

CHAPTER THIRTEEN

Disease Effects on Landscape and Regional Systems: A Resilience Framework

*F. Stuart Chapin III, Valerie T. Eviner, Lee M. Talbot, Bruce A. Wilcox,
Dawn R. Magness, Carol A. Brewer, and Daniel S. Keebler*

SUMMARY

IN THIS CHAPTER WE PRESENT and evaluate a conceptual framework intended to improve predictability of the role of disease in landscape processes of socioecological systems. On a local scale, disease tends to increase the interactions among patches on a landscape, particularly through changes in the frequency and severity of disturbances and increases in the vulnerability of ecosystems to fundamental changes in state in response to such disturbances. In addition, human activities that alter landscape structure or connectivity often increase the likelihood of disease epidemics or landscape sensitivity to disease. In contrast, on global and regional scales, disease tends to reduce landscape connectivity because the social response to these ecological changes is often to restrict trade and migration. Both the *increase* in connectivity on the local scale and the *decrease* in connectivity on regional to global scales can profoundly affect ecosystem structure and functioning.

Resilience theory addresses the factors that make systems either resilient or vulnerable to radical changes in state by considering interactions between the ecological and social components of systems. This provides a framework for predicting the regional impacts of disease and reducing their social consequences. Resilience is facilitated by fostering cultural and ecological legacies that provide seeds for recovery; by maintaining biological, social, institutional, and economic diversity, which increases the options for alternative pathways of recovery; and by fostering learning and innovation, which reduces the potential impacts of disease and increases the likelihood of favorable social change.

INTRODUCTION

Many of the key drivers of landscape and regional processes are changing at unprecedented rates and in ways that are strongly influenced by human activities (Foley et al. 2005; Steffen et al. 2004; Vitousek et al.

-1—
0—
+1—

1997). Diseases of plants, animals, and people often play a key role in these changes, both as an integral component of socioecological systems (Evimer and Likens, chapter 12, this volume) and as a trigger for changes in state. Yet disease is often viewed as a surprise that cannot be anticipated and therefore is not incorporated into predictive process-based frameworks. Earlier chapters in this book described the impacts of disease on individual organisms, communities, and ecosystems. In this chapter we extend these effects to larger spatial scales—landscapes and regions. We first assess the role of disease in landscape processes through a conceptual framework that relies on the integration of social and ecological systems. Human activities are an integral component of system dynamics on regional scales, as delineated in previous Cary Conferences (Groffman and Likens 1994; McDonnell and Pickett 1993), so we explicitly consider the social and ecological processes that characterize the reciprocal interactions of socioecological systems (Berkes et al. 2003; Machlis et al. 1997) (figure 13.1) and determine the resilience of these

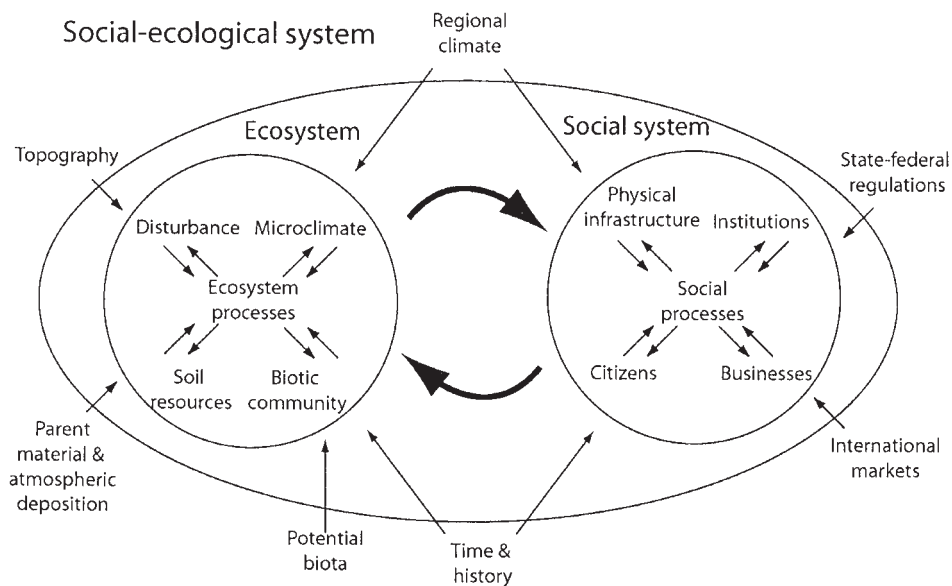


Figure 13.1. A socioecological system. The oval represents the socioecological system and the circles delineate its ecological and social subsystems. Several independent factors, such as climate, history, and international markets, determine the properties of the system; these properties are further modified by interactive controls that determine the internal dynamics of the system. (Reprinted with permission from Whiteman et al. 2004.)

—1
— 0
—+1

systems. Resilience is the capacity of a system to absorb shocks such as disease outbreaks without changing its fundamental properties, such as its social norms, its typical economy, and the types of species it supports (e.g., grain crops or forests). Using this framework, we describe the effects of disease on landscape processes. We then use resilience theory to explore the role of disease and insect pests in causing changes in the state of socioecological systems, using bark beetles, rinderpest, malaria, and AIDS as examples.

CONCEPTUAL FRAMEWORK

Pathogen and parasite interactions with their hosts are such an integral component of community dynamics that their chronic role in ecosystems is nearly invisible (Horwitz and Wilcox 2005; Lafferty, chapter 9, Eviner and Likens, chapter 12, this volume). As discussed in earlier chapters, diseases often modify competitive interactions, trophic dynamics, disturbance probabilities, and succession. Disease epidemics emerge when the pathogen-host balance shifts to be seriously deleterious to the host (Horwitz and Wilcox 2005), often creating unanticipated surprises (Gunderson 2003) that act as disturbances to alter the structure, composition, and functioning of ecosystems and landscapes (Wilcox and Gubler 2005). Many disease epidemics are triggered by human-induced environmental or biotic changes that shift the host-pathogen balance (Patz 2002; Patz et al. 2000). Here we examine disease from this perspective, considering its role in ecosystems and how ecosystem resilience influences and is influenced by disease events.

Diseases with the greatest immediate ecosystem impacts are generally those that selectively remove or suppress the dominant and keystone plant species (figure 13.2), which, by definition, are the plant species with the greatest effects on ecosystem processes (Chapin et al. 2002). Diseases can have equally dramatic impacts by selectively removing animals that control the abundance of dominant and keystone plants through trophic cascades (Polis 1999). In many aquatic ecosystems, bacteriophages (viruses that attack decomposer organisms) have a profound immediate direct effect on nutrient cycling by stimulating bacterial turnover (Middelboe, chapter 11, this volume). Over longer time scales, diseases influence ecosystem dynamics through their effects on organisms that influence disturbance regimes or species interactions (Eviner and Chapin 2003; Eviner and Likens, chapter 12, this volume).

Disease has equally profound effects on the human component of socioecological systems (figure 13.3). Disease has its greatest effects on social systems when it alters human population densities and activities,

-1—
0—
+1—

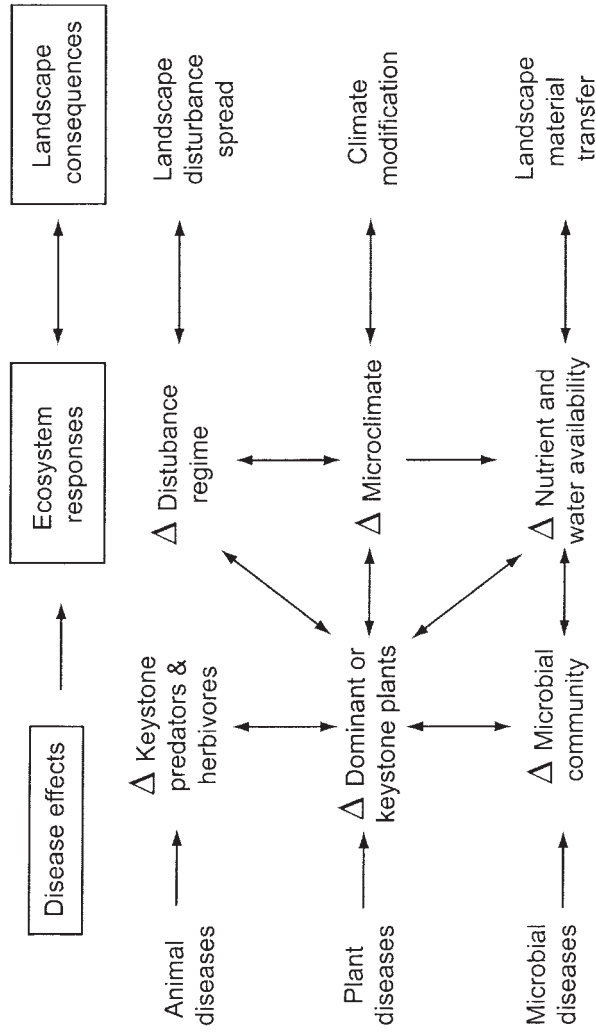


Figure 13.2. Major ecological pathways by which disease outbreaks affect landscape processes.

+1
0
-1

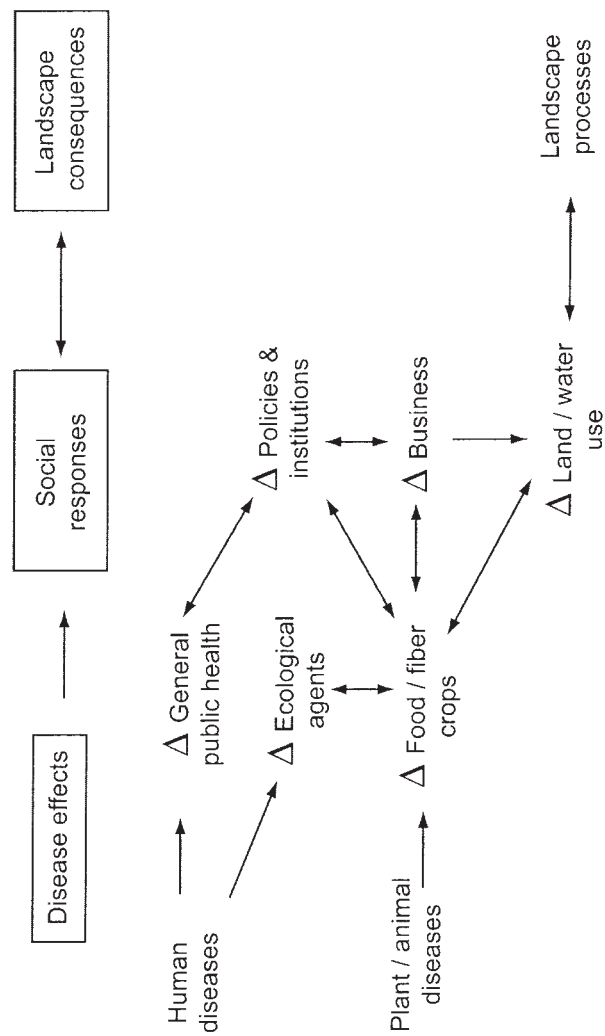


Figure 13.3. Major social pathways by which disease outbreaks affect landscape processes. The effects of disease on social responses are largely mediated by learning and education.

either by directly infecting humans (e.g., bubonic plague, *Yersinia pestis*, malaria, *Plasmodium*, tuberculosis, *Mycobacterium tuberculosis*, sleeping sickness, *Trypanosoma brucei rhodesiense* and *T. b. gambiense*) or by disrupting the food supply (e.g., the Irish famine precipitated by potato late blight, *Phytophthora infestans*, which led to the death of more than a million people and the migration of a million more) (McNeil 1989). Pathogens exert many other effects, including those that alter ecosystem and landscape processes (see figure 13.2) in ways that affect the delivery of ecosystem services to society (Millennium Ecosystem Assessment 2005).

Human diseases often have differential effects on particular segments of society (Turshen 1977). Those diseases that directly affect strong ecological agents, such as farmers, foresters, or pastoralists, have disproportionately large ecological consequences. Malaria and schistosomiasis, for example, have their greatest impacts on rural populations and therefore on agricultural land use (Sachs and Malaney 2002). In addition, diseases that are perceived as posing a general health risk (particularly a risk to privileged segments of society) are more likely to influence policy than are diseases that are largely restricted to disenfranchised populations (Turshen 1977). These policies in turn often influence public health decisions, land and water management, travel, trade, and other human activities. AIDS, for example, initially received only modest research funding in the United States because it was viewed primarily as a disease of homosexuals. It received more attention by policy makers after it became recognized as a health risk for broad segments of society. In contrast, severe acute respiratory syndrome (SARS), which was immediately perceived as a health risk for the general public, particularly global travelers, received more immediate control efforts.

Plant and animal diseases also have important consequences that are mediated by socioecological feedbacks (figure 13.3). Economically important diseases (e.g., foot-and-mouth disease, *Aphthovirus*, soybean rust, *Phakopsora*, white pine blister rust, *Cronartium ribicola*) decrease the productivity of hosts that support the human food and fiber supply and the stability of economic and social systems. These diseases often trigger management actions that remove diseased organisms or alter landscape linkages in an attempt to isolate areas with the disease. An outbreak of foot-and-mouth disease in England, for example, reduced beef exports and severely restricted regional travel in 76% of the country. The restriction on the movement of cattle led to overgrazing of pastures (Fraser of Allander Institute [FAI] 2005). On the flip side, the establishment of Uruguay as a foot-and-mouth disease-free country led to a doubling of its beef exports and a corresponding expansion of pasturelands (Food and Agriculture Organization [FAO] 2001). In this

—-1
— 0
—+1

way, trade barriers in one region of the world can alter land use by increasing production of that commodity in distant areas free of the disease (FAO 2001; Yuill 1991). Meanwhile, disease-prone areas change land use to accommodate another economic base. Diseases can have additional longer-term effects by altering lifestyles, policies, institutions, or business frameworks (figure 13.3). The death of livestock in Africa as a result of a short-term outbreak of Rift Valley fever led to the migration of young men from rural to urban areas, altering family structures and increasing the spread of HIV (Preslor 1999). The outbreak of Rift Valley fever in 1997–98 led to a ban on livestock products from eastern Africa by Saudi Arabia, leading to a 75% decrease in livestock exports, which constitute 90% of the foreign exchange in Somaliland. This virtually halted imports of medicine, sugar, and grains, causing the closure of many stores in urban centers (FAO 2001). These examples demonstrate the critical nature and large magnitude of change in socioecological interactions that can be triggered by disease outbreaks.

DISEASE EFFECTS ON LANDSCAPE PROCESSES

Diseases affect all classes of interactions among patches on a landscape. In the absence of disease outbreaks, gravitational movement of materials such as water, nutrients, and sediments often dominate the short-term interactions among patches in a landscape (Chapin et al. 2002; Turner et al. 2001). Diseases act like other disturbances that substantially reduce the activity or biomass of dominant plants. In general, this reduces the capacity of ecosystems to retain these materials (Eviner and Likens, chapter 12, this volume), thereby increasing fluxes from one patch to another and increasing overall landscape connectivity. Dieback in Australian jarrah caused by the introduced pathogen *Phytophthora cinnamomi*, for example, increased runoff by 20% (Bari and Ruprecht 2003), and elsewhere long-term dieback caused by this disease increased water yield by 75% (Batini et al. 1980). Disease-associated diebacks can also substantially increase stream nitrate concentrations (Hobara et al. 2001; Ohte et al. 2003). In Alaska, yellow cedar decline led to a 3.8-fold increase in landslides when roots decomposed fifty years after tree death (Johnson and Wilcock 2002). Human diseases that foster migration from rural areas to cities (e.g., Rift Valley fever; FAO 2001) would also likely augment the movement of food and wastes between urban and rural areas—another increase in landscape connectivity.

Landscape processes in turn influence disease (e.g., spatial distribution, infection rates), mainly by limiting or facilitating the movement of organisms among patches (McCallum, chapter 5, this volume). Emerging

-1—
0—
+1—

infectious diseases are those that have recently expanded geographically, increased in epidemic activity, increased in virulence, or are caused by new pathogen variants or novel pathogens. About a third of these diseases are associated with natural or anthropogenic ecotones, that is, boundaries between habitat patches (Despommier and Wilcox in press). Ecotones result in more frequent contact among novel species, diverse selection pressures, and distinct controls over population densities, dispersal, and movements (Risser 1995). All these factors facilitate pathogen transmission, spread, and evolution and therefore the potential for disease emergence. Malaria and schistosomiasis are examples of diseases whose emergence has been facilitated by ecotonal processes (expansion of forest edge and aquatic-terrestrial zones due to deforestation and water development and dam projects). Disease can also influence landscape structure in ways that alter landscape connectivity. In Africa, for example, the introduction of rinderpest (Morbillivirus) from domestic animals to African wildlife in the nineteenth century profoundly altered the balance of shrubs and grasses, leading to changes in the structure and connectivity of both ecological and social systems. Disease can mediate interactions among landscape processes occurring on different scales. Barriers between landscape patches (e.g., roads, streams, lakes) reduce the likelihood of flea-vectored plague among prairie dog colonies (Johnson and Collinge 2004), thereby promoting the fine-scale heterogeneity created by these colonies. Conversely, policies intended to reduce disease spread can reduce the movement of people and other organisms among landscape patches.

The most dramatic impact of disease and insect pests on landscape processes is through changes in disturbance spread across landscapes. Bark beetles, for example, increase the probability of forest fires, often with longlasting and profound effects (Dickman 1992). In coastal marine ecosystems, coral bleaching in combination with diseases of sea urchins that would otherwise have grazed on reef algae led to catastrophic mortality of reef corals in the western Atlantic in the 1980s (Jackson 2001), making coastal areas more vulnerable to erosion. Kelp forests are sensitive to several impacts of disease. Sea urchins that expand in response to sea star or sea otter diseases (Conrad et al. 2005; Eckert et al. 2000) can graze down kelp (Estes and Palmisano 1974), whereas sea urchin diseases shift the balance in favor of kelp (Lafferty 2004). Kelp forests reduce current speeds, storm surges, and coastal erosion, thereby increasing the suitability of these areas for suburban development (Kay and Alder 1999). This in turn can increase public support for marine habitat protection. A shifting mosaic of disease might therefore lead to a complex matrix of changes in multiple landscape processes.

—-1
— 0
—+1

The net effect of disease outbreaks is to increase connectivity of patches in a landscape through multiple avenues of patch interactions, particularly the propagation of disturbance. If the disease spreads rapidly, the increased connectivity of landscapes might reduce landscape heterogeneity and diversity. If the disease moves slowly because of inherent dispersal limitations or disease management, it might increase landscape heterogeneity. The landscape effects of disease therefore depend on the rate and extent of disease spread relative to other process controls (Marcogliese 2004).

DISEASE-INDUCED CHANGES IN STATE

Resilience Framework

Disease epidemics are disturbances that can radically alter the state of ecosystems and landscapes. Resilience theory, which addresses the factors that make systems either resilient or vulnerable to radical changes in state, therefore provides an appropriate framework for examining the role of epidemic diseases in socioecological systems (Carpenter 2003; Gunderson and Holling 2002; Walker et al. 2004). Resilience is the capacity of a system to absorb shocks such as disease outbreaks without changing its fundamental properties, for example its social norms, its typical economy, and the types of species it supports (e.g., grain crops or forests). These fundamental properties typically change slowly, but, when modified, they alter the nature of the system (Carpenter and Turner 2000; Chapin et al. 1996). Sustaining these slow variables reduces the likelihood that disease or other major perturbations will have irreversible consequences.

Most systems periodically experience severe shocks and disturbances and typically have seeds for recovery. These include propagules of important species, institutions and rules for managing crises, and memories and stories of how previous crises were managed or averted. Sustaining these legacies reduces the potential impact of disease and other disturbances and promotes recovery. Diversity of biological, social, and economic options is another mechanism for promoting recovery by increasing the number of pathways by which recovery can occur. For example, in areas where the economic base is not diversified, there is greater susceptibility to disease-induced state changes in socioeconomic systems (Department for Environment, Food and Rural Affairs [DEFRA] 2001; FAO 2002). Diversity also provides options for adapting to change when the system has been altered so substantially that recovery to the original state is unlikely.

-1—
0—
+1—

Disease interacts with other stresses and disturbances. Systems that are already stressed are more vulnerable to disease-induced state changes. For example, industries such as agriculture that are already economically stressed and poor farmers within the agricultural sector are less resilient to disease outbreaks (DEFRA 2001; FAO 2002). The global increase in emerging infectious diseases is largely a consequence of unprecedented population growth, resulting in novel conditions that promote pathogen transmission and persistence (Wilcox and Gubler 2005). Effective management of these diseases requires a flexible approach based on an understanding of changing social and ecological conditions. When vector control programs are implemented in an inflexible manner, they may augment rather than reduce the reemergence of diseases such as malaria (Holling 1986).

In the remainder of this chapter, we highlight how resilience theory contributes to our understanding of disease-induced state changes in socioecological systems.

Social Learning to Enhance Resilience and Adaptation

Human perceptions about disease have a large effect on disease spread. How can education influence, mediate, and moderate this response? Anticipating and responding to the causes and consequences of disease epidemics requires an understanding of environmental complexity, as well as of the roles that uncertainty and variability play in environmental and social processes (Clark et al. 2001). Innovation and learning are critical to successful adaptation. This learning occurs most readily when biological, landscape, and socioeconomic diversity provide alternative possibilities for resilience or adaptation. There are at least two modes of learning that are important: (1) understanding of the dynamics of disease in socioecological systems and (2) enhancing the social and institutional capacity to respond to crises effectively.

In almost any region facing disease outbreak, a key challenge is to capture the imagination and interest of local people in a way that stimulates cooperation and appropriate action (Winch et al. 2002). It is difficult to engage the public in a meaningful dialogue about the hazards of disease outbreaks to humans and to ecosystems if policy makers and others do not have a basic understanding of the ecology and epidemiology of the disease and the environment into which it is introduced. Ideally, effective broad-scale education programs would occur before a disease reached epidemic status. Such programs would consider people's cognitive understanding of the linkages between ecology and disease, people's perceptions of the disease and health with respect to the environment,

—-1
— 0
—+1

prevailing and pervasive attitudes and misconceptions, and worldviews that shape and constrain understanding of ecology and disease (Brewer et al., chapter 22, this volume). The potential to affect decision making and behavior related to disease epidemics may be enhanced, for example, by visual or other devices that promote understanding of the processes that influence disease spread, or by forecasts of how much a system might be disrupted by the disease (to this end, maps and other images are now readily available through the use of geographic information systems). Moreover, an informed public would benefit from improved communication of how disease outbreaks and epidemics are modeled, model assumptions, and how assumptions influence confidence in resulting predictions (Brewer and Gross 2003; Smith et al. 2005). The ready availability of Web-based tools to display complex data could be used to promote public understanding of disease, its influence on ecosystems, and the influence of decision-making scenarios on possible future outcomes.

When rapid changes occur as a result of disease outbreaks, most effort is applied to reducing the rates of transmission or promoting recovery. These crises, however, also represent opportunities for institutional changes that might otherwise be difficult to implement (Gunderson et al. 1995). Taking advantages of crises to implement change requires an understanding of the multiple factors that constrain human well-being and the capacity of individuals or institutions to explore innovative solutions, as described later with respect to managing the AIDS crisis in Africa.

In the following sections we provide four examples of pest and disease outbreaks that modify the thresholds of resilience in socioecological systems.

Bark Beetle

In the Kenai Peninsula of south-central Alaska, gradual climatic change led to a sudden eruption of spruce bark beetle (*Dendroctonus rufipennis*). This insect pest blocks phloem transport of sugars to roots, and its vectored bluestain fungus blocks water transport in the xylem. Massive outbreaks of this beetle-fungus combination killed the dominant tree (white spruce, *Picea glauca*) across 0.8–1.2 million ha within a decade (Berg et al. 2006). Climate warming appeared to trigger the recent outbreak by allowing the beetle to complete its life cycle in one rather than two years, suddenly altering the dynamic balance between beetles and the plant defense system. Spruce bark beetle outbreaks have occurred frequently on the Kenai, including a massive historical outbreak in the late 1870s. Outbreaks kill large-diameter trees, resulting in a growth release of pole-size trees that are less vulnerable to attack because larvae cannot develop in young trees with thin phloem. Outbreaks are limited

-1—
0—
+1—

by the availability of large-diameter trees even if favorable beetle conditions persist, causing discrete time intervals between outbreaks.

Human interactions with the ecosystem have changed since the last beetle outbreak because of the increased size and dispersion of the human population. In the past, stand-replacing fires have not occurred in beetle-kill areas (Berg et al. 2006). However, warming conditions may change fire behavior, and human settlements increase the fire ignition rate (DeWilde et al. in press). The broad expanses of dry, dead trees greatly increase the risk of wildfires in what has become a wildland-urban interface. In addition, the loss of the tree canopy and the increased nutrient return to the forest floor have accelerated nutrient cycling and fostered the growth of grasses, which increase the risk of spring fires (when dry grass litter provides a ground fuel) and compete with tree seedlings, reducing the potential for stand regeneration. Widespread public concern about wildfire has led to changes in forest management policies to subsidize salvage logging to remove dead trees. In summary, the beetle outbreak substantially modified ecological and social processes on regional scales and increased the risk of disturbance spread (by fire and logging) across the landscape.

Rinderpest in Africa

Rinderpest is a highly contagious, often fatal, viral disease that infects most artiodactyls. Although it affects both domestic (e.g., cattle, water buffalo) and wild (e.g., antelope and gazelles) animals, cattle are probably its natural host. Rinderpest was apparently introduced into Africa with livestock accompanying military operations in 1884 and 1889. It rapidly became an epizootic, devastating cattle and wild ruminants throughout the continent. In East Africa, for example, it appeared in 1890, and within about two years 95% of the domestic cattle had died. In the next few years, most wild artiodactyls followed suit. Simultaneously, the loss of domestic livestock impoverished and caused famine among the pastoral Masai and subsequently among the adjacent agriculturalists both because of loss of livestock and because of resultant warfare. Weakened, the Masai and others were then hit by a smallpox epidemic, resulting in massive starvation and the consequent abandonment of large areas of the country (Branagan and Hammond 1965; Ford 1971; Sinclair and Norton-Griffiths 1979; Talbot 1963).

These ecological and social changes triggered many secondary effects. In these East African grasslands, moderate grazing and browsing combined with human-caused fires reduce woody vegetation, which will return rapidly in the absence of fires. Loss of domestic and most wild herbivores removed the grazing and browsing pressure, which, along

—-1
— 0
—+1

with the cessation or reduction of fires formerly set by the people, allowed woody vegetation to take over vast areas that had been open grassland or savanna. Woody areas provide habitat for tsetse flies (*Glossina swynnertoni*), carriers of the blood parasite (*Trypanosoma*) that transmits sleeping sickness in both humans and cattle. The loss of the wildlife may have temporarily reduced the numbers of tsetse flies. However, in time, the wild ungulates increased in number. This population increase in turn provided hosts for the tsetse flies, which spread through the now extensive woodlands. The presence of the flies kept humans with their livestock out of large areas of East Africa. Control programs that reduced tsetse flies led to the return of livestock and humans, and with them came fire, which reopened much of the woodland, reexpanding savanna and grasslands. A subsequent rinderpest outbreak in the late 1950s temporarily reduced the wildebeest numbers, allowing an accumulation of grass fuel that carried hotter fires, further reducing woody vegetation. Subsequently the wildebeest numbers increased about five-fold. Their heavy grazing removed much grass fuel and thereby reduced the impact of human-ignited fires, again allowing the resurgence of some woody vegetation (Dublin 1995; Sinclair and Norton-Griffiths 1979; Talbot 1963; Talbot and Talbot 1963). These events dramatically demonstrate how disease responds to and causes complex webs of landscape-level changes in socioecological systems.

Malaria and Schistosomiasis

Malaria impacts landscape processes through its effects on people. It is the preeminent tropical parasitic disease and one of the top three killers among communicable diseases (Sachs and Malaney 2002). The incidence of malaria in the tropics is increasing rapidly for many reasons, including increasing drug and insecticide resistance, population movements into malarious regions, changing agricultural practices (including dam building and irrigation), deforestation, and weakening of public health systems in some poor countries. Malaria increases most rapidly in poor countries that have insufficient wealth for personal expenditures and government programs to reduce the incidence and provide for the treatment of disease. Malaria affects landscape processes through multiple pathways. On a local scale, malaria increases absenteeism from work and school, reducing levels of education and training. Malaria also increases the proportion of children in the population, as couples choose to have more children to compensate for anticipated malarial deaths. Together, these trends reduce agricultural productivity, savings, and human well-being. Tourism, mining, and business avoid malarial areas, further increasing the wealth disparity between malarial and

-1—
0—
+1—

nonmalarial regions (Gallup and Sachs 2001). In South Africa, malaria has caused large shifts in landscape distributions of agricultural types and people. Prior to World War II, malaria limited large-scale commercial agriculture by wealthy farmers, allowing black Africans to use this land for small-scale agriculture and herding. With increased malaria control after World War II, there was an increase in the extent of commercial farming and migration of poor white farmers onto land previously farmed by black Africans, causing black Africans to shift from small-scale agriculture to wage labor (Packard 2001).

Schistosomiasis is a water-borne disease that is increasing in the tropics, in part as a result of landscape changes associated with building of dams and expansion of irrigation. Different species of *Schistosoma* are specific to humans or cattle (in some cases both). Increases in morbidity and mortality and declines in productivity have landscape-level consequences similar to those of malaria. In Nigeria, for example, schistosomiasis reduces worker productivity, cash income, rates of land clearing, and farm size (Umeh et al. 2004).

These socioecological consequences of disease constrain the capacity of these systems to achieve economic and social changes in well-being. In this case, disease contributes to the resilience of a poverty trap that constrains changes toward a more desirable socioecological state.

AIDS

The HIV/AIDS pandemic in sub-Saharan Africa has drastically altered traditional family and community structures, leaving many orphans, whose parents died before they could pass on local knowledge of agricultural techniques best suited to local circumstances. In Zambia's Southern Province, where one-third of households care for orphans, those households not affected by HIV/AIDS can afford twice as many livestock and farming implements as female-headed households caring for orphans (FAO 2004). Potential increases in tick-borne diseases caused by a loss of local knowledge of their distribution and dynamics further reduce the availability and usefulness of livestock. In general, adult mortality has deprived families and communities of three major assets: knowledge, a strong labor force, and capital (Jayne et al. 2004).

In Zambia, aid organizations have attempted to fill this gap in the transfer of intergenerational knowledge by integrating HIV/AIDS education into agricultural education campaigns and introducing both new and traditional agricultural practices that involve labor-saving techniques. These include crop diversification (resulting in multiple harvests over the course of a year rather than a single, labor-intensive harvest) and the introduction of easier to use ploughs and tools (particularly important for

—-1
— 0
—+1

children, women, and the elderly), with techniques such as minimal tillage, direct planting of seeds in pits rather than in rows, the introduction of weed-suppressant soil cover, and preparation of the soil during the dry season, which distributes labor still more evenly over the course of the year. Additional innovations include the introduction of for-profit vegetable gardens, increased husbandry of small livestock such as goats and chickens, seed multiplication, and the enhancement of “homestead gardens” that supplement staple gardens (FAO 2004). The proposed introduction of fish farming would require the digging of numerous ponds and would likely bring about significant change in local landscape processes. All of these agricultural innovations alter socioecological interactions and landscape processes.

Without these interventions, communities lose knowledge about the cultivation of traditional crops, resulting in a reduction in the planting and use of these crops (Waterhouse et al. 2004). The corresponding decrease in crop diversity and increased dependence on external seed sources reduces agricultural and household resilience. Traditional crops are especially appropriate for poorer, risk-averse households. This example highlights the importance of learning and innovation in coping with disease.

CONCLUSIONS

Disease epidemics are disturbances that alter interactions among ecological and social components of regional systems. The ecological impacts of disease are largely mediated by changes in dominant and keystone plant species or in animals that regulate these plant species. Loss of these species due to disease generally augments the fluxes of water and nutrients among patches on a landscape, increasing landscape connectivity. Diseases affect the social components of regional systems through their effects on ecological agents—farmers, foresters, and pastoralists—and the agroecosystems they manage. Over longer time scales, diseases affect policies and institutions that influence human activities and land use. Diseases have the potential to affect all pathways of interactions among patches on the landscape, but their impacts on disturbance regimes have the largest long-term consequences, sometimes leading to changes in ecosystem state. Resilience theory provides a framework for predicting, preparing for, and managing the consequences of profound changes in the state caused by disease and other perturbations. Unless we understand the feedbacks between social and ecological responses to and effects on diseases and the components of socioecological systems that foster resil-

-1—
0—
+1—

ience, we will fail both in predicting future disease patterns and in managing their impacts.

ACKNOWLEDGMENTS

We thank the Integrative Graduate Education and Research Training program supported by (NSF grant No. DGE-0114423 to the University of Alaska) for support of the Resilience and Adaptation program.

LITERATURE CITED

- Bari, M. A., and J. K. Ruprecht. 2003. Water yield response to land use change in SW western Australia. Salinity and Landuse Impact Series 31. Perth, Australia: Department of Environment.
- Batini, F. E., R. E. Black, J. Byrne, and P. J. Clifford. 1980. An examination of the effects of changes in catchment condition on water yield in the Wungong catchment, Western Australia. *Australian Journal of Forest Research* 10:29–38.
- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227:219–32.
- Berkes, F., J. Colding, and C. Folke. (Eds.). 2003. *Navigating Social-Ecological Systems: Building Resilience for Complexity and Change*. New York: Cambridge University Press.
- Branagan, D., and J. A. Hammond. 1965. Rinderpest in Tanganyika: A review. *Bulletin of Epizootic Diseases of Africa* 13:225–46.
- Brewer, C. A., and L. J. Gross. 2003. Training ecologists to think with uncertainty in mind. *Ecology* 84:1412–14.
- Carpenter, S. R. 2003. *Regime Shifts in Lake Ecosystems: Pattern and Variation*. Lodendorf/Luhe, Germany: International Ecology Institute.
- Carpenter, S. R., and M. G. Turner. 2000. Hares and tortoises: Interactions of fast and slow variables in ecosystems. *Ecosystems* 3:495–97.
- Chapin, F. S., III, P. A. Matson, and H. A. Mooney. 2002. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag.
- Chapin, F. S., III, M. S. Torn, and M. Tateno. 1996. Principles of ecosystem sustainability. *American Naturalist* 148:1016–37.
- Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. A. Pielke, Jr., W. Pfizer, C. Pringle, et al. 2001. Ecological forecasts: An emerging imperative. *Science* 293:657–60.
- Conrad, P. A., M. E. Grigg, C. Kreuder, E. R. James, J. Mazet, H. Dabritz, D. A. Jessup, F. Gulland, and M. A. Miller. 2005. Sea otters serve as sentinels

—-1
— 0
—+1

- for protozoal pathogens transmitted from the terrestrial hosts to marine mammals (abstract). *In* Cary Conference 2005: Infectious Disease Ecology, 56. Millbrook, NY: Institute of Ecosystem Studies.
- Department of Environment, Food and Rural Affairs. 2001. Tackling the Impact of Foot and Mouth Disease on the Rural Economy. London: Department for Environment, Food and Rural Affairs.
- Despommier, D., and B. A. Wilcox. In press. The role of ecotones in emerging infectious diseases. *EcoHealth* 3.
- DeWilde, L., F. S. Chapin, III, and T. S. Rupp. In press. Regional variation in human impacts on the fire regime of interior Alaska. *International Journal of Wildland Fire*.
- Dickman, A. 1992. Plant pathogens and long-term ecosystem changes. *In* *The Fungal Community: Its Organization and Role in the Ecosystem*, ed. G. C. Carroll and D. T. Wicklow, 499–520. New York: Marcel Dekker.
- Dublin, H. T. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: The role of elephants, fire, and other factors. *In* *Serengeti II*, ed. A. R. E. Sinclair and P. Arcese, 71–90. Chicago: University of Chicago Press.
- Eckert, G. L., J. M. Engle, and D. J. Kushner. 2000. Sea star disease and population declines at the Channel Islands. *In* *Proceedings of the Fifth California Islands Symposium*, ed. D. R. Browne, K. L. Mitchell, and H. W. Chaney, 390–93. Santa Barbara, CA.: Minerals Management Service.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185:1058–60.
- Eviner, V. T., and F. S. Chapin III 2003. Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Reviews of Ecology and Systematics* 34:455–85.
- Fraser of Allander Institute. 2005. Economic Impact of the 2001 Foot and Mouth Disease Outbreak in Scotland. Aberdeen, Scotland: Fraser of Allander Institute, University of Strathclyde, and Macauley Land Use Research Institute, Arkleton Centre for Rural Development Research, University of Aberdeen.
- Food and Agriculture Organization. 2001. The State of Food and Agriculture 2001. Part III. Economic Impacts of Transboundary Plant Pests and Animal Diseases. Washington, DC: Food and Agriculture Organization.
- Food and Agriculture Organization. 2002. Improved Animal Health for Poverty Reduction and Sustainable Livelihoods. FAO Animal Production and Health Paper 153. Washington, DC: Food and Agriculture Organization.
- Food and Agriculture Organization. 2004. Strengthening Institutional Capacity in Mitigating HIV/AIDS Impact on the Agricultural Sector: Potential Mitigation Interventions. Lusaka, Zambia: Ministry of Agriculture and Cooperatives, Food and Agriculture Organization of the United Nations.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, III, M. T. Coe, G. C. Daily, et al. 2005. Global consequences of land use. *Science* 309:570–574.
- Ford, J. 1971. *The Role of the Trypanosomiases in African Ecology*. Oxford: Clarendon Press.

-1—
0—
+1—

- Gallup, J. L., and J. D. Sachs. 2001. The economic burden of malaria. *American Journal of Tropical Medicine and Hygiene* 64:85–96.
- Groffman, P. M., and G. E. Likens. (Eds.). 1994. *Integrated Regional Models: Interactions between Humans and Their Environment*. New York: Chapman and Hall.
- Gunderson, L. H. 2003. Adaptive dancing: Interactions between social resilience and ecological crises. *In Navigating Social-Ecological Systems: Building Resilience for Complexity and Change*, ed. F. Berkes, J. Colding, and C. Folke, 33–52. Cambridge: Cambridge University Press.
- Gunderson, L. H., and C. S. Holling. (Eds.). 2002. *Panarchy: Understanding Transformations in Human and Natural Systems*. Washington, DC: Island Press.
- Gunderson, L. H., C. S. Holling, and S. S. Light. 1995. *Barriers and Bridges to the Renewal of Ecosystems and Institutions*. New York: Columbia University Press.
- Hobara, S., N. Tokuchi, N. Ohte, K. Koba, M. Katsuyama, S. J. Kim, and A. Nakanishi. 2001. Mechanism of nitrate loss from a forested catchment following a small-scale, natural disturbance. *Canadian Journal of Forest Research* 31:1326–35.
- Holling, C. S. 1986. Resilience of ecosystems: Local surprise and global change. *In Sustainable Development and the Biosphere*, ed. W. C. Clark and R. E. Munn, 293–317. New York: Cambridge University Press.
- Horwitz, P., and B. A. Wilcox. 2005. Parasites, ecosystems, and sustainability: An ecological and complex systems perspective. *International Journal of Parasitology* 35:725–32.
- Jackson, J. B. C. 2001. What was natural in the coastal oceans? *Proceedings of the National Academy of Sciences of the United States of America* 98: 5411–18.
- Jayne, T. S., M. Villareal, P. Pingali, and G. Hemrich. 2004. Interactions between the agricultural sector and the HIV/AIDS pandemic: Implications for agricultural policy. ESA Working Paper 04–06. Rome: Agricultural and Development Economics Division, Food and Agriculture Organization.
- Johnson, A. C., and P. Wilcock. 2002. Association between cedar decline and hillslope stability in mountainous regions of southeast Alaska. *Geomorphology* 46:129–42.
- Johnson, W. C., and S. K. Collinge. 2004. Landscape effects on black-tailed prairie dog colonies. *Biological Conservation* 115:487–97.
- Kay, R., and J. Alder. 1999. *Coastal Planning and Management*. London: Routledge.
- Lafferty, K. D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Applications* 14:1566–73.
- Machlis, G. E., J. E. Force, and W. R. Burch. 1997. The human ecosystem: The human ecosystem as an organizing concept in ecosystem management. *Society & Natural Resources* 10:347–67.
- Marcogliese, D. J. 2004. Parasites: Small players with crucial roles in the ecological theater. *EcoHealth* 1:151–64.

—-1
— 0
—+1

- McDonnell, M. J., and S. T. A. Pickett. (Eds.). 1993. *Humans as Components of Ecosystems: The Ecology of Subtle Human Effects and Populated Areas*. New York: Springer-Verlag.
- McNeil, W. H. 1989. *Plagues and Peoples*. New York: Anchor Books/Random House.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Synthesis*. Washington, DC: Island Press.
- Ohte, N., N. Tokuchi, M. Katsuyama, S. Hobara, Y. Asano, and K. Koba. 2003. Episodic increases in nitrate concentrations in streamwater due to the partial dieback of a pine forest in Japan: Runoff generation processes control seasonality. *Hydrological Processes* 17:237–49.
- Packard, R. 2001. “Malaria blocks development” revisited: The role of disease in the history of agricultural development in the Eastern and Northern Transvaal lowveld, 1890–60. *Journal of Southern African Studies* 27:591–612.
- Patz, J. A. 2002. A human disease indicator for the effects of recent global climate change. *Proceedings of the National Academy of Science of the United States of America* 99:1506–8.
- Patz, J., T. K. Graczyk, N. Geller, and A. Y. Yittor. 2000. Effects of environmental change on emerging parasitic diseases. *International Journal of Parasitology* 30:1395–405.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86:3–15.
- Preslor, D. B. 1999. Lessening the impact of animal diseases on developing country agriculture. *In Sustainable Agriculture Solutions: Action Report*. London: Noello Press.
- Risser, P. 1995. The status of the science examining ecotones. *BioScience* 45:318–26.
- Sachs, J., and P. Malaney. 2002. The economic and social burden of malaria. *Nature* 415:680–85.
- Sinclair, A. R. E., and M. Norton-Griffiths. 1979. Dynamics of the serengeti ecosystem. *In Serengeti: Dynamics of an Ecosystem*, ed. A. R. E. Sinclair and M. Norton-Griffiths, 1–30. Chicago: University of Chicago Press.
- Smith, K. F., A. P. Dobson, F. E. McKenzie, L. A. Real, D. L. Smith, and M. L. Wilson. 2005. Ecological theory to enhance infectious disease control and public health policy. *Frontiers in Ecology and the Environment* 3:29–37.
- Steffen, W. L., A. Sanderson, P. D. Tyson, J. Jäger, P. A. Matson, B. Moore III, F. Oldfield, K. Richardson, H.-J. Schellnhuber, et al. (Eds.). 2004. *Global Change and the Earth System: A Planet Under Pressure*. New York: Springer-Verlag.
- Talbot, L. M. 1963. *Ecology of the Serengeti-Mara savanna of Kenya and Tanzania, East Africa*. PhD dissertation, University of California–Berkeley.
- Talbot, L. M., and M. H. Talbot. 1963. The wildebeest in western Masailand, East Africa. *Wildlife Monographs* 12:1–88.
- Turner, M. G., R. H. Gardner, and R. V. O’Neill. 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*. New York: Springer-Verlag.
- Turshen, M. 1977. The political ecology of disease. *Review of Radical Political Economics* 9:45–60.

-1—
0—
+1—

- Umeh, J. C., O. Amali, and E. U. Umeh. 2004. The socio-economic effects of tropical diseases in Nigeria. *Economics & Human Biology* 2:245–63.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737–50.
- Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability, and transformability in social-ecological systems. *Ecology and Society* 9(2):5 (<http://www.ecologyandsociety.org/vol9/iss2/art5>).
- Waterhouse, R., E. M. Devji, D. A. X. A. de Carvalho, and C. de S. P. Tinga. 2004. The Impact of HIV/AIDS on Farmers' Knowledge of Seed: Case Study of Chókwe District, Gaza Province, Mozambique. Maputo, Mozambique: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).
- Whiteman, G., B. C. Forbes, J. Niemelä, and F. S. Chapin III. 2004. Bringing feedback and resilience of high-latitude ecosystems into the corporate boardroom. *Ambio* 33:371–76.
- Wilcox, B. A., and D. J. Gubler. 2005. Disease ecology and the global emergence of zoonotic pathogens. *Environmental Health and Preventive Medicine* 10:263–72.
- Winch, P. J., E. Leontsini, J. G. Rigau-Perez, M. Ruiz-Perez, G. G. Clark, and D. J. Gubler. 2002. Community-based dengue prevention in Puerto Rico: Impact on knowledge, behavior, and residential mosquito infestation. *Journal of Tropical Medicine and Hygiene* 67:363–70.
- Yuill, T. M. 1991. Animal diseases affecting human welfare in developing countries: Impacts and control. *World Journal of Microbiology & Biotechnology* 7:157–63.

—-1
— 0
—+1