Chapter 3 Ecology in Global Scenarios

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Main Messages

Ecosystems are essential to the survival of human societies and economies. Ecosystems provide a range of economic and cultural services to humans. These include such basic necessities as clean air, clean water, and the production of food. Ecosystems also enhance human well-being through a diverse range of services that include climate and disease regulation, flood and erosion control, pollination, recreational areas, and enhancement of spiritual and aesthetic experiences.

The inclusion of ecology in past global scenario exercises has been limited. Previous global scenario exercises (see Chapter 2) have largely focused on social and economic drivers and consequently have presented an incomplete picture of the world.

Ecological change affects scenario outcomes. Ecosystems have a significant influence on societies and economies, and people modify ecosystems. One of the goals of the Millennium Ecosystem Assessment is to develop the first set of global scenarios to explore the importance of ecosystems and ecological change for human well-being while maintaining an awareness of the importance of social and economic change.

There are substantial risks that ecological degradation will diminish the future well-being of humanity. Much of our current socioeconomic progress is not sustainable because it reduces the capacity of the biosphere to provide the ecological services that we depend on. Irreversible ecological changes, such as extinctions and species invasions, are of particular concern. It is likely that changes in production systems, ecological management, and social organization will be necessary if we are to sustain human well-being.

Regime shifts in ecosystems cause rapid, substantial changes in ecosystem services and human well-being. Ecosystem services that have been impaired by regime shifts include fisheries and food production in drylands and the quality of fresh waters. Other types of ecological regime shifts with important effects on people include regional climate changes and the emergence of disease. Increasing pressure on these ecosystems will increase the frequency of regime shifts that affect ecosystem services and human well-being.

Ecological feedbacks may accentuate human modifications of ecosystems. Changes in ecological functioning produced by unintended ecological feedbacks from human actions appear likely to amplify climate change, decrease agricultural productivity, reduce human health, and increase the vulnerability of ecosystems to invasive species.

Although ecological theory is well developed, an improved understanding of the relationships between ecosystems and human well-being would facilitate sustainability. There are numerous ecological theories, described in this chapter, that help us understand ecological processes and their relevance for thinking about ecosystem services in global scenarios. Recent developments in complex systems theory offer further insights into the relationships between ecosystems, economies, and societies. Research on resilience, adaptive management, political ecology, and ecological economics offers guidance on linkages between ecosystems, societies, and economies. Although we believe that the inclusion of ecology in global scenarios is a big step forward, further research is needed to better understand the connections among the production of multiple ecosystem services, the local and global impact of ecological processes, and the determinants of ecological resilience.

3.1 Introduction

It is easy for us to take for granted the complex environment that has given rise to our species. Although life on Earth has persisted far longer than we have, and will probably outlast us, recent years have brought an awareness that ecosystems may be more fragile than we had thought. Some of the changes that humans have caused in ecosystems are now affecting people directly. Continuing human impacts on ecosystems cast doubt on the capacity of ecosystems to continue to provide the goods and services that we depend on. We need to pay attention to changes in ecosystems, even if only because our social and economic systems are embedded within them.

The direct importance of ecosystem services to humans is explained in Chapter 1 and is summarized in the MA conceptual framework. Ecosystem services emerge from the interactions of diverse ecological structures and processes. They are not independent of one another; what may be most important for people is the continued existence, or resilience, of an entire bundle of interdependent services. It is possible to affect a range of ecosystem services when attempting to manage or change only a single service.

Many ecosystem services interact with one another through trade-offs, in which increasing the provision of one service causes declines in provision of another service. Decisions concerning the economic benefits of ecosystem modification often require us to address trade-offs between different types of ecosystem service. For example, Fearnside (2000) describes how climate regulation (carbon storage, evapotranspiration) may conflict with food production (such as clearing of woodlands to create pastures); similarly, the use of river systems as conduits for the removal of wastes can have severe impacts on water quality and human health (e.g., Donnison and Ross 1999).

Changes in ecosystems may have both direct and indirect effects on human health and well-being. These changes are often more complicated than direct provision of food and fiber, recreational areas, or clean water. For example, a decrease in flow variability caused by an impoundment on the Vaal River in South Africa contributed to an outbreak of the blackfly *Simulim chutteri*, the vector of river blindness (Carr 1983; Chutter 1968), and destruction of wetlands has resulted in higher levels of heavy metals in table fishes (Brant et al. 2002; King et al. 2002). In Ecuador, destruction of mangroves for the aquaculture of shrimps for the export market has contributed to declining food security through the loss of coastal fisheries (Parks and Bonifaz 1994).

Ecosystem services are intricately related to poverty (Martinez-Alier 2002). People with few financial resources are more likely to rely on the direct provisioning services of ecosystems, such as bushmeat and unpurified water. They may also be less able to manage resources effectively if they have been resettled in unknown areas (Angelsen and Kaimowitz 1999; Deininger and Binswanger 1999), are denied full tenure (Lawrence 2003; Parks and Bonifaz 1994; Robinson and Bennett 2002), or lack the political power to prevent imports of externally generated pollutants (Martinez-Alier 2002). Effective ecosystem management will require policies that take poverty into account. Similarly, effective poverty alleviation requires realistic policies that take into account the capabilities of different ecosystems to provide bundles of ecosystem services. In this chapter we describe the future of ecosystem services, the motivation for developing scenarios that consider ecological services, some of the ecological theories that may be useful for integrating ecosystem services into scenarios, the integration between ecology and related disciplines, and the relevance of ecological theories and scenarios for the development of management and policy approaches. Our aim is to provide a cohesive summary of relevant ecological thinking (and its relationship to other disciplines) for readers who are interested in understanding the motivation for the MA scenarios and the current limitations and future needs for the development of ecological scenarios.

3.2 The Future of Ecosystem Services

There is increasing evidence that the activities of humans can alter a range of ecosystem services at global and regional scales. Well-documented impacts of human activities on ecosystem services at a variety of scales include changes in Earth's climate (Watson and Team 2001), the number and distribution of species (Chapin et al. 2000; Higgins et al. 2003; Sala et al. 2000), the quality and quantity of fresh water (Meyer et al. 1999; Brinson and Malvarez 2002), and air quality and pollution levels (Sinha et al. 2003). Human activities also affect ecosystems in ways that have diverse effects on bundles of ecosystem services, for instance through changes in the ability of organisms to disperse (Hill and Curran 2003) and by disrupting food webs through species translocations (Simon and Townsend 2003; Zavaleta et al. 2001).

Sustainable development has become a mantra for many development organizations, although (or perhaps because) the concept of sustainability has proved difficult to pin down and apply (Goldman 1995). Given projected increases in human population and the slow rate of change of many human behaviors, it seems increasingly likely that human impacts on ecosystem services will affect the quality of life of the majority of the human population within the next 50 years. Our current lack of knowledge concerning the resilience of ecosystem services makes it difficult to assess the degree to which we should be concerned about this. If ecosystems are relatively robust, it is possible that current trends may not greatly alter the provision of the more vital ecosystem services. By contrast, if ecosystems are relatively brittle and if the relationship between ecological impacts and ecosystem services is nonlinear, we run the risk that cumulative human impacts will some day push ecosystems over one or more thresholds, resulting in the collapse of a bundle of ecosystem services (Peterson et al. 2003a).

The true state of affairs probably lies somewhere between these two extremes and will differ for different ecosystem services. Current understanding suggests that there are high levels of uncertainty concerning the relative magnitude of human impacts on ecosystems, that rates of habitat destruction and species extinctions are higher than they have ever been in the history of humanity (McNeill 2000), and that ecosystem services may be intricately linked to one another in surprising or unforeseen ways. For example, in Australia, deforestation has led to the unexpected rise of a saline water table, severely affecting food production (Keating et al. 2002).

One of the most worrying aspects of the loss and modification of natural habitats is that we risk damaging our own life-support systems irreversibly. This is particularly true in situations where cross-scale interactions (and other kinds of nonlinearity) are possible. Cross-scale interactions occur from broad scales to fine scales, and vice versa. For example, a broad-scale process such as the formation of clouds may be tightly linked to a fine-scale process such as evapotranspiration (Heck et al. 2001; Wang and Eltahir 2000). Rainfall affects the moisture that is available to plants, driving evapotranspiration. At the same time, increases in evapotranspiration make the air more humid, affecting circulation patterns and potentially making rainfall more likely. Although we typically assume that the broad-scale process drives (or constrains) the small-scale process, this is not necessarily the case in every instance or at all times. Small-scale disturbances can affect broad-scale processes either by individual action (for example, a single highway blocks an important migration corridor for the Florida black bear) or, more commonly, by the combined effects of smallscale contagion (for example, a single lightning strike starts a fire that burns a vast area of forest).

Cross-scale interactions occur between fine- and broadscale processes, as in the rainfall-evapotranspiration example. Where the effect influences the cause, these interactions are termed cross-scale feedbacks. Cross-scale feedbacks often start with large-scale stressors (such as droughts, glaciers, or floods) that cause local ecosystem change. Local change leads in turn to a contagious spread of ecological responses that collectively cause an upscaling of the problem. Positive feedback loops, in which fine- and broadscale processes amplify one another, can lead to escalating changes. For example, Foley et al. (2003) and Higgins et al. (2002) explore the ways in which land use and land cover change may affect the global climate. (See Box 3.1.)

A second example of a cross-scale feedback involves schistosomiasis, a debilitating parasitic disease in the Lake Malawi area (Stauffer et al. 1997). Until the early 1990s, schistosomiasis was thought to be absent from Lake Malawi. By 1994, however, nearly 80% of all schoolchildren evaluated had schistosomiasis. The change in human schistosomiasis levels was caused by an increase in the abundance of snails, the intermediate hosts of the Schistosoma parasite, in the nearshore regions of the lake. Snail populations increased following a decline in the fish that preved on them, which in turn occurred as a result of introductions of nonnative fish and intensified fishing. Ironically, intensive fishing was facilitated by a program that was intended to protect local people from malaria-carrying mosquitoes, when mosquito nets were converted to fishing nets by enterprising fishers.

3.3 Why We Need to Develop Ecological Scenarios

3.3.1 Ecological Critique of Existing Scenarios and Statement of What Value We Add

Chapter 2 of this volume presents the motivations for developing scenarios and the main tenets of scenario building.

BOX 3.1 Green Surprises: Climate, Ecology, and Carbon

The dynamics of terrestrial ecosystems can have both physical and chemical influences on climate. Albedo, which is the proportion of incident radiation that is reflected by Earth's surface, is modified by changes in land cover. For example, ice caps and bare sand (high albedo) tend to reflect far more radiation than a multilayered tree canopy and understory (low albedo). Changes in albedo affect energy exchange between atmosphere and land, and so they can modify surface temperatures. Changes in surface temperatures affect heat transfer via evapotranspiration and air movement. Surface structure also affects air currents, altering the movement and mixing of the atmosphere near Earth's surface. Rougher surfaces produce more mixing, and so cool Earth's surface more effectively. Changes in vegetation, such as deforestation, affect both albedo and surface structure and thus can influence climate.

Chemical transformations in terrestrial ecosystems influence the climate by changing the composition of the atmosphere. The amount of carbon absorbed by the biosphere is the difference between the amount of carbon plants absorb through photosynthesis and the amount released to the atmosphere by plant and microbial respiration. Disturbances such as fire, wind, and insect outbreaks, in conjunction with human modification of land cover, alter carbon absorption and respiration and frequently release additional carbon. The terrestrial biosphere appears to have acted as a net carbon sink for the last few decades, absorbing nearly 20% of anthropogenic emissions (Prentice et al. 2001). Whether terrestrial ecosystems continue to provide this service will depend on land use and land cover change, as well as on changes in climate and atmospheric CO_2 concentrations.

The cumulative impacts of local changes in land cover can combine to produce regional or global changes (Brovkin et al. 2004). Agriculture cur-

As it makes clear, although there are a number of detailed, carefully constructed global scenarios in existence, their focus is largely on social, economic, and immediate environmental issues. Scenarios are usually designed to differ in a way that is important to the issue being addressed (van der Heijden 1996; van Notten et al. 2003). Where the central issue relates to the environment, however, previous scenarios have tended to downplay the importance of ecosystem dynamics. Environmental changes, as distinct from ecosystem dynamics, are incorporated in many existing global scenarios. They are explicitly included in the biodiversity scenarios of Sala et al. (2000) and the Intergovernmental Panel on Climate Change's global climate change scenarios (Watson and Team 2001). They are implicitly incorporated as drivers of societal change in most of the Global Scenarios Group scenarios (Raskin et al. 2002).

While the IPCC's global emissions take into account global feedbacks between climate, land use, and emissions, the many complex feedbacks that characterize real ecosystems (Higgins et al. 2002) are not explored or tested in detail in existing global scenarios. Such feedbacks can result in nonlinear system behaviors that differ profoundly from those of models that do not include feedbacks. Local ecosystem feedbacks may be important for global processes in several ways. (See Box 3.2.) In general, although previous scenario exercises have been environmentally aware, they have largely ignored the role of ecological feedbacks. A

rently occupies about 35% of Earth's land surface, and deforestation continues to reduce the area of the world's remaining large areas of forest. The impacts of these patterns on regional climate (and hence on the dynamics of terrestrial ecosystems) are not well understood. However, the presence of climate-vegetation feedbacks creates the potential that changes in land cover may trigger a cascade of biophysical feedbacks to climate. For instance, the northward expansion of forest could decrease the albedo of northern areas, enhancing global warming (Levis et al. 2000).

Modeling studies have shown that anthropogenically forced climate change could cause the biosphere to switch from being a net sink to a net source of CO_2 , further accelerating the process. This positive feedback would occur as a consequence of changes in rainfall that reduce forest productivity and increase soil respiration, causing some regions to switch from being sinks of CO_2 to sources (Cox et al. 2000).

The relative importance of the interaction between biogeochemical and biophysical processes appears to vary by region. Changes in terrestrial ecosystems may either dampen or amplify the effects of anthropogenic climate change (Foley et al. 2003). An integrated model that includes both biogeochemical and biophysical feedbacks shows that deforestation in the tropics tends to result in warming due to biophysical feedbacks, while boreal deforestation tends to result in cooling due to biogeochemical feedbacks (Claussen et al. 2001). These loops suggest that climate-ecosystem feedback processes may act to resist change driven by external forcing, but when change occurs it can be abrupt and surprising, as positive feedback processes move regional climate and vegetation away from its historical state. There is some evidence that Amazonian deforestation may be approaching such a threshold (Rial et al. 2004).

more detailed discussion of the role of ecology in previous global scenario exercises is presented in Cumming et al. (in press).

Ecological feedbacks matter for global scenarios because the continued provision of ecological services is central to human well-being. Ecological science has demonstrated that certain kinds of anthropogenic ecological change can radically transform the ability of ecosystems to provide ecosystem services (Turner et al. 1993). The unintended consequences of attempts to increase food production include alterations to rainfall patterns, increases in soil erosion and populations of agricultural pests, introductions of new diseases, and reduced water quality and quantity. These changes represent feedbacks from one part or scale of the ecosystem to another; perturbations in one part of the system are translated by ecological dynamics into environmental changes. Ecological feedbacks have the potential to become important drivers of human action, although they may be difficult to include quantitatively in scenario exercises because their likelihood and their strength are uncertain (Bennett et al. 2003).

From the perspective of scenario development, one type of ecosystem change that is of greatest concern involves regime shifts. These occur when an entire system flips into an alternative stability domain or stable state (Scheffer et al. 2001). Such changes occur rapidly and are often a strongly nonlinear response to gradual changes in the variables that

BOX 3.2

Local and Global Ecosystem Feedbacks

One of the central messages of this chapter is that ecosystems are active entities that can cause extensive changes in socioeconomic systems. Although the relevance of ecosystems for human societies at a local scale is well documented, the relevance of ecology at a global scale (and hence for global scenarios) is less obvious. We suggest that ecosystem feedbacks matter most for global scenarios when they are cumulative, nonlinear, or interactive.

Cumulative feedbacks. Small-scale changes become broad-scale changes when they are sufficiently widespread. For most socioeconomic drivers, such as stock markets and human population growth rates, local fluctuations have little significance until a global trend emerges. The same is true of ecological drivers like deforestation or infectious diseases. Local ecosystem changes that are usually considered to have local impacts will have global impacts if a global trend develops. Global scenarios will need to consider the overall scale of ecological feedbacks, rather than continuing to categorize all ecosystem feedbacks as local.

Nonlinear feedbacks. Gradual changes in ecosystems may either elicit gradual and corresponding changes in global systems (linear responses) or appear to have no effect until a threshold is crossed and a strong, relatively sudden global response occurs (nonlinear responses). System responses that are strongest at particular scales are typically nonlinear. For example, the total area that a fire can burn from a single ignition is a nonlinear function of the number of flammable habitat patches in the land-

scape. The potential exists for small-scale ecosystem feedbacks to have disproportionately large effects, particularly as the effective scale of the problem changes from one hierarchical level to another. One of the challenges for global scenarios is to try to determine where important thresholds are located and at what point the net impact of local and regional feedbacks becomes global in nature.

Interactive feedbacks. Ecosystem feedbacks have the potential to interact with one another and to compound socioeconomic problems at global scales. Ecosystem feedbacks are unlikely to occur singly or in a way that is independent of context. For example, extensive clearing of woodlands for sheep pastures in Australia has resulted in a rise of the saline water table and a widespread soil salinity problem. Technological replacement of the ecological service of groundwater regulation (through pumping and water recycling) has been expensive and has reduced the profitability of farming in the area, with ramifications for social and economic systems that were already in a state of flux.

Although it is currently difficult to make rigorous predictions in each of these areas for most ecosystem feedbacks, we can at least conclude that local ecosystem feedbacks with effects that are cumulative, interactive, or nonlinear will lead to greater uncertainties in global models. One of the challenges for the future quantitative development of global scenarios will be to establish which ecosystem feedbacks are significant enough to warrant inclusion in global and regional models and which can safely be ignored.

have defined a system's stability domain. The stability domain can be conceptualized as a cup in which the ecosystem moves like a rolling ball. If the shape of the cup is altered, or the ball is knocked hard enough by some external agent, the system can escape its current stability domain and enter a new state. For example, gradual increases in phosphorus levels in a shallow lake can result in a regime shift that propels the lake from a clear water system to a turbid water system in a relatively short period of time (Carpenter et al. 1999b). Regime shifts have been documented in lakes, woodlands, deserts, coral reefs, and oceans (Scheffer et al. 2001). They are of high importance for scenarios because they usually have large impacts on ecosystem services and human well-being; because they often occur rapidly and with little warning, making them hard to predict and manage; and because they may be irreversible or extremely expensive to reverse, raising the possibility of long-term ecosystem degradation and the effective loss of ecosystem services.

The kinds of ecological feedbacks that either maintain system stability or result in regime shifts are incompletely understood. Three key areas in which further understanding would be valuable are the connectivity of ecosystem services, the role of cross-scale connections, and the question of what determines ecological resilience. It is unclear to what extent ecosystem services can be examined in isolation or should be considered as a coproduced ensemble. For example, differentiation in species (biodiversity) is the basis for variety in ecosystem services (Kinzig et al. 2001), because no single organism provides all ecosystem services; groundwater depletion may affect certain components of the biota but leave others untouched; and many organisms may be able to cope relatively well with a change in the variability of the global climate. Some case studies of tradeoffs between different ecosystem services are described in Chapter 12.

Cross-scale interactions complicate the analysis of ecological feedbacks. Systems may be highly resilient to human impact at one scale and very brittle at others. It is difficult to establish definitively the probability and plausibility of different scenarios without a more comprehensive understanding of the cross-scale properties of resilience, a topic that is currently a frontier in ecological research. The ways in which ecological processes interact to determine ecological resilience are poorly understood, and we have little ability to identify, detect, or monitor changes in the resilience of ecosystems—especially in the face of novel types of disturbance (Carpenter et al. 2001).

Difficulties also emerge in assessing the contribution of ecological feedbacks at a global scale. Global systems are hugely complex and may be highly resistant to change. It took a large amount of research to demonstrate that anthropogenic activities have influenced carbon dioxide levels in the atmosphere, and even more to demonstrate that these changes have altered global temperatures (Weart 2003). The significance of the contribution to global processes made by any system component, including ecosystems, is difficult to establish because of the multivariate complexity of the global system. Furthermore, many ecological processes are essentially homeostatic within a wide range of conditions, serving to regulate global systems and maintain their stability, and hence there may be few global signals that can be strongly linked to ecosystem change unless a major regime shift occurs. The lack of extensive evidence for global ecological feedbacks should not, therefore, be interpreted as implying that no such feedbacks exist.

One of the main themes of several previous global scenarios is that people will respond to environmental change rather than ignoring it. Societal responses to change, and the potential for changes in human values, are of central importance in the future. Existing values may themselves be either highly resilient or refreshingly adaptive. For example, the development of China's current forestry policy was initiated in part by severe dust storms in the seat of government, Beijing (Zhang et al. 2000; Zhuang et al. 2001).

If governments continue to act only when such clear and unmistakable signals of ecological degradation become apparent, then changes to the status quo may only come through an ecological perturbation of a magnitude greater than anything that we have yet experienced-which implies that the change in values that would be necessary for the formation of a true ethic of sustainability might only occur in response to the local destruction of a significant component of the environment. This Catch-22 situation is not explicit in the scenario literature and may make some existing global scenarios excessively optimistic. On the other hand, remedial actions have been taken rapidly in the past without a fundamental change in values. For example, the specter of a hole in the ozone layer led to the speedy adoption of the Montreal Protocol, which restricted the use of ozone-destroying chemicals (Beron et al. 2003; Mullin 2002; Powell 2002), although this response occurred in conjunction with the understanding that the industry creating the problem would in turn be the one to most profit from its solution.

Adoption of the Montreal Protocol required a rapid and coordinated institutional response. It was fortunate that the capacity for such a response existed. The capacity of institutions to respond to ecological change across a variety of scales is central to the creation of global scenarios. A mismatch in the scales of social, economic, and ecological processes may create inconsistencies in scenarios. For example, a true reformation of global markets (to incorporate evaluations of ecosystem services) would require a substantial rearrangement of the institutions responsible for managing economies and ecosystems. This would have to occur at many different scales, from global to local. Scenarios that envisage the emergence of ecological sustainability under the invisible guidance of the market would require that local institutions were able to manage ecosystem processes at the appropriate scales in order to avoid the kinds of scale mismatch problems described here (Spaargaren and Mol 1992).

To some extent, the idea that development will result in ecological concerns being addressed assumes that there are relatively direct and manageable links between ecological cause and effect that allow the causes of negative ecological outcomes to be identified and addressed. Ecological science suggests that while this is true in some cases, frequently ecological causation is complex, with impacts being produced at locations distant in time and space from their causes. If such complex causation is common, the costs of reactive approaches to ecological issues are likely to be high.

The capacity of institutions to respond to change often depends on the resources that are available to them and hence may be linked to the wealth of the society in which they occur. Economists have proposed that an inverted Ushaped relationship exists between the per capita income of a country and the environmental impact of its economic activities. This relationship, which has aroused controversy, is termed the Environmental Kuznets Curve after the relationship that the economist Kuznets found between income inequality and per capita income (Canas et al. 2003).

The model underlying the Kuznets Curve views environmental services as a luxury. It assumes that when people are poor the environment provides many services, and that development represents a trade-off between ecosystem services and economic growth; as societies become richer and can afford to sustain a wider range of environmental services, they are assumed to invest more money in environmental protection. Empirical research has supported the environmental Kuznets model for a number of regional atmospheric pollutants (Selden and Song 1994), but not for many other types of environmental degradation (Agras and Chapman 1999; Arrow et al. 1996; Dietz and Adger 2003). Gergel et al. (2004) show that an Environmental Kuznets Curve may be more likely for phenomena that are ecologically reversible or of concern for human health. Our current understanding of the Environmental Kuznets Curve may simply reflect the absence of studies designed to distinguish between alternative hypotheses; for instance, Bruvoll and Medin (2003) identify a range of other relevant covariates that do not necessarily parallel economic growth.

3.3.2 Value of Ecological Scenarios

Ecological scenarios will take into account existing ecological knowledge while recognizing the uncertainties that are present in any complex scientific analysis. One of the greatest contributions to be made by ecological scenario exercises will be to thoroughly work through the likely impacts of current resource exploitation and habitat conversion on the long-term sustainability of future human societies. Various estimates of the current human impact on Earth suggest that it is impossible to greatly expand human consumption of ecological production (Haberl et al. 2002; Rojstaczer et al. 2001; Vitousek et al. 1986). Wackernagel et al. (2002) have estimated that humanity is already exceeding the carrying capacity of the biosphere.

Contrary to the assumptions made by many economic models, continued increases in the production of ecosystem services over the long term will simply not be possible. Global ecological scenarios will highlight the regions in which declines in ecosystem goods and services are most likely to have significant impacts on human health and well-being. In particular, they will clarify the trade-offs that must be made between ecological, economic, and social capital, while also identifying the key ecological processes and ecological thresholds that can be used to guide policy responses. We also anticipate that ecological scenarios will aid in the development of appropriate measures (indicators) of change, relevant monitoring programs, and realistic policy and management goals by working through the range of multivariate interactions that may occur between ecosystems and people.

3.4 Relevant Ecological Theories and Ideas for Global Scenarios

Ecosystems have been defined by Tansley (1935) as "the fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment." (See also the MA Glossary in Appendix D.) Ecology is defined as the study of the distribution and abundance of organisms (Andrewartha and Birch 1954) or, more broadly, as "the scientific study of the processes influencing the distribution and abundance of organisms, the interactions among organisms, and the interactions between organisms and the transformation and flux of energy and matter" (IES 2004).

Ecology has produced numerous ideas that are relevant to the development of global scenarios. The ecological theories and ideas that are of the greatest importance for global scenarios are those that relate to global processes and broadscale spatial and temporal patterns. They can be categorized in four main groups: fundamental frameworks that underpin ecological thinking; community ecology theories, especially those that relate specifically to biodiversity, abundance, and other aspects of community composition that are of particular importance in the provision of ecosystem services; landscape and ecosystem ecology theories, especially those that deal with broad-scale spatial patterns and the movements of organisms or substances; and a more general set of ideas relating to prediction, forecasting, and uncertainty. This section summarizes the theories and ideas from ecology that we consider most important for global scenario exercises. In each instance we explain a little about the theory and its relevance to the development of scenarios. This list is necessarily incomplete; in particular, we have focused on ecological theories that are not described in detail elsewhere in this volume. We conclude this section with a short discussion of some of the topics that we still need to learn more about.

3.4.1 Fundamental Frameworks

3.4.1.1 Evolution

The theory of evolution is the central organizing idea in biology (Mayr 1991). We understand and interpret the diversity of organisms in the world according to the principles of descent, variation, and selection. Evolution gives us numerous insights into the nature of change in the natural world. Macroevolution (the origin and extinction of species) and microevolution (the adaptation of species to their environment) are both important to ecological scenarios.

Although the rate of speciation is slow by comparison to the time frames for which we design global scenarios, the rate of extinction is not. Rates of extinction currently exceed rates of speciation by around four orders of magnitude (Lawton and May 1995). This asymmetry in evolutionary processes explains why ecologists have become increasingly concerned about the recent accelerations in extinction rates; once lost, species that perform particular functions cannot be replaced at time scales that have any meaning for human society. Despite recent advances in genetics and biotechnology, we do not consider it plausible that these technologies will be able to restore extinct species effectively within the time period of this assessment. The many failures of attempts at species reintroductions from small numbers of captive individuals serve to underline this point.

Microevolutionary theory describes how natural selection drives changes in species attributes. Through natural selection, changes in the environment can produce changes within populations of species over a relatively short time period. Consequently, microevolutionary theory is particularly important for understanding possible changes in the behavior of short-lived species in response to anthropogenic modification of their environment, such as in predicting how ecological change will alter the epidemiology of disease (Anderson and May 1991; Daily and Ehrlich 1996) and how changes in ecosystems will affect the evolution of agricultural pests and their predators (Conway 1997). For example, many species of pests have rapidly evolved resistance to pesticides and appear to be evolving resistance to transgenic crops that incorporate the organic insecticide Bacillus thuringiensis (Wolfenbarger and Phifer 2000). Numerous examples of microevolution also exist for plants.

Few scenario exercises have considered either macroor microevolution directly. Speciation usually occurs slowly enough that it is not perceived as relevant over the time scales of most assessments. However, since evolution is the sole mechanism for the replacement of biodiversity, reductions in genetic diversity (including species extinctions and loss or reduction of distinct populations) are of extremely high concern. Microevolution is also an important issue for scenarios in which organisms with short life spans and relatively simple genomes may play an important role. In particular, the emergence of new infectious diseases and more virulent or drug-resistant pathogen strains has the potential to influence global scenarios, not only because of the possibility for the occasional massive epidemic but also because pathogen microevolution places a continuing burden on the economies of developing nations. (See Box 3.3.)

3.4.1.2 Hierarchy Theory

The issue of scale lies at the center of ecology (Levin 1992). As an ecosystem is examined at larger or smaller scales, the apparent magnitudes and rates of ecological processes change. The relationships between pattern (variation, heterogeneity) and process may also change as a function of scale. Hierarchy theory offers a way of organizing and visualizing the world as a series of scale-dependent units (Allen and Starr 1982).

The units that make up hierarchies are typically ordered from big to small or from fast to slow. In most hierarchies, the general principle applies that "upper levels constrain, lower levels explain." In other words, the mechanisms that

BOX 3.3

Ecology of Emerging Infectious Disease

The ecology of infectious disease has shaped human history. Diseases can have large effects on human populations, and humans have often facilitated the emergence of new diseases (McNeill 1976). Human diseases are concentrated in the tropics; about 75% come from other animals (Taylor et al. 2001). Disease has both direct and indirect social and economic consequences. For example, malaria kills and incapacitates millions of individuals every year and greatly reduces the economic growth of countries where it is endemic (Sachs and Malaney 2002). Understanding epidemiology depends not only on medicine and molecular biology, but also on disease ecology: the ways in which transformation of ecosystems alters the distribution and abundance of pathogens. Human interactions with ecosystems have changed over time through four main eras of disease (McMichael 2004):

- Agriculture brought people in close contact with domestic animals, such as cows and pigs, and parasitic species that occupied agricultural settlements, such as lice and rats. This contact provided the opportunity for the ancestors of many of the pathogens that cause disease (such as influenza, tuberculosis, leprosy, cholera, and malaria) to adapt from their animal hosts to infect humans.
- Conflict and trade among civilizations in Eurasia connected populations, allowing the spread of epidemic disease, and began a process that led to the co-evolution of people and their pathogens. Many epidemic diseases became endemic diseases, and urban populations developed disease resistance.
- European colonization connected diverse populations more tightly, spreading infectious disease to people with little previous exposure and causing horrific epidemics of measles, smallpox, and influenza on small oceanic islands, Australia, and most famously in the Americas. These epidemics affected entire civilizations and facilitated the European colonization of the temperate Americas, Australia, and New Zealand (Crosby 1986).
- Over the twentieth century, the expansion and increasing mobility of the human population produced a globalized community of pathogens. The ecology of infectious disease is currently being shaped by four main drivers: land use and land cover change, urbanization, human migration and trade, and diet.

People alter their disease environment in many ways, of which road construction, water control systems, and the conversion of forest to agriculture are of particular importance (MA *Current State and Trends*, Chapter 14). These ecological changes affect the abundance and distribution of both pathogens and their hosts, changing the timing and location of encounters between people and pathogens and altering disease dynamics.

Many emerging infectious diseases have spread from their animal hosts to people as people have cleared disease-rich tropical forests. Clearing disrupts existing host-parasite interactions and encourages the selection of strains suited to new, human-dominated environments by increasing the exposure of people and their domestic animals to diseases (Daszak et al. 2001). For instance, deforestation has coincided with increases in malaria in Africa, Asia, and Latin America. This increase is due in part to the creation of new areas of mosquito habitat in cleared land (Patz et al. 2004), as has occurred during the expansion of irrigation in India (MA *Current State and Trends*, Chapter 14). Leaky irrigation systems increase standing water, fields are often leveled to improve production, and irrigation has raised the water table (Tyagi 2004). Roads further impede the flow of water, creating pools of standing water that can increase populations of disease-transmitting mosquitoes and snails; people are also more likely to come into contact with water near roads and may encounter or introduce pathogens as they enter new areas (Patz et al. 2000).

Urbanization is an important component of recent patterns of land use/ land cover change. The world's urban population has been steadily increasing since reaching 1.7 billion in 1980 and is expected to reach 5 billion by 2030. At this time, 30% of humanity is projected to be living in cities of more than 5 million people. (See Chapter 7.) Drainage and water supplies are critical factors that determine the extent to which many diseases are either contained or propagated in urban communities. A combination of poverty and rapid, unplanned growth of urban populations can produce high-density areas that lack infrastructure for the safe storage and distribution of water and the drainage of wastewater. Failure to collect garbage increases the number of small pools of water that provide habitat for mosquitoes and can, for example, lead to epidemics of dengue fever (Patz et al. 2004).

Tourists and business travelers can carry infectious diseases from one region of the world to another, as has been the case with AIDS and SARS. The introduction of new diseases and new disease-transmitting organisms into a region is a form of "pathogen pollution" that places an increased pressure on public health efforts (Daszak et al. 2001). Furthermore, some researchers have suggested that today's rapid changes in the distribution of pathogens could favor the evolution of virulent diseases (Ewald 1994).

Human dietary demands and production practices can also influence disease emergence. Bushmeat hunting—the commercial hunting of wild animals—has lead to outbreaks of Ebola and monkeypox and has been linked to the emergence of HIV 1 and 2 (MA *Current State and Trends,* Chapter 14). Human-animal contact in production systems has been implicated in the emergence of Avian flu and SARS. Feeding herbivores to other herbivores that humans then eat has further contributed to the emergence of diseases of both livestock and humans. In recent times, one of the most notable of these has been the prion-caused bovine spongiform encephalitis, which manifests itself as Creutzfeldt-Jakob disease in humans and is thought to have been caused by feeding cattle with protein obtained from sheep with scrapie. All these emerging diseases have been facilitated by an increasing societal demand for meat.

explain a particular event usually originate at smaller scales (faster rates, smaller areas) while the potential of a particular unit is constrained by the levels above it in the hierarchy. For example, outbreaks of spruce budworm (a herbivorous caterpillar) in the northeastern United States and Canada can result in the defoliation and subsequent death of spruce trees over large areas. The lower-level mechanisms that explain budworm population dynamics are the reproductive rates of budworms and predation by birds (Holling 1988). Once the spruce trees grow sufficient foliage to provide protection from predation for the budworms, the budworm population can increase rapidly. The amount of food available for budworms to consume and the degree to which they are protected from predation by slow-growing foliage act as upper-level constraints on the ultimate size of the budworm population (Holling 1986).

For global scenarios, awareness of the hierarchical arrangement of the world is essential. In many cases the re-

gional properties of a particular location will constrain possible events at that location. Crop production in higher latitudes is constrained by the number of growing days in a season; growth rates of small towns are constrained by the national economy; and innovative management of natural resources may be constrained by tenure and property systems that operate at a higher hierarchical level than the individual. Many of the impacts in which we are interested involve top-down effects, such as where changes in a nation's economy can influence small-scale mining activities in remote regions (Heemskerk 2001). There are also bottomup effects where the cumulative impacts of small-scale changes result in changes at larger scales. Examples include the effects of individual car engines on the gas composition of the atmosphere, the fragmentation of landscapes by individual clear-cuts, and, in political systems, individual discontent rising in turbulent revolutions such as those in China and East Germany (Kuran 1989). It is essential that global scenarios are not naive about the possibilities for cross-scale effects, meaning both that such effects are invoked only where they are plausible and that their potential as agents of sweeping change is not ignored.

As an ecosystem changes, its dynamics vary in rate. Periods of slow accumulation of natural capital, such as biomass or soil, are interrupted by its abrupt release and reorganization (Holling 1986). Ecological disturbance releases natural capital that was tightly bound in accumulations of biomass and nutrients. Rare events, such as hurricanes or the arrival of invading species, can unpredictably shape structure at critical times or at locations of increased vulnerability. As resources enter and leave the system, and as system components enter new relationships with one another, ecological innovation can occur.

This dynamic tension between growth and destruction, between stabilization and disruption, appears to represent a key aspect of ecological dynamics. Stabilizing forces (those that push a system toward an equilibrium) maintain productivity and biogeochemical cycles. Destabilizing forces (those that push systems away from equilibrium conditions) serve to maintain diversity and create opportunity by removing portions of a population, reducing competition, making habitats available for colonization, and creating new niches (Gunderson and Holling 2002). For example, organisms may take advantage of unusual climatic events, fluctuating habitat conditions, or predator-free environments to achieve rapid increases in numbers (e.g., Bakun and Broad 2003). Similarly, forested areas that are cleared by fires or landslides offer opportunities for early successional species.

From the perspective of the MA, the key aspect of this conceptualization of ecological dynamics is that the connections between an ecosystem and the context in which it is embedded will change over time. Although ecosystems are typically constrained by top-down processes, there will be some periods during which they are vulnerable to disruption from bottom-up change (Peterson 2000b). A smallscale disturbance can trigger a larger-scale collapse if the larger system is vulnerable to disturbance. The introduction of shrimp into lakes in the Columbia River Basin provides an example of a small event triggering large-scale reorganization. The shrimp have caused the reorganization of the lake and surrounding ecosystems, as salmon populations and the species feeding upon them have declined and been replaced by bottom-feeding fish (Spencer et al. 1991).

As an ecosystem reorganizes following a disturbance, the remaining ecosystem legacies and surrounding large-scale systems provide the components and constraints out of which a system reorganizes. For example, the 1934 destruction of a dam on the Salmon River allowed salmon from neighboring watersheds to colonize the restored river and establish new populations (Wilkinson 1992). Without the maintenance of source populations in neighboring watersheds, recolonization would have been extremely unlikely.

We are not aware of any previous scenario exercises that have explicitly considered hierarchy theory. However, choosing spatial and temporal scales for analysis is a continual issue in any modeling exercise. Since processes at different scales can interact with one another in complex and unexpected ways, awareness of the hierarchical arrangement of ecosystems is essential for scenario exercises. Hierarchy theory will also provide the conceptual basis for models that predict the cumulative effects of local ecosystem feedbacks.

3.4.2 Theories from Community Ecology

3.4.2.1 Island Biogeography

Since the early work of Darwin and Wallace, island communities have been used as model systems in ecology (Quammen 1996). The theory of island biogeography has been the inspiration for many of the quantitative approaches currently used in population and landscape ecology. Mac-Arthur and Wilson (1967) noted that small oceanic islands tended to have communities that were composed of a subset of the species that were present on nearby mainland areas. They argued that community composition would be limited by the dispersal ability of its constituent species; poor dispersers would not be able to travel from mainland to island. As the distance of islands from the mainland increased, colonization by new species would become increasingly less likely. Similarly, species living on larger islands would be able to maintain larger populations and would be less likely to become extinct.

MacArthur and Wilson (1967) proposed that the community of species living on an island would be determined by the balance that was reached between the processes of colonization and extinction. They argued that island size was the principal determinant of the overall species extinction rate on the island and that the distance of the island from the mainland was the prime factor driving colonization. According to their framework, variations in these two factors would explain differences in community composition among islands. While a number of the extensions of this theory (such as the importance of the arrival sequence of new species on an uncolonized island) have been contested, its basic predictions have been strongly supported.

Island biogeography was one of the first formal, quantitative recognitions of the role of space and dispersal in determining community composition. Many theories that are currently used to predict the long-term persistence of communities rely on the same basic mechanisms of reproduction and distance-dependent dispersal. Islands of species habitat are not identical to oceanic islands because the degree of isolation is less, the area surrounding a patch of habitat on the mainland is likely to be habitable by many terrestrial species, and changes in terrestrial vegetation will not present the same type of barrier as the ocean provides to the dispersal of terrestrial species. Despite these differences, however, the basic tenets of island biogeography have been used to predict species richness and changes in biodiversity on continents as well as on oceanic islands (e.g., Davis et al. 2002; Fragoso et al. 2003; Lomolino and Weiser 2001; Sanchez and Parmenter 2002).

Global scenarios inevitably involve changes in the location and spatial pattern of human settlement and either the destruction or restoration of natural areas. Some areas are naturally patchy while others are naturally continuous but may be fragmented by humans. Island biogeography tells us how different populations of organisms will respond to these different conditions as a function of their dispersal ability and their proximity to potential sources of colonization. There are numerous models that allow quantitative estimation of the likelihood of population persistence in patchy landscapes (Bascompte 2003; Husband and Barrett 1996; Wennergren et al. 1995).

In scenarios, recognition of the impacts of land cover change on the distribution and abundance of species is integral to making connections between economic and social changes and likely changes in the provision of ecosystem services. This point is further elaborated in Chapter 10, where the species-area relationship and its relevance for the estimation of biodiversity are described in detail. Island biogeography makes it clear that scenarios must consider not only the amount of habitat change, but also its spatial pattern, since equivalent amounts of habitat reduction that occur in different spatial configurations can have very different implications for the provision of ecosystem services.

As far as we are aware, island biogeography has not been incorporated in previous scenario exercises. The relevance of island biogeography and related ideas (such as metapopulation theory and the design of corridors and reserve networks) for studies of ecosystem function is becoming increasingly apparent as humans fragment systems that were formerly continuous (Sanderson et al. 2002). Predictions about the sustainability of biodiversity and the continued provision of ecosystem services in fragmented landscapes will have to rely on island biogeography theory. Island biogeography and its offshoots will also provide the bridge for linking broad-scale satellite remote sensing assessments of land cover change directly to populations, communities, and ecosystems. Although the methods are at an early stage, Chapter 10 raises the possibility that future scenario exercises will be able to link quantitative simulations of land cover change to changes in biodiversity and the provision of ecosystem services.

3.4.2.2 Disturbance, Succession, and Patch Dynamics

One of the debates that has surrounded studies of small islands is whether they are more vulnerable to disturbances, in which case they would have an elevated extinction rate and should contain fewer species than expected from their location (Herwitz et al. 1996; Jones et al. 2001; Komdeur 1996; Whittaker 1995). Island biogeography recognizes disturbance as a major influence on ecosystems. The importance of disturbance has also been apparent in studies of vegetation succession as an answer to the question of why old-growth forests tend to be highly diverse instead of dominated by a single, highly competitive species.

The continual disturbance of areas within the boundaries of a particular ecosystem or community creates a mosaic of vegetation patches, each at different stages of succession. Successional processes create predictable temporal changes in communities, where hardy earlier colonizers are gradually replaced through time by slower-growing competitors (Vanandel et al. 1993). The spatial and temporal diversity that is produced by disturbance and succession allows a range of species to survive within the system (Levin 1992), even though individual patches may tend toward homogeneity. The development of patchiness (heterogeneity, variation) within an ecosystem, and the ways in which patches change through time and interact with one another, is termed patch dynamics.

Disturbance, succession, and patch dynamics are integral components of ecosystems. Human managers are often uncomfortable with processes that are not strongly regulated or controllable. Consequently, many management strategies have resulted in reductions in the number, intensity, and duration of natural disturbances such as floods, fires, and pest outbreaks. The net consequence of such decreases in natural disturbances is frequently to create a system that becomes increasingly vulnerable to other kinds of disturbance (Holling and Meffe 1996). For example, fire suppression in the United States in the middle of the last century allowed fuel loads to increase beyond their normal densities, resulting in huge and potentially catastrophic fires.

For global scenarios, it is important to recognize not only that disturbance regimes are integral parts of ecosystems, but also that systems tend to cope well with some kinds of disturbance but not others. Feedbacks may occur between the properties of landscapes and the kinds of disturbance that they experience. Disturbance regimes and their interactions with ecosystems can be major sources of surprises and shocks in scenario storylines.

Broad-scale ecological disturbances have been considered as drivers of change in previous scenario exercises. However, the focus of these analyses has typically been on anthropogenic drivers of change, such as CO_2 emissions, and abiotic responses, such as changes in the frequencies of extreme rainfall events or hurricanes. Ecosystems are often perceived as dependent on socioeconomic forces rather than as independent systems that can cause change in their own right. This perspective ignores the degree to which ecosystem characteristics influence their susceptibility to disturbance. For example, changes in albedo in Alaskan and Australian habitats can influence the frequency of lightning strikes that forests and grasslands experience and hence the number of fires that occur (Bonan et al. 1995; Higgins et al. 2002; Kasischke et al. 1995; Lafleur and Rouse 1995; Rabin et al. 1990). The vital role of natural disturbance regimes and patch dynamics in maintaining biodiversity and the continued provision of ecosystem services, as well as the two-way interactions between ecosystems and disturbance regimes, have not been considered in depth in any global scenario exercise.

3.4.2.3 Food Webs, Bioaccumulation, and Trophic Cascades

Each species within an ecosystem eats and is eaten by a limited set of the other species within an ecosystem. This network of feeding relationships constitutes a food web. The relative position of a species within a food web is termed its trophic level. Photosynthetic organisms, which receive their energy directly from the sun, are at the lowest trophic level. Trophic levels increase as organisms become more removed from primary production. Organisms at different trophic levels play different roles in ecosystems. Species at lower trophic levels tend to be abundant producers; those at higher trophic levels tend to be rarer and to act more as regulators of other populations.

The trophic level of a species predicts, to some extent, the response of the entire system to changes in the population of that species. For example, overfishing of Caribbean coral reefs has lowered populations of many herbivorous fish species. When sea urchin populations were suddenly affected by pathogens and hurricanes around the same time as several coral bleaching events, many reefs became dominated by algae (McClanahan et al. 2002). Changes in the composition and abundance of species at the top of the food web can have consequences that resonate through the food web in surprising ways (Pinnegar et al. 2000; Schmitz 2003; Snyder and Wise 2001). Species at high trophic levels are often large, long-lived predators with slow population growth rates. A decline in the populations of these species can initiate a trophic cascade, in which the abundance of species at lower levels of the food web increases as they are released from predation and species in the next lower trophic level in the food web are suppressed (Carpenter and Kitchell 1993b).

The trophic level of a species in the food web can also be used as a guide to the vulnerability of that species to contaminants in the food web. For example, mercury is concentrated in living tissue as it moves up the food web. Small fish in a lake may be unaffected by their low concentrations of mercury, but birds that eat piscivorous fish will accumulate a much higher level of mercury (Brant et al. 2002). This process is called bioaccumulation and is often associated with contaminants that are fat-soluble. Species at the top of a food web are more vulnerable to bioaccumulation than those at lower trophic levels. Humans, for example, are potentially vulnerable to the consumption of biomagnified contaminants that have accumulated in farmed salmon (Fairgrieve and Rust 2003).

An understanding of food web interactions, the feeding relationships between organisms, is important for global scenarios because disruption of individual food web components may have surprising effects on other organisms. For example, the removal of birds from a system can lead to increases in the abundance of the insect species on which they feed, resulting in pest outbreaks and reduced productivity of agriculture (Battisti et al. 2000; Crawford and Jennings 1989; Mols and Visser 2002). Similarly, the removal of large predators has resulted in increases in herbivore densities in many areas, reducing densities of plants (Terborgh et al. 2001).

Many trophic interactions have immediate importance for humans. An interesting example comes from the c. 50year periodic masting (flowering and fruiting) of *Melocanna bambusoides* bamboo plants in India. The ready availability of nutritious bamboo seeds after masting events can lead to rapid increases in rodent populations. High rodent abundance creates a subsequent problem for farmers, whose grain crops are vulnerable to rats once the brief pulse of bamboo production is over. Plagues of rats associated with bamboo masting have been blamed for famines in the northeastern state of Mizoram in 1861, 1911, and 1959 (John and Nadgauda 2002).

Trophic cascades and food web dynamics have entered into previous global scenarios where depletion of food stocks has been considered important, particularly in scenarios that have considered fisheries; but in general, the potential for nonlinear food web change (and its impacts) has been ignored.

3.4.3 Systems Approaches: Landscape Ecology and Ecosystem Ecology

Landscape and ecosystem ecology are focused on the study of broad-scale processes and patterns in ecology. Ecosystem ecology has traditionally focused on the movements of matter and energy through ecosystems. It has already made many important contributions to global scenarios, including models that describe fluxes of carbon, nitrogen, and phosphorus from soils through plants, animals, and decomposers.

Landscape ecology has been less on the agenda of scenario planners, although it also has potentially valuable contributions to make. One of its central tenets is the idea that the locations at which ecosystem processes occur and the spatial relationships between locations are important. Although habitat amount is of primary importance in determining the size and ultimately the persistence of populations, habitat arrangement becomes increasingly more important as habitat is lost (Flather and Bevers 2002). Percolation theory (Stauffer 1985) and neutral landscape models (Gardner et al. 1987) predict that the ease of movement of animals through a given habitat type should follow a logistic function, with a rapid decline in connectivity once 30-50% of habitat is lost (Plotnick and Gardner 1993). Recent studies have suggested that habitat arrangement may also affect equilibrial population densities (Cumming 2002; Flather and Bevers 2002) and predator-prey dynamics (Cuddington and Yodzis 2002). Ecosystem services are provided by populations of organisms. Consequently, global scenarios that seek to link ecosystems and human wellbeing will have to take into account the potential for local extinctions and population changes as a consequence of habitat arrangement, not just as a function of habitat amount.

The impacts of anthropogenic activities can be pervasive at broad scales. For example, Forman (1999) has estimated that up to a fifth of the United States is affected by roads. The relevance of this kind of habitat fragmentation will differ for different species, depending on their dispersal capabilities and habitat requirements (Poiani et al. 2000). Animals perceive and move through landscapes at distinct scales that relate to their body size (Holling 1992; Roland and Taylor 1997); habitat fragmentation is likely to have different effects on animals at different trophic levels. Larger terrestrial species will have larger home ranges and require more habitat; the relatively coarse grain at which they perceive the landscape suggests that they will be among the first species to be affected by habitat fragmentation. However, larger species may also be less vulnerable to predation and more capable of traveling through areas of suboptimal habitat (as witnessed by the persistence of the Florida black bear, for example).

Anthropogenic changes in landscapes have altered the ways in which plants and animals disperse. Human modification of the landscape has separated areas that were formerly continuous. For example, roads and cities create barriers to dispersal for a variety of organisms, forestry clearcuts and agricultural land conversion may disrupt landscapes that were formerly continuous, and impoundments reduce the connectivity of streams and lakes. Humans have also created novel connections between ecosystems that were formerly separate. Roads and trade (both terrestrial and marine) have resulted in the translocation of many species into new habitats, with huge consequences for people and the world's ecosystems (Crosby 1986).

Understanding the flows of energy, material, and organisms across landscapes integrates ecosystem and landscape ecology. In many instances, the continued provision of ecosystem services in a given area is dependent on exchanges of organisms, substances, or materials with other areas. This effect is termed a spatial subsidy. For example, many cities are built on the banks of large rivers. The continued provision of water by the river depends on the spatial subsidy provided by the upper watershed. Changes in the upper watershed, such as deforestation or increased numbers of livestock, can result in changes in the quality and quantity of water provided downstream, as well as affecting siltation, nutrient influxes to floodplains, and eutrophication of lakes. In small oceanic islands, soil fertility may be maintained by dust blown in from mainland areas (Chadwick et al. 1999), and recolonization by tree species after a hot fire may depend on dispersal from nearby forests.

There are a number of approaches to thinking about these kinds of phenomena, including ideas about boundaries and flows of substances and organisms through landscapes (Cadenasso et al. 2003); the spread of invasions (Muller-Landau et al. 2003), colonization, metapopulation, and island biogeography; and biogeochemical cycles that describe the movements of essential substances (such as water, carbon, calcium, nitrogen, and phosphorus) through ecosystems (Krug and Winstanley 2002; Newman 1995; Schimel et al. 1991; Singh and Tripathi 2000). Subsidies may also be temporal, such as through seeds that are stored in the soil.

Global scenarios will inevitably depict a variety of spatial patterns of anthropogenic activity and different degrees of infrastructure development, human settlement, and urbanization. They will also vary in levels of resource exploitation and the ability of communities or governmental organizations to cope with the management issues that are raised by changes in ecosystem connectivity. As connectivity between different areas changes, ecological processes will be influenced by increases or decreases in the variety and amount of spatial subsidies that they receive.

The responses of people to such changes may in turn create either positive or negative feedbacks between management actions and ecosystem services. For example, declines in water quality and the increased likelihood of flooding in rivers such as the Yangtse have largely been blamed on environmental changes in the upper catchment. The Chinese response to this problem has taken several forms. The ban on logging on the Tibetan plateau, which will serve to stabilize soils and improve water quality, may result in further positive feedbacks toward ecological enhancement (Zhang et al. 2000). By contrast, the construction of large impoundments such as the Three Gorges Dam is likely to create further ecological and social problems (resettling 2 million people, creating an impassable barrier for fish and mussel species, altering the natural variability of the downstream flow regime, affecting coastal fisheries and food security) while potentially solving the problem of flooding. This type of destabilizing ecological feedback, in which the anthropogenic modification of one set of ecological subsidies alters another set, can have important implications for ecological scenarios. Ecological trade-offs are described in more detail in Chapter 13 of the MA Multiscale Assessments volume.

Although global climate models and emissions scenarios have taken account of spatial patterns and flows of substances, in general the roles of ecosystem subsidies and changes in the configuration of habitats have been ignored in global scenario exercises.

3.4.4 Prediction, Forecasting, and Uncertainty

Human action now dominates the dynamics of many ecosystems. People generally make decisions based on their current knowledge and their expectations about the future. The heterogeneity, nonlinear dynamics, and cross-scale feedbacks that occur within ecosystems make ecosystem behavior difficult to predict (Holling 1978; Levin 1999). Although management decisions are often constrained by the amount of information that is available about the system, monitoring is frequently perceived as an irrelevant or excessively costly activity. In reality, people seldom have enough information to make reliable forecasts of ecosystem behavior (Sarewitz et al. 2000).

Even in situations where large amounts of data exist and there are relatively reliable and accepted ecosystem models, unexpected environmental variation can falsify predictions. Exogenous variables, such as changes in climate or disturbance regimes, can have enormous impacts on ecosystems and are often difficult to predict with great accuracy. For example, the El Niño-Southern Oscillation is a global weather pattern driven by the interaction between the ocean and the atmosphere in the central and eastern Pacific. ENSO alternates on a two- to seven-year period and exerts a strong influence on the productivity of fisheries in the eastern Pacific (Bakun and Broad 2003). Although our understanding of ENSO events is improving, it is still difficult to make precise and accurate predictions about its onset and impacts.

A considerable amount of variation in different variables can also be generated by processes that are endogenous to ecosystems. For instance, relatively high levels of variability in the relationship between phosphorus and chlorophyll production in freshwater lakes can be generated by changes in food web structure (Carpenter 2002), and ecosystemclimate coupling can produce complex behaviors in weather systems (Higgins et al. 2002). Predictions about social systems may also be falsified by both exogenous and endogenous drivers. For example, fluctuations in the global market (an exogenous driver) can have unexpected effects on local communities, and the formation of new political organizations (an endogenous driver) can result in broader societal change, such as when the organization of rubber tappers in the Amazon stimulated new approaches to forest management.

The uncertainty associated with ecological statements about the future is seldom evaluated in a rigorous manner. In particular, the problem of model uncertainty is often ignored in ecology, even though statistical methods are available to address the issue (Clark et al. 2001). Rigorous evaluation of the uncertainty associated with an ecological prediction usually indicates that a forecast is quite uncertain, meaning that it assigns roughly equal probability to a wide range of different outcomes. The weaknesses of ecological predictions are typically exacerbated by their reliance on drivers that are difficult to predict, such as human behavior. The reflexivity of human behavior further constrains the reliability of ecological predictions (Funtowicz and Ravetz 1993); if predictions are made and taken seriously, people will change their actions in response to the predictions, making accurate forecasts difficult (Carpenter et al. 1999a). For example, a coordinated global response to climate change could make current predictions based on highemissions scenarios incorrect.

Despite the difficulties of producing reliable forecasts, people need to make decisions about the future. Carpenter (2002) suggests that three ways in which science can contribute to decision-making include obtaining a better understanding of ecological thresholds and dynamics, assessing uncertainty more rigorously, and using scenarios as tools for thinking through the possible consequence of decisions and the ways in which unexpected events may influence their outcomes. The narrative form of scenarios makes them more accessible than many other kinds of scientific information. Their accessibility provides a forum for dialogue between scientists, the public, and decision-makers, which can be useful for addressing complex issues of high public concern (Funtowicz and Ravetz 1993; Kinzig et al. 2003).

Questions of prediction, forecasting, and uncertainty have been major concerns in several past scenario exercises, most notably the IPCC scenarios (Nakićenović and Swart 2000). These questions relate more to the applications of scenario planning than to their internal consistency. One of the main benefits of attaching estimates of uncertainty to the events that are envisaged in scenarios is that uncertainty estimates give scenario users an indication of the degree of scientific confidence in individual forecasts. The risk of presenting uncertainty estimates is that they may become an excuse for failing to act. In general, since the risks of mismanaging ecosystems are so large, the precautionary principle should be applied (Harremoes et al. 2001); managers should try, where possible, to keep systems well clear of key thresholds that might lead to ecosystem degradation.

3.4.5 The Application of Ecological Theories in Scenarios

The ecological theories just described are relevant to global scenarios. We envision that they will be applied in different ways and at different scales of analysis in different contexts. Evolution and hierarchy theory provide a basic context for thinking about ecosystems and their interactions with social systems. Evolution (including the study of the fossil record) offers a long-term perspective on environmental change and the ways in which species responded to it in the past and provides a frame of reference for thinking about how species may respond in the future. Microevolution is a likely source of ecological feedbacks, particularly those relating to pests and pathogens. Hierarchy theory is relevant in any context in which some kind of change in space or time is posited. Hierarchies offer a structured approach to problems of scale and for thinking about the interactions of processes and patterns that occur at the same scales or different ones. Scenarios will need to justify the lower-level mechanisms that create system changes and to take into account the upper-level constraints on what is possible. Coping with the concept of scale and the dynamics that are generated by cross-scale interactions, particularly the possibility for broad-scale regime shifts, remains a major challenge for scenario development.

Theories from community ecology, ecosystem ecology, and landscape ecology are especially relevant for scenarios that incorporate anthropogenic impacts on the environment. They will be applicable in situations where humans extract resources, alter the flows and movements of energy and materials, or change land use or land cover. Hunting and fishing, logging, fruit and nut extraction, and other activities that have focused impacts on particular components of the ecosystem will set in train a series of knock-on effects that may be transmitted through the food web. Alterations in temperature and rainfall regimes will have profound effects on nutrient cycles, the domain of ecosystem ecology. Changes in land use and land cover will affect the broaderscale context in which communities of organisms live and may disrupt processes such as migration and gene flow. Although many of these feedbacks are typically characterized as local, they may have larger impacts under certain conditions.

3.4.6 What Don't We Know?

Consideration of uncertainty makes it clear that in many cases we know less than we think we do. There are also areas of ecology about which we are spectacularly ignorant or whose true importance we have only recently started to recognize. One of the most critical areas for global scenarios concerns the connections between ecosystem patterns and ecosystem processes. Current global models for ecological variables produce estimates of changes in patterns based on a mixture of correlative and mechanistic understanding. We urgently need better models that link likely changes in landscape patterns to likely changes in essential ecosystem processes, including nutrient cycles, primary production, and community dynamics (such as predator-prey cycles, trophic cascades, and pest outbreaks).

The loss of species and the functions that they perform is closely related to changes in habitat. There has been considerable debate over the question of whether higher species diversity results in greater community stability and/or resilience (Ives and Hughes 2002; Ives et al. 2000; Pimm 1984). Relevant questions include whether more diverse communities are better able to survive extreme disturbances. whether more diverse communities are more vulnerable to invasion by introduced species, and whether ecosystem function is more likely to be maintained in a diverse community, assuming that diversity includes "redundant" species that perform similar functions to one another but have different environmental tolerances (Huston 1997; Loreau et al. 2001; Naeem 2002; Tilman et al. 1996; Walker et al. 1999). Furthermore, there is little understanding of how changes in the interactions between species at different scales influence ecosystem function (Peterson et al. 1998).

Our current understanding of ecology is also weak in the area of long-term and large-area ecological dynamics (Carpenter 2002). Studies of ecological processes at very large spatiotemporal scales are rare, partly because the necessary data are so hard to obtain. Our understanding of the relative importance of different variables may change when analyses are undertaken at broader scales. For example, local studies of the Caribbean Sea often ignore the impact of the Amazon and Orinoco outflows on water quality and circulation patterns (Hellweger and Gordon 2002). At broad scales, the magnitude and even the direction (positive versus negative correlation) of relationships that have been established at finer scales may change (Allen and Starr 1982). Broad-scale processes are of high importance for global scenarios because they often provide the slowly changing variables that can force ecosystems from one state to another (Bennett et al. 2003).

3.5 Placing Ecology in a Socioeconomic Context

Ecological knowledge arises and is applied in a socioeconomic context. In each of the MA scenarios, the causes and consequences of ecological change depend on the nature of the interactions between ecosystems and socioeconomic systems. The scenarios explore not only the importance of ecological dynamics for human societies, but also the consequences of alternative approaches to ecosystem management. Approaches to ecological management can be organized using the concepts of uncertainty and controllability.

3.5.1 Ecological Uncertainty and Control

In human societies there are different ways of knowing, ranging from the formal structures of science to less formal knowledge systems such as customs and traditions. Regardless of the variety of knowledge in question, however, knowledge is used whenever decisions are made. People who make decisions about natural resource management generally take into account both what they know and what they are capable of achieving. It is difficult to track ecological knowledge through global scenarios, but it is clear that ecological knowledge is more likely to increase in scenarios in which people work with ecosystems and have structured ways of learning from their experiences. (See MA *Multiscale Assessments*, Chapter 5.)

High levels of uncertainty correspond to a lack of ecological knowledge and hence an inability to predict future aspects of system behavior. The degree to which aspects of system behavior are predictable affects both the likelihood that a given management action will achieve its desired aim and the ease of obtaining social approval for the action to be taken. Where uncertainty is high, costly interventions are less likely to be approved and a command-and-control management approach is unlikely to be successful. Depending on the context, high levels of uncertainty may have different effects on management. Uncertainty can lead to inaction because it can be hard to determine the best course of action when uncertainty is high. Uncertainty can also provide opportunities that inspire action by fostering the belief that the future is malleable and that desired futures are attainable (Ney and Thompson 2000). Last, uncertainty can encourage humility and tolerance, because managers and stakeholders are ignorant of what the future will bring and may find that the plans and beliefs of others are more effective or correct than their own.

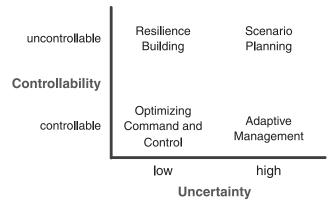
The controllability of ecological processes by management actions depends on aspects of both the ecosystem and the social system. Available technologies influence the controllability of ecosystems; for example, it is currently easier to add nutrients to a system than to remove them, to control access to an island than to an offshore fishery, and to monitor and regulate a stream rather than groundwater. A second component of controllability is the willingness and ability of a group of people to coordinate their ecological management actions. Changes in ecological controllability can occur due to social change, such as increased agreement on what constitutes fair or good management, or changes in technologies relating to ecosystem services (e.g., Kiker et al. 2001). Throughout history, groups of people have organized ways of managing water, game, and fisheries (Berkes 1999), with varying degrees of success. Governments have

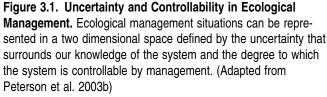
frequently expropriated resources from local people and then been unable to manage the resources effectively, as a consequence of passive or active resistance to their policies. The increased level of interest in community-based conservation in recent decades is largely due to the failure of coercive and nonparticipatory environmental management practices (Agrawal and Gibson 1999).

The appropriateness of a given approach to ecosystem management depends largely on the degree of uncertainty about a system's behavior and the degree to which the system can be controlled. (See Figure 3.1.) Optimizing approaches make sense when a system is controllable and known. Resilience-building approaches to management are more appropriate when a system is difficult to control but understanding of its dynamics is high. When understanding is lacking, learning-based approaches are appropriate. If control is possible, adaptive management can be useful; if control is difficult, however, more exploratory and dialogue-centered techniques are likely to be needed and the focus shifts from ecosystem management to societal adjustment. Many of our most pressing environmental problems, such as concern over the ecological impacts of transgenic organisms or the local impacts of climate change, are situations in which control is difficult and uncertainty is high. These problems appear best suited to open ecological management practices that engage an extended community in defining and analyzing the socioecological context (Funtowicz and Ravetz 1993).

3.5.2 Command and Control

Managers have historically tended to view ecosystems as places in which isolated, individual provisioning ecosystem services exist and can be enhanced. This optimization approach has largely been implemented via the goal of "maximum sustained yield." The MSY approach combines quantification and technical understanding with commandand-control management to attempt to produce the maximum achievable continuous supply of an ecosystem service.





It has been the guiding philosophy of agriculture, forestry, hunting, and fishing.

Fisheries management provides many rich examples of MSY applications. The concept of MSY in fisheries was developed in the early twentieth century but was formalized, extended, and extensively applied following World War II (Clark 1985; Ricker 1975; Schaefer 1954). MSY approaches were largely based on fitting a population growth curve using estimates of current numbers of fish and their reproductive rates and then setting a level of exploitation that maximized the biomass or the monetary value (or some other criterion determined by the manager) of the catch. Difficulties in measuring fish populations, identifying stocks, enforcing regulations, and coping with environmental variation all present challenges to the MSY approach, as does managing political intervention in the process of setting sustainable catches.

Despite good progress in fisheries stock assessment in addressing many of these challenges (Hillborn 1992), it is difficult to find a case where MSY fisheries management has unequivocally succeeded. Indeed, the concept of MSY appears to be an idea that is more resilient than the fisheries it has been used to manage. For example, Larkin (1977), a prominent fisheries scientist, argued nearly 30 years ago that MSY should be abandoned because it risks the catastrophic decline of populations, it fails to recognize the role of trophic interactions, and it is not necessarily desirable in economic terms. Despite these warnings and the poor track record of MSY, it has continued to dominate fisheries management.

More generally, the command-and-control approach adopted by MSY views ecological management as a straightforward process of problem definition, solution development, and solution implementation (Holling and Meffe 1996). Solutions are expected to be direct, appropriate, feasible, and effective over relevant scales. Command and control is expected to solve the problem either through control of the processes that lead to the problem (such as hygiene to prevent disease) or through mitigation of the problem after it occurs (such as pathogens killed by antibiotics). A command-and-control approach assumes that the problem is well bounded, clearly defined, relatively simple, and follows a linear or nearly linear relationship between cause and effect. Most of the problems with command and control arise when it is applied to complex, nonlinear systems that show low levels of predictability. Unfortunately, many ecosystems (and most ecological problems) fit this description. Societal recognition of the weaknesses of command and control approaches to natural resource management, and the degree to which the search for alternatives is successful, is a key aspect of the MA scenarios.

3.5.3 Managing for Resilience

Managing for resilience is intended to increase the ability of a system to cope with stress or surprise. It is an approach that has been advocated in situations where control is difficult but where there is understanding about how the system works. This approach has arisen in response to failures of command-and-control management. It is based on the argument that rather than maximizing production of individual ecosystem services, the central goal of ecological management should be to maintain a range of supporting and regulating ecosystem services to ensure the reliable supply of provisioning services. Resilience theory offers a framework for understanding the supporting and regulating systems that maintain ecosystem organization (Holling 1973; Peterson et al. 1998).

The aim of management for resilience is to maintain ecosystems that can persist despite environmental changes, management mistakes, and unexpected events (Gunderson and Holling 2002). Managers can do so by enhancing the ecosystem services that regulate and maintain the ecosystem. For example, lakes in the U.S. Midwest can be managed for resilience by the manipulation of lake food webs. Many of the agricultural areas in the Midwest have experienced large increases in soil phosphorus, and lakes in the region are vulnerable to eutrophication from high-nutrient runoff. Controlling runoff is very difficult. An alternative approach to coping with the increased stress on lake ecosystems is to increase lake resilience to phosphorus loading. This can be done by ensuring that lakes have a robust food web that includes substantial populations of piscivorous (fish-eating) fish (Carpenter and Kitchell 1993). An increase in these leads, via a trophic cascade, to increases in populations of the large herbivorous zooplankton that prey on lake algae. Increases in zooplankton populations decrease the likelihood that increased phosphorus loading will tip lakes into an alternate state where undesirable algal blooms occur.

The ability of a service to persist depends heavily on its response diversity—the variation of responses to environmental change among species that contribute to the same ecosystem service (Elmqvist et al. 2003). Increasing response diversity, such as by allowing the recovery of a diverse set of fish species with different responses to environmental change, can further increase resilience. While ecosystem management is increasingly aimed at managing for resilience, the capacity for managers to do so has been limited by a lack of models and tools for understanding resilience in ecosystems (Carpenter 2002). Socioecological researchers are actively working to fill this gap (Berkes et al. 2003).

3.5.4 Adaptive Management

A second alternative to command and control is adaptive management. This is a systematic process for continually improving management policies and practices by learning from the outcomes of operational programs. It is particularly appropriate when there is uncertainty about how an ecosystem functions and managers have some ability to manipulate the environment.

Adaptive management regards policies as alternative hypotheses and management actions as experiments (Holling 1978; Lee 1993; Walters 1986; Walters and Hilborn 1978; Walters and Holling 1990). This approach is very different from the typical "informed trial-and-error" approach, which uses the best available knowledge to generate a risk-averse, "best guess" management strategy that is only changed as new information becomes available. Practicing adaptive management involves identifying uncertainties and then establishing ways to reduce them. It is a tool not only to change the system, but also to learn about the system. The key scientific and social aspects of adaptive management include the following: a link to appropriate temporal and spatial scales; a focus on statistical power and controls; use of computer models to synthesize and build an embodied ecological consensus; use of embodied ecological consensus to evaluate strategic alternatives; and communication of alternatives to the political arena for the negotiation and selection of a management action (Holling 1978; Lee 1993; Walters 1986). In its strongest form-"active" adaptive management—interventions are designed to experimentally evaluate alternative hypotheses about the system being managed (e.g., Prato 2003).

Adaptive management is particularly useful in situations where management intervention is possible and there is a focus on the development of scientific knowledge for ecological intervention. These processes are appropriate in social contexts where technical understanding is used as the basis for ecosystem manipulation, but they are less likely to be successful in situations where ecological dynamics are not considered in decision-making or where ecosystem manipulation is unfeasible.

3.5.5 Social Learning

The degree to which learning, adaptation, and innovation can occur in socioecological systems shapes the ability of that system to cope and respond to the emergence of poorly defined and understood ecological problems. Resilience theory identifies three types of social learning (Gunderson and Holling 2002): incremental, lurching, and transformational.

Incremental learning occurs during phases of gradual system change. In this instance, the process of learning involves the collection of data or information to refine existing models. It is based on the assumption that models of how the world works are structurally correct, but imprecise. Incremental learning is similar to the process of single-loop learning described by Argyris and Schoen (1978). In many cases, organizations view this type of change and learning as problem solution (Westley 1995).

Lurching learning is episodic, discontinuous, and surprising. It often occurs when a system changes, making inadequacies in a previously acceptable model more apparent. For example, inadequacies in food production and distribution systems often emerge during drought years. Lurching learning is frequently stimulated by an environmental crisis that makes policy failure undeniable (Gunderson et al. 1995). In this case, where the underlying model is questioned and rejected, the learning process is described as double-loop (Argyris and Schoen 1978). It is also characterized as problem reformulation. In organizations, lurching learning is frequently facilitated by outside groups or charismatic leaders.

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Transformational learning is the most profound type of learning and is often a consequence of dramatic system changes. It is characterized by the emergence of novel or unexpected outcomes from complex, nonlinear, and/or cross-scale interactions. Transformational learning involves the identification of the variables that define the domain, in multivariate space, of the system of interest (Ludwig 2001). Defining or bounding variables are typically broad-scale and slow to change. For example, phosphorus levels in sediments are a bounding variable for lake eutrophication (Carpenter et al. 1999b). Transformational learning occurs via the assimilation of knowledge about slowly changing variables into the views of managers and policy-makers, including recognition of the possibility that slow variables may create surprises (such as the nonlinear shift from clear to turbid lake water). Examples of transformational learning in the ecological sciences include the discovery of and response to the Antarctic ozone hole and the discovery of the bioaccumulation of DDT and the resulting control of the use of DDT and other persistent organic pollutants. Transformational learning has also been described as evolutionary learning (Parsons and Clark 1995), where not only new models but also new paradigmatic structures are developed (Kuhn 1962). Transformational learning differs from doubleloop learning in that it involves substantial alterations to a dominant worldview.

Social learning processes allow groups of people to develop new adaptive responses to various types of surprising situations. Consequently, the possibilities for social learning present in each scenario will determine the capacity of people to respond to ecological surprises.

3.6 Ecosystem Management and Economics

Ecological and environmental economics have sought to understand how economics shape people's interactions with ecosystems, and how economic incentives can be used to improve ecological management. The complexities of both human behaviors and ecosystems make the application of economic theory to economic management difficult. For example, indicators commonly monitored by governments are unlikely to accurately reflect ecosystem resilience (Deutsch et al. 2003). Three of the more active areas of research at the nexus of ecology and economics are the use of economics to improve the efficiency of ecological management, the assessment of the value of ecosystem services to improve decision-making, and conflicts over property rights to nature.

3.6.1 Economics and Ecology

Understanding human behavior is important for natural resource management because ecology alone is insufficient to explain the dynamics of human-dominated ecosystems. Humans, individually or in groups, can anticipate and prepare for the future to a much greater degree than ecological systems can (Brock and Hommes 1997; Westley et al. 2002). Human views of the future are based on mental models of varying complexity and completeness. People have developed elaborate ways of exchanging, influencing, and updating their mental models of both the past and the future. Individual and societal perspectives on the future can create complicated dynamics that are influenced by access to information, ability to organize, and power.

By contrast, although some components of ecosystems are capable of "anticipating" future changes—for instance, many bats undergo reproductive delays that allow their offspring to be born at a time of year when food is abundant (Bernard and Cumming 1997)—the behavior of ecological systems is based primarily on the past. Ecological dynamics are the products of the mutual reinforcement of many interacting structures and processes. The behavior of ecosystems emerges from the successes of past evolutionary experimentation at the species level. The fundamental differences between human and ecological behavior mean that understanding the role of people in ecological systems requires not only understanding how people have acted in the past, but also what they think about the future.

Many economic ideas have been applied to understanding the dynamics of socioecological systems. One key distinction that economists have drawn from coupled economic-ecological models is the need to consider that economic activity anticipates the future. Economic criticisms of the early global environmental modeling work *The Limits to Growth* (Meadows et al. 1972) argued that the conclusions were flawed because people's views of the future were not incorporated into the models. Specifically, economists argued that people will shift their spending and investments as their perceptions of their current and future situation change. Many global models of ecosystem and economic change have not included these dynamics.

The economic concept of rational expectations proposes that people's actions are based on what they think will change in the future and how other people will respond to those changes. If people's behaviors are based on their expectation of what will happen, and this expectation is based on a prediction of the behaviors of other people, then when the world is well understood, such expectations will cause individual behaviors to converge rapidly. However, when the world is poorly understood many possible behaviors become equally likely. Consequently, when the world is unknown and difficult to understand, the consequences of individual rational behavior can make the future more difficult to predict (Brock and Hommes 1997). Game theory is one area of economics that allows for an analysis of this type of socioecological dynamic, but game theory for ecological management is still at an early stage (Brock and de Zeeuw 2002; Roth 2002; Supalla et al. 2002).

Another key insight from economics is the value of markets for distributing knowledge, observations, and decisionmaking for ecological management (Scott 1998). The successful development of markets for ecosystem services is an exciting advance in economics that shares important similarities (and some differences) with the economics of public and club goods, such as policing and intellectual property rights. Recent work has examined the design of markets for pollution emissions and genetically modified crops (Batie and Ervin 2001).

3.6.2 Valuation of Ecosystem Services

A second area in which the integration of ecology and economics may make a large contribution to scenarios is through the valuation of ecosystem services. Many decisionmaking processes involve some sort of cost-benefit analysis that attempts to convert all costs and benefits into a single currency that can easily be compared. Doing this with ecosystem services is difficult, however, as most ecosystem services are not traded in markets and consequently do not have prices. To improve people's ability to evaluate ecological management decisions involving a mix of market and nonmarket values, it is sometimes useful to illustrate the nonmarket economic value of services provided by ecosystems. Valuation is not necessary for many types of decisions, as people do not place economic values on many things they prize, such as freedom or democracy, and do not necessarily conserve things that they value. The valuation of ecosystem services is difficult, and only appropriate in specific situations, but it can illustrate the value of investing in natural capital. (For more details on ecological valuation, see MA 2003, Chapter 6.)

Some types of evaluation use market prices to estimate the value of ecosystem services. Hedonic prices, travel costs, and replacement costs all use techniques that estimate the marginal value people attach to a service (Heal 2000; Wilson and Carpenter 1999). That is, these approaches estimate how much a small change in the supply of a specific ecosystem service would be worth. They can be difficult to apply in cases where market data are lacking. In such situations, contingent valuation—the statistical analysis of questionnaires that ask people how much they would pay or spend for a specific ecosystem service—is used to estimate the marginal value of services.

Ecological valuation usually differentiates between use and non-use values. Use values derive from the use of a service, such as clean water. Non-use valuation of ecosystem services arises from diverse cultural, religious, ethical, and philosophical sources. Some of these values are strongly held and have endured for centuries. Some have decreased over time, while other new values have emerged. Worldwide concern for animal rights is an example of a relatively new movement that has had major impacts on how many societies view their relationship with animals. Intrinsic values can complement or counterbalance utilitarian values. For example, the Endangered Species Act in the United States is an expression of the view that human action should not directly cause extinction. This value is distinct from the economic value of the species that it protects. Similarly, many people donate money for tiger conservation because they value the existence of tigers in the wild, without expecting that they will derive an economic benefit from the presence of tigers.

Valuation does not solve the problem of who should have rights to use ecosystem services. Nor does it define good management or answer the question of how to construct institutions or markets that provide economic incentives to manage ecosystem services well (Martinez-Alier 2002). These issues, along with the technical and definitional problems surrounding ecosystem services, can lead to large differences between the values placed on an ecosystem service by different parties (Wilson and Carpenter 1999). Despite these difficulties, even the gradual and partial assignment of new property rights to ecosystem services (such as carbon credits and emissions trading) is likely to have substantial impacts on future scenarios.

One concern is that the partial incorporation of property rights for ecosystem services may have perverse or unexpected impacts on ecological services that remain open access. For example, assigning property rights to forests based solely on their role as producers of timber has been partially responsible for the undervaluation of the many other ecosystem services that forests provide (Scott 1998). However, valuation can provide useful information for dialogues about complex ecological management issues, which may help people develop better assessments of the trade-offs and synergisms among different sets of ecosystem services.

The complex interrelationships of ecosystem components complicate the creation and allocation of property rights that provide social and economic benefits. Ecosystems produce many different services, often at different scales, and the maintenance of ecosystem function may also depend on spatial or temporal subsidies that occur between systems. For example, a forested watershed can simultaneously provide clean water to downstream ecosystems, a habitat for migrating songbirds, and timber for a property owner. Conflicts over ecosystem change and use frequently relate to issues of who should own or control different ecosystem services (Martinez-Alier 2002). These questions are largely political; little economic theory has been developed to cope with them, although there has been substantial research on understanding common pool resources (Committee on the Human Dimensions of Global Change 2002; Levin 1992; Ostrom 2003).

3.6.3 Ecosystem Management and Political Ecology

Political ecology—the study of the relationship between nature and society—arose out of a theoretical need to integrate local situations into a political economy that often transcended the local (Blaikie and Brookfield 1987; Peet and Watts 1993; Schmink and Wood 1992; Watts 1983; Wolf 1972). Its basic theoretical framework encompasses "the constantly shifting dialectic between society and landbased resources, and also within classes and groups within society itself" (Blaikie and Brookfield 1987).

A focus on the structure of human systems has dominated much recent writing about political ecology (Martinez-Alier 2002; Pred and Watts 1992; Rocheleau et al. 1996). These approaches could be described as the political economy of natural resources, rather than political ecology, because they consider ecosystems primarily as passive objects that are transformed by human actors. An ecological political ecology should incorporate the active role of ecosystems as agents of political change, and an understanding of their diversity and dynamics (Peterson 2000a; Robbins 2004). The ecological services and resources that are available at a given time and place determine the alternatives that are available to people. This set of alternatives shapes the politics, economics, and management of ecosystems. However, constraints imposed by ecosystems are fluid, because ecosystems are dynamic and variable.

Ecological approaches to management will be strengthened by an understanding of political dynamics as they relate to human actions. Natural scientists frequently disregard the politics of human societies (Martinez-Alier 2002). This attitude can lead to scientific recommendations that ignore important determinants of human behavior, such as the political forces that influence what and how people learn, the political dimensions that determine which events are considered crises, and what kinds of things are considered to be property. Such blind spots may cause scientists to provide advice or formulate policy that is either spectacularly inadequate or may be open to disastrous misuse (Gunderson et al. 1995; Ludwig et al. 1993). The social consequences of such failures can be severe.

3.7 Application of Theory to Scenario Storylines

The ecological concepts described in this chapter are relevant to the MA scenario storylines in many different ways. A number of valuable insights relating to the role of ecology and ecosystem services in scenario exercises have emerged from the MA process (summarized in Table 3.1). This list is not exhaustive; it is intended as a summary for decisionmakers who are wondering why they should be concerned about ecosystems.

Differences in the relationships between people and ecosystems are the main driver of differences among the MA scenarios. Key aspects of the relationship between people and ecosystems include the ways in which people learn about ecosystems, the approaches people take toward ecological management, and the extent to which ecosystem services are incorporated in economies and economics. The nature of ecosystem management will inevitably change as societies accumulate knowledge. Approaches to ecological management depend on people's abilities to control ecosystems as well as their certainty about ecosystem dynamics and their confidence or risk adversity in applying this knowledge. The degree to which future decision-making considers ecological trade-offs will be an important determinant of ecosystem and societal change. The scenarios explore these differences by considering alternative futures under different degrees of societal learning.

3.8 Synthesis

The importance of ecosystems as a sustaining, interactive partner to human social and economic systems emerges strongly from this volume. In Chapter 1 the necessity of ecosystem services for human well-being is described. Society has not always given enough thought to its future need for ecosystem services. In recognition of this failing, the MA scenarios have built on past scenario exercises (see Chapter 2), acknowledging both their strengths and their weaknesses.

In this chapter, we first explain why the future of ecosystem services should be of particular concern as the human population increases and resource scarcity becomes increasingly more likely. Since ecosystem services play an essential role in our societies, greater consideration of ecosystems is needed in policy and management decisions. The rigorous inclusion of ecology in global scenarios is an important step toward bringing ecosystems back onto the stage of global decision-making. Previous scenario exercises have not given ecosystems adequate consideration or recognized the potential for the disruption of social and economic processes that can occur when the flow of ecosystem services is reduced or removed. The discipline of ecology has made considerable progress over the last 50-100 years in developing and testing quantitative approaches and conceptual frameworks that can be useful in assessing and understanding the impacts of anthropogenic modification of our environment, although ecological theory needs further development in many areas to address newly emerging global issues.

Knowledge of ecology is not sufficient on its own to produce effective and sustainable management of natural resources. The future of ecosystems is also dependent on our achieving social, political, and economic awareness of their importance, and on placing ecology in a socioeconomic context, so that decision-makers who are not ecologists can apply ecological theory effectively. The need for interdisciplinary approaches to management and policy decisions that affect multiple spheres is in many ways self-evident. However, achieving the balanced view that we consider necessary for long-term sustainability will require that societies develop the capacity to learn and to adopt flexible management approaches that can be modified as environmental conditions change. Fostering a flexible learning approach is one of the greatest challenges facing managers and policymakers. Ultimately, although the social, ecological, and economic issues described in this chapter could play out in many different ways in the future, a number of key principles emerge that will be relevant in all instances.

The MA has used many of the same quantitative models (see Chapters 4–7) that have been applied in past scenario exercises, although the MA storylines attempt to introduce a greater awareness of ecological relevance into the process. Unfortunately, the majority of existing quantitative approaches for making socioeconomic projections at broad scales do not explicitly incorporate ecosystem feedbacks. Many of the principles that are described in this chapter are thus applied qualitatively rather than quantitatively in the scenario storylines. (See Chapters 8 and 9.) Ecologists have not always made the relevance of their research clear to practitioners in other disciplines and have frequently been naive about the causes of anthropogenic impacts.

Making detailed projections of the consequences of human impacts on biodiversity is difficult in its own right, and we are far from being able to make similar projections about the impacts of biodiversity loss on ecosystem services. A general principle that emerges from Chapter 10 is that ecosystem services depend on the abundance of individuals in populations of species rather than on simple species pres-

Ecological Principle or Insight	Relevance for Global Scenarios	Illustrative Example
Current rates of change (habitat destruction, ex- tinctions) are extremely high by comparison to	ecosystems are more likely to be near to bound- ary conditions than they were historically	Chapin et al. 2000
nistorical rates	baseline data collected in the last 50 years do not necessarily reflect unperturbed state	
Ecosystem services are interdependent	need to consider "bundles" of services and their relevance to society interactions among ecological processes can lead to surprises	interactions between climate and forests; con- flicts over climate regulation, timber production and harvesting of non-timber forest products
	attempts at making trade-offs between ecosys- tem services may not be successful	
evels of ecological uncertainty may be higher han traditional models have suggested; thresh-	risk associated with different magnitudes of human impacts is uncertain	collapse of major marine fisheries (cod, Atlantic salmon, sea turtle) (Jackson et al. 2001; Pauly et al. 1998)
olds are difficult to quantify precisely	current global models are naive about human im- pacts on ecosystems	
Relationship between biodiversity and ecosys- em function is unclear	uncertain whether projected losses of biodiver- sity will have high or low impact on provision of ecosystem services	trophic cascades in lakes have demonstrated high interconnectedness of aquatic food webs
Nany ecosystems exhibit nonlinear dynamics	ecological shocks and surprises are likely to emerge from unexpected threshold effects	shallow lakes can switch rapidly from clear to turbid with a slight, linear increase in P load (Carpenter et al. 1999b)
Cross-scale dynamics, particularly those driven by the interactions of variables with different	ecological impacts and drivers must be consid- ered at a variety of scales	multiple small-scale N inputs from farms on the Mississippi are creating dead zone in Gulf of Mexico decline in molluscivorous fishes leading to in- creases in snails that act as secondary hosts to <i>Schistosoma</i> spp. in Lake Malawi; resulting in- crease in schistocomiasis in human population (Stauffer et al. 1997)
cale-dependent rates and magnitudes, can pro- luce feedbacks and cascades	context of ecological impacts is key, especially when considering likelihoods of positive vs. neg- ative feedbacks	
	constraints and mechanisms needed to explain storylines will come from different scales	
	human learning about ecosystems is made harder by relevance of large-scale processes and slow variables	
Spatial and temporal variations are essential components of ecosystems	changes in mean trends may be less important than changes in timing and magnitude of varia- tions	major impacts of climate change on biota will come from extremes, rather than from changes in means
Evidence for "ecological Kuznets" is lacking	economic theory cannot be applied indiscrimi- nately to relationship between society and eco- logical services in scenarios	Bruvoll and Medin 2003
Command-and-control management approaches often decrease system resilience	inherent or unexpected vulnerabilities are more likely to influence storylines in systems where command and control is or has been practiced	fires in California; development of resistant strains of antibiotics (Holling and Meffe 1996)
Successful application of ecology to manage- nent/policy depends on political context	scenarios must ensure that political context is appropriate for the ecosystem management ac- tions that are envisaged	Walters (1997) presents a number of examples of situations in which adaptive management has succeeded or failed

Table 3.1. Relevance of Ecological Principle or Insight to the Development of Global Scenarios

ence or absence. Species loss is worrying, but declines in ecosystem services will become evident well in advance of species extinctions. Hence, the management of vital populations of organisms (and the abiotic environment they depend on) may be a more appropriate focus than entire species for decision-makers who are concerned about the contribution of ecosystems to human well-being.

As many of the chapters in this volume make clear, human well-being is intricately connected to the components and functions of ecosystems. Changes in ecosystems are likely to have a number of important impacts on human societies. (See Chapter 11.) Decision-makers must often balance short-term economic or societal gains against longterm ecosystem costs. (See Chapter 12.) By attempting to include ecology in the process of scenario development, we have learned many lessons about the relationship between ecosystem services and human well-being. (See Chapter 13.) These are translated into a set of possible responses and recommendations for policy-makers and managers. (See Chapter 14.)

Although ecology and related disciplines have much to offer in this context, there are a number of areas in which further exploration of ecosystem dynamics would be useful. For example, the ecological scope of the scenarios could have been greatly strengthened if we had a stronger quantitative understanding of such things as diversity-function relationships, the endogenous dynamics of ecosystems and the circumstances under which they cause unexpected perturbations, the role of cross-scale variation in sustainability, and the locations of thresholds in the provision of ecosystem services. The scenarios would also have benefited from more extensive quantification and analysis of the links between resource value, resource use, and resource management.

In conclusion, we have argued that the consideration of ecosystems in scenario exercises and in policy and management decisions is vital to the long-term sustainability of human society. Despite the progress that the MA has made in tackling the complexity of the global socioecological system, it is clear that this volume represents a beginning rather than an end in the ongoing process of learning to manage ecosystems to increase human well-being sustainably.

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