, road building and deforestation in tropical forests have been linked to the emergence of HIV/AIDS (through increased human activity in African forests and increased contact with the wildlife reservoir of HIV-1's nearest relative, the chimpanzee), and mining activities in tropical forests have led to the emergence of Ebola and Marburg viruses. The value of these ecosystems in preventing disease regulation is in not modifying them and preventing contact that would allow disease emergence (i.e., reducing socioeconomic pressure on a region with high biodiversity). This is supported by recent analyses of the drivers of EIDs. The emergence of zoonotic diseases from wildlife, which are among the most common and highest-impact EIDs, is significantly correlated with wildlife biodiversity and socioeconomic factors such as human population density and growth. Because human population density, deforestation, road building, and globalized travel and trade are all predicted to increase in the near future, the rate at which new zoonotic diseases emerge from these biodiverse "EID hot spots" is also likely to increase.

FURTHER READING

Anderson, P. K., A. A. Cunningham, N. G. Patel, F. J. Morales, P. R. Epstein, and P. Daszak. 2004. Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. Trends in Ecology and Evolution 19: 535–544.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife: Threats to biodiversity and human health. Science 287: 443–449.

Hudson, P. J., A. P. Dobson, and K. D. Lafferty. 2006. Is a healthy ecosystem one that is rich in parasites? Trends in Ecology and Evolution 21: 381–385.

Hudson, P. J., A. Rizzoli, B. T. Grenfell, H. Heesterbeek, and A. P. Dobson. 2002. The Ecology of Wildlife Diseases. Oxford: Oxford University Press.

Jones, K. E., Nikkita G. Patel, Marc A. Levy, Adam Storeygard, Deborah Balk, John L. Gittleman, and Peter Daszak. 2008. Global trends in emerging infectious diseases. Nature 451: 990–993.

Kilpatrick, A. M., A. A. Chmura, D. W. Gibbons, R. C. Fleischer, P. P. Marra, and P. Daszak. 2006. Predicting the global spread of H5N1 avian influenza. Proceedings of the National Academy of Sciences U.S.A. 103: 19368–19373.

Kremen, C., and R. S. Ostfeld. 2005. A call to ecologists: Measuring, analyzing, and managing ecosystem services. Frontiers in Ecology and the Environment 3: 540–548.

LaDeau, S. L., A. M. Kilpatrick, and P. P. Marra. 2007. West Nile virus emergence and large-scale declines of North American bird populations. Nature 447: 710–713.

Morse, S. S. 1993. Emerging Viruses. New York: Oxford University Press.

Ostfeld, R. S., and K. LoGiudice. 2003. Community disassembly, biodiversity loss, and the erosion of an ecosystem service. Ecology 84: 1421–1427.

Patz, J. A., P. Daszak, G. M. Tabor, A. A. Aguirre, M. Pearl, J. Epstein, N. D. Wolfe, A. M. Kilpatrick, J. Foufopoulos, D. Molyneux, D. J. Bradley, and The Working Group on Land Use Change and Disease Emergence. 2004. Unhealthy landscapes: Policy recommendations on land use change and infectious disease emergence. Environmental Health Perspectives 112: 1092–1098.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50: 53–65.