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American Naturalist, Volume 148, Issue 6 (Dec., 1996), 1016-1037.

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American Naturalist

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PRINCIPLES OF ECOSYSTEM SUSTAINABILITY

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Submitted June 22, 1995; Revised January 16, 1996; Accepted February 22, 1996

Abstract.—Many natural ecosystems are self-sustaining, maintaining a characteristic mosaic of vegetation types for hundreds to thousands of years. In this article we present a new framework for defining the conditions that sustain natural ecosystems and apply these principles to sustainability of managed ecosystems. A sustainable ecosystem is one that, over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, and rates of biogeochemical cycling. These traits are determined by a set of four "interactive controls" (climate, soil resource supply, major functional groups of organisms, and disturbance regime) that both govern and respond to ecosystem processes. Ecosystems cannot be sustained unless the interactive controls oscillate within stable bounds. This occurs when negative feedbacks constrain changes in these controls. For example, negative feedbacks associated with food availability and predation often constrain changes in the population size of a species. Linkages among ecosystems in a landscape can contribute to sustainability by creating or extending the feedback network beyond a single patch. The sustainability of managed systems can be increased by maintaining interactive controls so that they form negative feedbacks within ecosystems and by using laws and regulations to create negative feedbacks between ecosystems and human activities, such as between ocean ecosystems and marine fisheries. Degraded ecosystems can be restored through practices that enhance positive feedbacks to bring the ecosystem to a state where the interactive controls are commensurate with desired ecosystem characteristics. The possible combinations of interactive controls that govern ecosystem traits are limited by the environment, constraining the extent to which ecosystems can be managed sustainably for human purposes.

The increasing human modification of the Earth's surface requires that we understand how the productivity and biotic diversity of both natural and managed ecosystems can be sustained (Lubchenco et al. 1991). Many ecosystems exhibit long-term changes in response to intense human use, as seen from desertification of overgrazed lands (Schlesinger et al. 1990), eutrophication of lakes (Schindler et al. 1990), loss of soil organic matter following agricultural conversion (Paul and Clark 1989), and loss of salmon fisheries following hydroelectric or forestry development (Francis 1990). Ecosystem sustainability is of growing concern to ecologists who study the cumulative global impact of widespread environmental change and to social scientists attempting to develop policies to sustain the production of goods and services for a growing human population (Goodland 1995). Research on agroforestry and sustainable agriculture is beginning to bridge this

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gap (Ramakrishnan 1992; Hartshorn 1995; Vandermeer 1995). However, to date the concept of sustainability has not been applied to natural ecosystems, nor have the basic principles of their sustainability been clearly enunciated. The issue of sustainability revives an earlier debate as to whether an ecosystem is simply a collection of organisms that responds to environment (Engelberg and Boyarsky 1979) or is integrated by processes that control and sustain ecosystem traits (Patten and Odum 1981). In an effort to develop an ecological framework that is useful in managed systems, we explore the following questions: Do natural ecosystems sustain themselves? If so, what principles govern their sustainability? Does application of these principles increase the sustainability of human-modified ecosystems?

DEFINITIONS

We define a sustainable ecosystem as one that, over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, soil fertility, and rates of biogeochemical cycling. We include all stages of succession in our definition of an ecosystem, including disturbance, colonization, and successional development (Holling 1986). We consider spatial scales that are relevant to direct human management (e.g., watersheds). Definitions of sustainability related to the long-term yield of commodities for human consumption (e.g., sustainable agriculture or forestry; Gale and Cordray 1991; Goodland 1995) are less relevant to unmanaged ecosystems, although there is a continuum from natural to intensively managed ecosystems (all of which are modified by human activities and provide benefits to people; Vitousek 1994). Even in the most intensively managed ecosystem, rates of biogeochemical cycling must be maintained if other, more narrow management objectives (e.g., seed yield of corn, persistence of an endangered species) are to be met over the long term (Ramakrishnan 1992; Goodland 1995).

Few ecosystems are sustainable longer than a few tens of thousands of years, because factors such as climate, soil development, and species gene pool, which shape ecosystems, change significantly over these time periods (Jenny 1941, 1980), as each species migrates according to its unique environmental requirements and dispersal capabilities (Davis 1981; COHMAP 1988). The current species composition and structure of any ecosystem and its pattern of successional development are transitory assemblages that are not sustainable indefinitely. Sustainability is, however, a relevant and important concept over timescales of many generations of the dominant species (i.e., decades to centuries in most ecosystems, the timescales most relevant to human interactions with ecosystems).

We define functional groups as groups of species that have similar effects on ecosystem processes. For example, homeotherm herbivores eat plants and return nutrients to soil in a highly available form because their high respiration rate burns off most of the carbon contained in the original food material. Evergreen trees have leaves available to capture carbon at all times of year, are generally well defended against herbivores, and produce chemically defended litter that decomposes slowly (Coley et al. 1985; Chapin 1991). Important ecological differ-

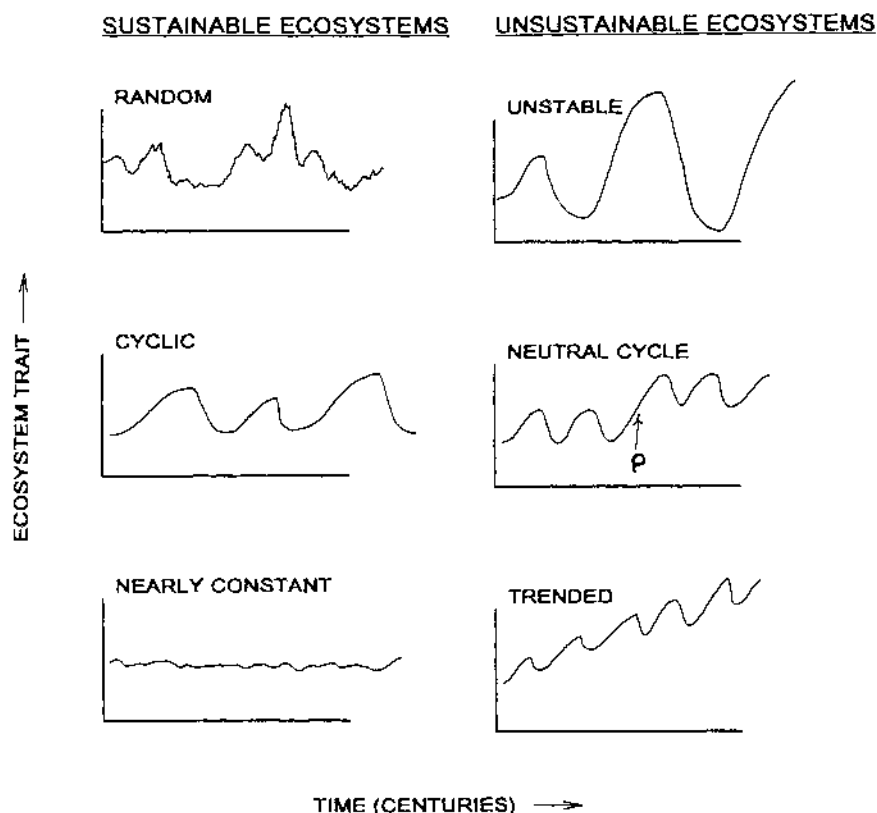


FIG. 1.—Examples of temporal fluctuations in ecosystem traits in sustainable and unsustainable ecosystems (May 1973; Holling 1986). Here *P* indicates the time of an external perturbation.

ences exist within and among functional groups. However, functional groups are a useful way to describe general ecological effects that organisms have on ecosystem processes (Chapin 1993; Smith et al. 1996). The ecosystem processes we address in this article are the flows of energy and materials in an ecosystem (e.g., plant productivity, leaching of nitrate in ground water, the release of nutrients from soil organic matter by decomposition).

Ecosystems are not static. Plant and animal species composition, productivity, and nutrient cycling all change in response to stochastic events and successional change. Sustainable ecosystems, however, maintain these traits within stable bounds (fig. 1). For example, outbreaks of Scandinavian vole populations every 3–4 yr cause corresponding changes in predator density, plant productivity, and nutrient cycling but cause no long-term trend in these characteristics because the decrease in plant growth and increase in predators both act as negative feedbacks to the vole population (Laine and Henttonen 1983; Oksanen 1990). Stochastic variation in rainfall causes sediment transport by streams to vary among years

by orders of magnitude in undisturbed watersheds, but these nutrient losses are balanced by inputs from weathering over the long term (Bormann and Likens 1979). Plant succession following tree falls creates a heterogeneous mosaic of vegetation in forest ecosystems (Denslow et al. 1990) but maintains a characteristic vegetation pattern at the landscape scale. Similarly, in many ecosystems predictable successional changes in ecosystem parameters follow natural wildfires (Stark and Steele 1977; Van Cleve et al. 1991; D'Antonio and Vitousek 1992). However, the landscape as a whole does not change because fires in some patches are balanced by successional development in other patches (Watt 1947; Turner 1989).

THE BASIS OF SUSTAINABLE ECOSYSTEMS

Ecosystem properties are governed by both internal interactions and external factors. Jenny (1941) suggested that five independent *state factors* (parent material, climate, topography, potential biota, and time) determine soil and ecosystem processes. This approach has proven extremely useful in explaining why soils differ among ecosystems (fig. 2A). We introduce an extension of the state factor approach in which each ecosystem is characterized by four dynamic elements, or *interactive controls*: local climate, soil resource supply, major functional groups of organisms, and disturbance regime. In contrast to state factors, interactive controls both control and respond to ecosystem characteristics (fig. 2B). Interactive controls are constrained by state factors and interact dynamically with ecosystem processes. Similarly, Billings (1952) described holocoenotic factors, all of which affect each other and plants. We contend that interactive controls must be conserved if an ecosystem is to be sustained. Major changes in any interactive control will lead to a new ecosystem with distinctly different properties. Specific ecosystems will respond more strongly to some interactive controls than others (e.g., temperature sensitivity of tundra, phosphorus sensitivity of lakes, sensitivity of islands to invasion of new species). Each interactive control changes over the course of a disturbance-succession cycle. However, the set of interactive controls operates within bounds that are representative for that ecosystem and form negative feedbacks preventing larger changes in interactive controls. In this section we outline how the connections among interactive controls govern ecosystem processes.

Climate

On broad geographical scales, climate is the interactive control that most strongly governs the structure, productivity, and biogeochemistry of ecosystems (Schimper 1898; Holdridge 1947; Woodward 1987). Climatic changes through glacial-interglacial cycles have caused massive ecosystem changes (Davis 1981). The productivity and vertical structure of vegetation, in turn, govern microclimatic factors like water and temperature gradients within the canopy and soil and influence regional climate through energy and water exchange with the atmosphere (Jarvis and McNaughton 1986; International Geosphere-Biosphere Programme [IGBP] 1990; Chapin 1993; fig. 2B). There is a continuum between the global

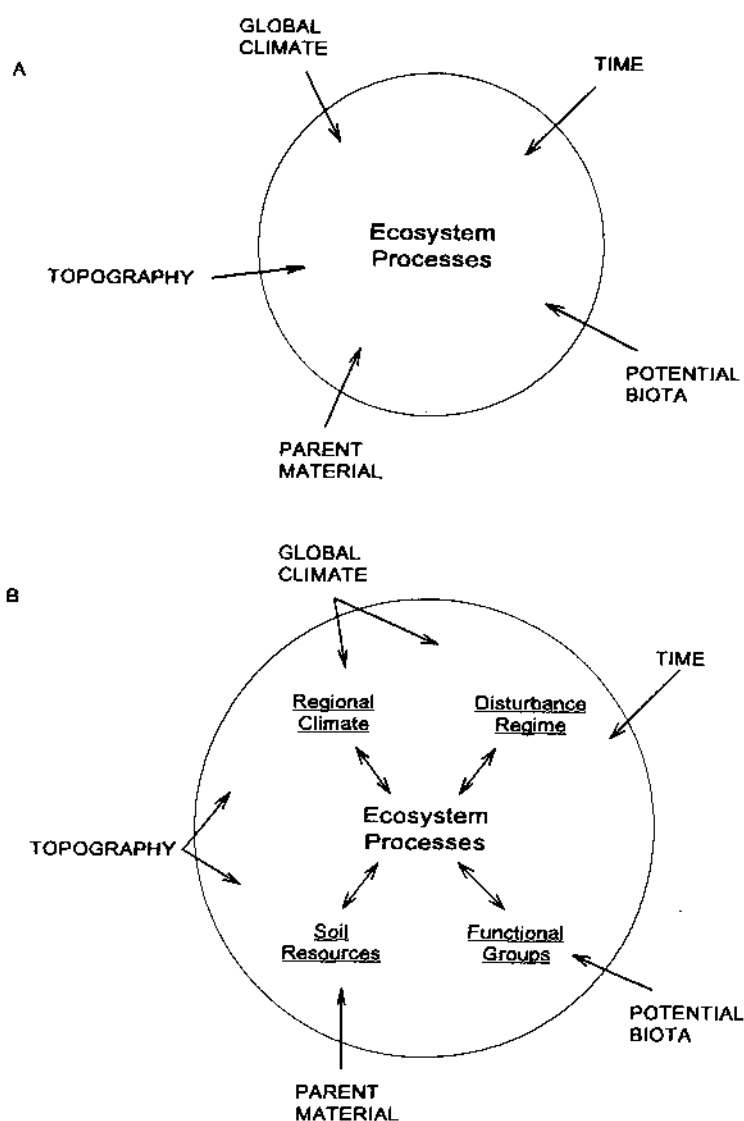


FIG. 2.—The relationship (A) between state factors and ecosystem processes and (B) among state factors, interactive controls, and ecosystem processes. See text for explanation. State factors are capitalized, interactive controls are underlined, and the circle represents the boundary of the ecosystem.

climate that is determined largely by latitudinal gradients in solar input, land-ocean interactions, and topography (climate as a state factor) and those climatic attributes that may be influenced by ecosystems (climate as an interactive control).

Ecosystems and climate interact in a coupled fashion. Widespread overgrazing of arid lands (Charney et al. 1977; Schlesinger et al. 1990) or tree harvest in boreal forests (Bonan and Van Cleve 1992) could alter regional albedo and energy absorption sufficiently to change the regional climate and create a stable relationship between the new climate and the new vegetation type. Similarly, a change in regional water balance caused by conversion of tropical forest to grassland might lead to a permanently drier regional climate that retards forest regeneration (Shukla et al. 1990). Change in the position of the arctic treeline may have had as large an effect as changes in solar input in causing climatic change 6,000 yr ago (Foley et al. 1994), and the current position of treeline may determine the position of the arctic front (Pielke and Vidale 1996). These potential changes in climate, which are initiated by altering vegetation, can occur more rapidly (e.g., decades to centuries) than natural glacial-interglacial cycles in climate and thus are relevant to issues of ecosystem sustainability.

Soil Resources

Soil resource supply (or water quality in aquatic ecosystems) determines the maximum productivity and structural diversity of vegetation (Van Cleve et al. 1991; Field et al. 1992; Chapin 1993). Rates of biogeochemical cycling and water loss from vegetation generally correlate closely with productivity (Miller et al. 1976) because the uptake of these nutrients supports productivity, and transpirational water loss is an inevitable consequence of the photosynthetic carbon gain that drives production (Field et al. 1992). Thus, productivity, nutrient cycling, and water loss are closely intercorrelated and causally linked to the availability of soil resources (Field et al. 1992; Chapin 1993). Climate strongly influences soil moisture through the balance between precipitation and evaporation and determines latitudinal patterns of nutrient availability through effects on weathering rate, soil nutrient turnover, and leaching loss (Meetenmeyer 1978; Meetenmeyer and Berg 1986; Vitousek and Howarth 1991). However, within a given climatic regime, soil resource supply (water and nutrients) is governed by parent material, topography, and activity of nitrogen (N)-fixing organisms (Jenny 1941).

Change in soil resources is perhaps the most widespread mechanism by which human activity has altered ecosystem sustainability. Erosional loss of soils following overgrazing or improper agricultural or forestry practices reduces nutrient supply and therefore productivity and rates of nutrient cycling. Increased input of nutrients from fertilizer applications, atmospheric N deposition, or agricultural runoff to aquatic systems may enhance the productive potential of these systems but may also permanently change the species composition of terrestrial (Aerts and Berendse 1988) and aquatic (Schindler 1978; Carpenter et al. 1992) communities and can alter the probability of insect outbreaks (Waring and Pitman 1985). Ecosystems that receive large anthropogenic nutrient inputs will change to some new ecosystem state unless intensively managed (Berendse and Aerts 1987). For

aquatic ecosystems, water supply and water quality, rather than soil resources, are the relevant interactive control.

Disturbance Regime

Landscape scale disturbance by fire, wind, insect outbreaks, hurricanes, and so forth, is critical to sustaining the natural structure and rates of processes in ecosystems (Sousa 1985). For example, fire is critical to the long-term maintenance of fire-prone ecosystems (e.g., chaparral, grassland, savanna) and landscape-scale habitat patterns (Turner 1989). Disturbance regimes interact strongly with climate and soil resources. Climate, including humidity, wind, soil moisture, and lightning, directly affects fire starts and spread rates (Torn and Fried 1992). Climate and soil resources also influence plant biomass, physiognomy, and moisture status and therefore fuel load characteristics and the propensity of trees to be toppled by wind. Conversely, disturbances influence soil resource supply, for example, by mineralizing nutrients through combustion of organic matter or distributing alluvial silt.

Change in either the intensity or frequency of disturbance can cause long-term ecosystem change. For example, woody plants often invade grasslands when fire suppression reduces fire frequency. In sequoia forests the development of an understory tree canopy and increased fuel load resulting from fire suppression can increase fire intensity to the point that dominant trees become vulnerable to fire (Kilgore and Taylor 1979). Building dams in rivers prevents winter flooding and scouring of stream channels. In California this loss of an annual disturbance allows larger populations of predator-resistant (armored or sessile) stream insect grazers to overwinter and prevents spring algal blooms that would otherwise support a food chain for trout and salmon (Power 1992). Clear-cutting of forests modifies patterns of nutrient cycling and nutrient inputs to rivers (Perry et al. 1989; Carpenter et al. 1992). Lighting of fires by hunters and gatherers increases the abundance of early successional vegetation and associated bird-dispersed shrubs and mammalian herbivores.

Functional Groups of Organisms

Because we define functional groups of organisms by their effects on ecosystem processes, it is not surprising that a change in functional groups has strong effects on ecosystems. It is noteworthy, however, that changes in functional groups often influence ecosystem processes just as strongly as do large differences in climate or parent material (Vitousek and Walker 1989; Chapin 1993; Foley et al. 1994). In the boreal forest, for example, successional increases in moss biomass create a negative feedback to increased production by reducing mineralization rates and nutrient supply, because of low litter quality of mosses and their effectiveness in insulating the soil from summer heat input (Oechel and Van Cleve 1986; Johnson and Damman 1991). Late-successional black spruce trees are resinous and more fire prone than earlier successional deciduous species, which increases the probability of disturbance in late succession (Van Cleve et al. 1991). During primary succession, invasion by N-fixing trees and shrubs substantially increases N supply and therefore the productivity of late-successional forests

(Walker 1993; Chapin et al. 1994). These effects of changing species composition in a single site are just as pronounced as changes in ecosystem processes associated with regional differences in parent material, topography, or latitude at any given successional stage (Flanagan and Van Cleve 1983).

Climate, soil resources, and disturbance regime strongly influence the types of functional groups that dominate a system (Holdridge 1947; Grime 1977; Chapin 1980; Tilman 1988). In general, high-resource environments are dominated by trees, given sufficient time since disturbance, whereas environments of low soil resource availability are often dominated by a mixture of low-statured functional groups (e.g., cactus, shrubs, annual forbs in a desert [Tilman 1988; Chapin 1993] or dwarf shrubs in an infertile heath [Chapman 1967]). Soil resources also influence trophic structure, with the number of trophic links often increasing with increasing productivity (Fretwell 1977; Oksanen 1990). For example, extremely unproductive habitats may be insufficient to sustain mammalian herbivores, habitats of intermediate productivity may be heavily grazed, and extremely productive habitats may be so productive that predators minimize the impact of herbivores on vegetation (Oksanen 1990).

A gain or loss of key functional groups (e.g., through introduction or extirpation of species with important ecosystem effects) can permanently change the character of an ecosystem through changes in resource supply or disturbance regime (Vitousek and Walker 1989; Vitousek 1990; Chapin et al. 1996). Introduction of the exotic N fixer, *Myrica faya*, into Hawaii substantially increased N supply and productivity and has permanently altered the species composition and productivity of invaded tropical forests (Vitousek et al. 1987). Invasion of exotic grasses can alter fire frequency, resource supply, trophic interactions, and rates of most ecosystem processes (D'Antonio and Vitousek 1992). Elimination of predators by hunting can cause outbreak of deer that severely overbrowse their food supply (Klein 1968). As described earlier, large changes in grazing regime can create increases in albedo sufficient to alter regional climate. Thus, functional groups respond to and affect most interactive controls and ecosystem processes.

Summary

Interactive controls determine the structure and productivity of ecosystems. If we wish to maintain natural ecosystems in their current state or manage an agroecosystem sustainably, we must maintain a stable pattern of interactive controls. Only in this way can the natural capital (e.g., soil, atmosphere, vegetation) of an ecosystem be sustained (Goodland 1995).

MAINTENANCE OF SUSTAINABLE ECOSYSTEMS

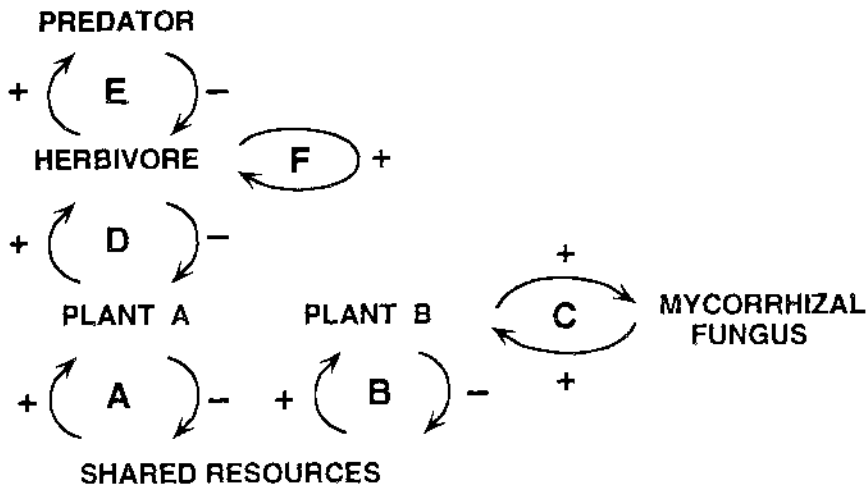
Given the natural variability in interactive controls and the sensitivity of ecosystem processes to these controls, it is perhaps surprising that many natural ecosystems sustain themselves over long time periods (decades to centuries). Negative feedbacks are the key to ecosystem sustainability because strong negative feedbacks provide resistance to natural or anthropogenic changes in interactive controls and maintain the potential for regeneration after perturbation. By

contrast, strengthened positive feedbacks amplify an initial change in conditions and push the ecosystem toward some new state (fig. 1). Natural ecosystems are complex networks of interacting positive and negative feedbacks (DeAngelis et al. 1986; DeAngelis and Post 1991) that operate over a range of temporal and spatial scales. Thus, both positive and negative feedbacks are important in determining the characteristics of natural ecosystems. Community dynamics, which operate within an ecosystem at any point in time, primarily involve feedbacks among soil resources and functional groups of organisms. Landscape dynamics, which govern changes in ecosystems through cycles of disturbance and recovery, involve additional feedbacks with microclimate and disturbance regime.

Interactions within and among interactive controls generate positive feedbacks (e.g., mutualisms and population growth) that are relatively well understood (DeAngelis and Post 1991), so we provide examples but do not review this literature. *Resource-based mutualisms* of plants with mycorrhizal or N-fixing symbionts create a positive feedback that maximizes productivity that can be sustained at a given resource supply (fig. 3) because both the host plant and the fungus or N-fixing bacterium benefit from the association (Allen 1991). *Demographic mutualisms* such as pollination and seed dispersal enhance population sizes in a community. Population growth acts as a positive feedback because increased population size tends to cause still greater population increase. In simple two-species microcosms, population growth creates instability because one species provided with a finite food supply increases its population until the food supply is exhausted, and the population crashes.

In sustainable ecosystems, negative feedbacks generated by soil resources, plants, and other interactive controls constrain positive feedbacks, such as those described earlier (Pimm 1984). The acquisition of water, nutrients, and light to support growth of one plant reduces availability of these resources to other plants (Tilman 1988), thereby stabilizing community productivity (fig. 3). Similarly, animal populations cannot sustain exponential population growth indefinitely, because declining food supply (Malthus 1798) and predation (Hairston et al. 1960; Oksanen 1990) reduce the rate of population increase. If these negative feedbacks are weak or absent (e.g., low predation rate), population cycles can amplify and lead to extinction of one or both of the interacting species (Holling 1992).

A diversity of species that compete for the same limiting resource (e.g., soil nutrients or a common prey species) generates negative feedbacks at the ecosystem level (*feedback A, B, D, or E* in fig. 3). Competition has sometimes been considered a positive feedback (DeAngelis and Post 1991) because, over short timescales, each competing individual has negative effects on its neighbor. However, if competition operates by the depletion of a shared limiting resource (Tilman 1988), competition is the net result of negative feedbacks between each competitor and the shared resource (fig. 3). Because each species in an ecosystem has a slightly different response to environment (Gleason 1926; Whittaker 1953), a change in interactive controls that is detrimental to one species will have less of an effect on another species or even a positive effect because of release from competition for the shared resource (Mellinger and McNaughton 1975; Chapin and Shaver 1985). These divergent responses of individual species to changes in



Process	Nature of Feedback	
Resource Uptake	A	—
Competition	A+B	—
Mutualism	C	+
Herbivory	D	—
Predation	E	—
Population Growth	F	+

FIG. 3.—Examples of linked positive and negative feedbacks in ecosystems (DeAngelis and Post 1991). The effect of each organism (or resource) on other organisms can be positive or negative. Feedbacks are positive when the reciprocal effects of each organism (or resource) have the same sign (both positive or both negative). Feedbacks are negative when reciprocal effects differ in sign.

interactive controls buffer the community against large changes in productivity or nutrient cycling because it is the level of the shared resource that constrains productivity. For example, climatic variation causes large changes in production of individual tundra or grassland species but only modest changes in ecosystem production (McNaughton 1977; Lauenroth et al. 1978; Chapin and Shaver 1985). Conversely, if there is only one species capable of using a resource, changes in the abundance of that species can have effects that propagate broadly through

the community (DeAngelis and Post 1991; Pimm 1993). For example, sea otters are the only major predator of sea urchins in parts of the Pacific coast of North America. Overhunting of sea otters caused a population increase in urchins that eliminated kelp forests, which were a habitat for hundreds of species of fish and invertebrates (Estes and Palmisano 1974). Thus, biodiversity within a group of species that are limited by the same resource provides insurance against radical ecosystem change in response to extreme events (e.g., frost or drought) that might eliminate a species (Tilman and Downing 1994).

Successional cycles of disturbance and ecosystem development in landscapes entail both positive and negative feedbacks. Following disturbance, the initial increase in plant biomass enables the vegetation to acquire more resources, which causes a further increase in plant production and potential to acquire resources. These and other positive feedbacks (e.g., mycorrhizal or N-fixing mutualisms between plants and microorganisms) can promote recovery of a degraded ecosystem (Bradshaw 1983; Perry et al. 1989). However, over the long term, negative feedbacks constrain these ecosystem changes (Odum 1969). The increase in plant biomass following disturbance induces a negative feedback to plant growth as light availability declines within the canopy, maintenance respiration increases owing to the increasing proportion of nonphotosynthetic support tissues, and nutrient availability declines because of nutrient sequestration in plant biomass and dead soil organic matter (Odum 1969; Tilman 1988; Van Cleve et al. 1991; Field et al. 1992). The increase in fuel load with time increases the probability of fire (D'Antonio and Vitousek 1992; Torn and Fried 1992). Declines in plant carbohydrate reserves in old-forest stands increase the probability of insect or pathogen outbreaks and fire (Holling 1992). If these long-term negative feedbacks are maintained, the mosaic of ecosystems in the landscape can be sustained.

Ecosystems in a landscape are linked by the movement of plants and animals, water, energy, and biogeochemical cycles (Turner 1989). Where these links are reciprocal between systems or form negative feedback, they enhance landscape sustainability. For example, if a stochastic or human-induced decline in the abundance of a species occurs in one patch on the landscape, corridors to similar ecosystems allow recolonization and recovery of the population (Tilman et al. 1994). Thus, the cascade of ecological effects associated with elimination of the sea otter from a coastal marine ecosystem might be minimized if linkages permitted recolonization from adjacent areas. Forest regeneration after fire or logging is enhanced by links to undisturbed forests, which provide seed rain and migration corridors for displaced species. Large animals often move readily among adjacent ecosystems, feeding in one place and seeking refuge from predators in a different ecosystem type. In all these examples, ecosystems have reciprocal effects on one another, many of which involve negative feedbacks.

Some interactions among ecosystems in a landscape are strongly asymmetric, as in the impact of uplands on lakes, streams, and wetlands. Similarly, coastal fisheries are influenced by stream inputs of freshwater and nutrients and by upwelling of deep ocean water but have little impact on their donor ecosystems. In these cases, there are few negative feedbacks from the recipient to the donor ecosystem. A landscape containing these asymmetric linkages is sustainable as

long as the donor ecosystem is unaltered. However, the recipient ecosystem is vulnerable to changes in the donor ecosystem because of a lack of negative feedbacks from the recipient to the donor ecosystem. For example, after clear-cutting of forests or introduction of high-intensity agriculture, aquatic ecosystems often receive additional nutrient inputs that lead to dramatic changes in fish, insect, and algal communities (Carpenter et al. 1992) but have only weak mechanisms to modify the terrestrial system in ways that reduce these inputs. By altering global cycles of carbon, nitrogen, and sulfur, we have developed asymmetric linkages among urban, agricultural, and unmanaged ecosystems that were formerly more discrete (Vitousek 1994). New asymmetric linkages are likely to reduce the sustainability of recipient ecosystems when interactive controls become governed by processes outside the ecosystem rather than by negative feedbacks generated within the ecosystem.

SUSTAINABILITY OF MANAGED ECOSYSTEMS

It has been sharply debated whether any ecosystem is sustainable when subjected to continuous human harvest (Ludwig et al. 1993; Rosenberg et al. 1993). However, management practices certainly influence the degree of sustainability, and an important goal of applied ecology is to increase sustainability of managed ecosystems (Lubchenco et al. 1991). Based on our analysis of natural ecosystems, we suggest three principles of ecosystem sustainability relevant to managed ecosystems.

First, the sustainability of productivity and other ecosystem characteristics requires that interactive controls be conserved. These interactive controls can be managed but are constrained by state factors that are outside the control of the manager. The interactive controls most readily managed are soil resources (e.g., fertilizer, irrigation), disturbance regime, and functional groups of organisms. Common state factor constraints to management objectives include climate, parent material, and steepness of topography.

Second, negative feedbacks among interactive controls increase the sustainability of ecosystem processes. Negative feedbacks important to management include the use of multiple species limited by the same resource (e.g., mixed cropping; Nambiar and Nethercott 1987; Ramakrishnan 1992; Swift and Anderson 1993) and predation (e.g., biocontrol; Huffaker 1957). When negative feedbacks are weakened, management must be intensified. Positive feedbacks such as mycorrhizal or N-fixing mutualisms that push an ecosystem toward some new state can also be constructive management tools in promoting recovery of degraded ecosystems (Perry et al. 1989).

Finally, linkages among ecosystems are most likely to enhance sustainability when they generate negative feedbacks among these ecosystems. Laws and regulations can create negative feedbacks and increase the sustainability of human harvest from natural ecosystems.

To test the utility of our hypotheses about ecosystem sustainability, we present four examples of ways in which natural ecosystems have been modified to support human activity with varying degrees of sustainability.

Slash-and-Burn Agriculture

Tribal societies of northeast India have maintained a culture based on slash-and-burn agriculture for centuries (Ramakrishnan 1992). Typically, plots of land are cleared, burned, and planted to a mixture of crops that are harvested for 1–2 yr. Then the plot is used less intensively (e.g., for fuel) and accumulates nutrients to original levels during a 20–40-yr secondary succession, whereupon the cycle repeats. The long history of the tradition and the similarity of primary production and litterfall between the 30-yr fallow and mature forest suggest that this agricultural practice may be relatively sustainable with a long fallow period (table 1). Because of recent population increases, land has become scarce, and the length of the fallow period has declined. This slash-and-burn agriculture appears unsustainable when the rotation cycle declines below 10 yr (Ramakrishnan 1992), judging from the decline in production and litterfall during the fallow stage (table 1) and the high frequency of desertification and abandonment of land (Ramakrishnan 1992).

Three interrelated changes in interactive controls reduce the sustainability of this agricultural practice when the rotation cycle is shortened: soil erosion following land clearing occurs more often, causing a decline in soil fertility; more frequent disturbance reduces the length of the fallow phase during which the ecosystem recovers its nutrient capital; and the functional groups of plants change, as the landscape becomes dominated by active cropland or early successional weedy species, eliminating seed sources of midsuccessional species, many of which are effective in fixing N (e.g., Nepalese alder) or retaining potassium (e.g., bamboo) or calcium (woody species). This change in species composition leads to arrested succession and a long-term decline in soil fertility. The cumulative consequences are significant depletion of soil resources and decline in productivity over time (table 1).

Interactions among plants, soil resources, and management practices generate positive feedbacks that accelerate a loss of soil fertility and productivity. For example, as soil fertility declines, farmers plant more root crops, which have a lower nutrient requirement but whose low plant biomass and low leaf allocation give less protection to the soil against rain and further erosion. Another response to declining land availability is a switch to more intensively managed continuous cropping systems (Ramakrishnan 1992). A mixed cropping system of pineapples and vegetables provides more consistent productivity than monocultures of tea, ginger, or coffee because each species within the mixed culture differs in its response to annual variation in weather (Sanchez and Benites 1987; Uhl 1987; Ramakrishnan 1992). The mixed cropping system requires less fertilizer input because of the recycling of plant residues, whereas herbicides minimize these plant inputs in the intensive monocultures and make the soils more prone to erosion (table 1).

Sustainable Forestry

Sustained productivity of managed forests requires management of disturbance regime, plant functional groups, and soil resources. Although forests are managed

TABLE 1

NITROGEN (N) INPUTS (FROM CROP RESIDUES, FALLOW LITTERFALL, AND FERTILIZER), LEAF AREA INDEX (LAI), BIOMASS PRODUCTION DURING THE CROP PHASE, LITTERFALL DURING THE FALLOW PHASE, AND SOIL EROSION IN A NATURAL FOREST AND SEVERAL TYPES OF AGRICULTURAL SYSTEMS FOR THE GAROS AT BURNIHAT IN NORTHEAST INDIA (RAMAKRISHNAN 1992)

ECOSYSTEM	NATURAL N INPUT (kg N ha ⁻¹ yr ⁻¹)		FERTILIZER N INPUT	LAI (m ² m ⁻²)	NET 1° PRODUCTION (mg ha ⁻¹ yr ⁻¹)			FALLOW LITTERFALL (kg ha ⁻¹ yr ⁻¹)	SOIL EROSION* (t ha ⁻¹ yr ⁻¹)
	Crop	Fallow			Crop	Fallow	Average*		
Natural forest	0	155	0	23.6	23.6	1,178	.8
Slash-and-burn agriculture:									
5-yr cycle	33	57	0	.59	18.5	2.3	5.5	480	6.9
10-yr cycle	43	92	0	1.49	14.7	5.8	6.7	710	3.0
30-yr cycle	48	109	0	3.20	17.7	14.8	14.9	976	1.5
Continuous mixed-crop	...	0	0	...	1.0	...	1.0	0	.1
Continuous monoculture:									
Coffee	4	0	12455	0	1.2
Tea	4	0	284	...	1.0	...	1.0	0	2.6
Ginger	19	0	213	...	1.9	...	1.9	0	20.0

* Averaged over the entire crop-fallow cycle.

TABLE 2

ORGANIC MATTER AND NITROGEN (N) ACCUMULATION IN VEGETATION AND SOIL COMPARTMENTS OF 55-YR-OLD CONIFER STANDS PLANTED WITH AND WITHOUT ALDER ON HIGH- AND LOW-FERTILITY SITES IN WASHINGTON (BINKLEY ET AL. 1992) AND A 450-YR OLD-GROWTH DOUGLAS FIR FOREST (COLE AND RAPP 1981)

COMPONENT	LOW-FERTILITY SITE		HIGH-FERTILITY SITE		OLD-GROWTH FOREST	
	Organic Matter (Mg ha ⁻¹)	N (kg ha ⁻¹)	Organic Matter (Mg ha ⁻¹)	N (kg ha ⁻¹)	Organic Matter (Mg ha ⁻¹)	N (kg ha ⁻¹)
Conifer stand:						
Alder	0	0	28	63	0	0
Conifer	151	109	530	400	802	566
Understory	5	52	1	13	6	14
Forest floor	16	104	26	243	219	445
Soil (0–9 m)	156	1,960	468	9,800
Conifer + alder stand:						
Alder	92	190	164	356
Conifer	177	146	154	138
Understory	1	7	2	26
Forest floor	29	350	21	301
Soil (0–9 m)	212	4,340	518	13,720

for many purposes, here we consider only wood harvest. In the northwestern United States, old-growth Douglas fir forests attain an age of more than 500 yr (Wills and Stuart 1994). Fire and windthrow of individual trees are the major natural disturbances, creating fine-, medium-, and coarse-scale mosaics of tree ages. Although total ecosystem N decreases after disturbance, N available to plants increases right after disturbance because of mineralization of dead plant biomass and soil organic matter. Nitrogen accumulation by N-fixing trees and shrubs early in succession compensates for the loss, so that overall N levels are stable over multiple successional cycles (Agee 1993).

In this region, logging is now the most widespread disturbance. Logging differs from the natural disturbance regime by affecting larger areas, occurring more frequently, removing the N bound in biomass, and accelerating erosion through disruption of the surface organic mat. Thus, logging has resulted in declines in average stand age and ecosystem nutrient levels. Functional groups planted during reforestation affect the rate at which these nutrients are recovered and therefore future productivity. After 55 yr of regeneration in a low-fertility site, a stand planted with a mixture of N-fixing alders and Douglas fir had higher productivity, biomass, soil carbon, and N accumulation in plants and soil than an adjacent stand planted with Douglas fir alone (Binkley et al. 1992; table 2). Results were similar in a high-fertility site, except that plant biomass and growth rate were lower in the mixed than in the pure conifer stands, apparently because the competitive impact of alders on conifer growth exceeded the benefit of N added to soils. The higher carbon and N contents of soils planted with alders suggest that later in succession, when alders are shaded out by conifers, the mixed alder-conifer stands may have higher productivity than the conifer-only stands even in the high-fertility sites. In each system, the sustainable harvest rate depends on the soil resource and the management of plant functional groups.

Sustainable Fisheries

Unrestricted harvest of plants and animals can reduce sustainability by replacing the natural negative feedbacks to population changes with positive feedback responses that drive harvested populations to low levels. For example, supply-and-demand economics and government subsidies often maintain or increase fishing intensity in response to declining fish populations (Ludwig et al. 1993; Hilborn et al. 1995; Pauly and Christensen 1995), as in the Pacific sardine and Peruvian anchovy fisheries (Hilborn and Walters 1992) rather than decrease predation pressure, as would be the typical population response of natural predators (Francis 1990).

The North Pacific salmon fishery appears relatively stable under current management. Commercial and subsistence fishing are allowed only after a specified escapement into spawning streams has been achieved. This strong negative feedback to fishing pressure, which allows fishing when adequate recruitment is obtained, may contribute to the recent record-high salmon catches from this fishery after 30 yr of management (Francis and Sibley 1991; Ludwig et al. 1993), although regulation of fisheries on the high seas is also important. Sustaining the fishery requires protection of spawning streams from changes in other interactive controls such as dams that prevent winter floods (disturbance regime), warming of streams by removal of riparian vegetation of logged sites (climate), species introductions (functional groups), and inputs of silt and nutrients in runoff or municipal sewage outfall (nutrient resources).

A current approach to sustainable management is to harvest only the production in excess of that which would occur when density-dependent mortality limits fisheries stocks, termed "surplus production" (Rosenberg et al. 1993; Hilborn et al. 1995). We suggest that the existence and magnitude of surplus production depend on the stability of interactive controls (e.g., physical environment, nutrients, predation pressure) and the extent to which these interactive controls respond to changes in fisheries stocks (Pauly and Christensen 1995). For example, the impact of fish on nutrient supply and zooplankton densities may differ between the open ocean and salmon-spawning streams. The major challenge in fisheries management is to estimate surplus production in the face of fluctuating interactive controls and uncertainty in the relationship between these controls and the population size of the fishery.

Preservation of Endangered Species

Human activities threaten the survival of many species. Although extinction is a natural process, current extinction rates from human activities greatly exceed those of the past several million years (National Research Council 1994). The most common human cause of species extinction is habitat destruction through land use and activities that alter the interactive controls that maintain critical habitat. We define the habitat of a species as the ecosystem and interactive controls that it depends on rather than simply the patch of vegetation where the organism spends most of its time. For example, some species depend directly on disturbance regime, such as herbs with long-lived seed banks that germinate only

after fire (Fenner 1985). Sustaining a population of these fire-adapted species requires protecting the natural fire regime as well as the land on which it grows.

The focus of endangered species protection has generally been the establishment of parks containing populations of the target species and vegetation associated with those species. However, establishment of parks is insufficient protection for species when humans continue to influence important interactive controls, such as fire regime, N supply from atmospheric deposition, water flows, or species introductions (Jensen et al. 1993). In addition, fence building, habitat fragmentation, and hunting alter the natural linkages among ecosystems inside and outside parks. Consequently, nearly all parks require management to compensate for human impact. For example, the boundaries of Yellowstone National Park block migration of elk to traditional wintering areas, so winter food supplements must be provided (Chase 1987). These winter food supplements are not subject to the natural negative feedbacks associated with changes in elk population size. In combination with the extirpation of natural predators, natural controls on the elk population and forage quality are lacking and have at times been replaced by hunting or relocation of elk. In general, it may be more biologically successful and less costly to protect species by conserving interactive controls than by replacing these controls with direct human management of the endangered species. Where interactive controls cannot be preserved, our framework suggests that management should try to create a stable set of interactive controls that will sustain desired habitat without relying on continued intensive intervention.

CONCLUSIONS

The structure and processes of natural ecosystems are sensitive to natural and human-induced changes in interactive controls (climate, disturbance, soil or water resources, and functional groups of biota). Positive feedbacks associated with exponential population growth and cumulative changes in rates of nutrient cycling are counterbalanced by negative-feedback processes such as predation, successional cycles of disturbance and recovery, and use of the same limiting resource by several competing species. The sustainability of an ecosystem depends on the complex interactions among interactive controls and the positive and negative feedbacks they generate. An ecosystem is sustainable under conditions and time-scales in which negative feedbacks constrain changes in interactive controls.

We assert that the general principles of ecosystem sustainability are critical to sound management of human-modified ecosystems. In particular, knowledge of interactive controls may assist management of natural resources and biological diversity. The most important step in enhancing the sustainability of a managed ecosystem is to preserve or manage interactive controls so they form negative feedbacks that maintain desired ecosystem characteristics. These negative feedbacks can be strengthened by maintaining historic linkages among ecosystems and by using regulations to produce negative feedbacks where human intervention strongly influences interactive controls of natural ecosystems.

Human activities are leading to global changes in all major interactive controls:

climate (global warming), soil and water resources (N deposition, erosion, diversions), disturbance regime (land use change, fire control), and functional groups of organisms (species introductions and extinctions). As a result, all ecosystems are experiencing directional changes in ecosystem controls, creating novel conditions, and, in many cases, positive feedbacks that lead to new types of ecosystems. These changes heighten the challenge of sustainably managing natural resources and threaten the sustainability of natural ecosystems everywhere.

ACKNOWLEDGMENTS

We thank F. S. Chapin, Jr., M. Chapin, G. Daily, A. Galo, J. Harte, S. Hobbie, D. Jensen, S. Lele, N. Martinez, P. Morrow, W. Post, T. Powell, M. Power, P. Ramakrishnan, A. Schultz, and P. Vitousek for helpful discussions and comments. These ideas resulted from research supported by the National Science Foundation (DEB-8205344, BSR-9122791, and DPP-9214906), the National Aeronautics and Space Administration, and the Department of Energy.

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Associate Editor: Wilfred M. Post