ECOSYSTEM FUNCTION, PRINCIPLES OF

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GLOSSARY

ecosystem All the individuals, species, and populations in a spatially defined area and the interactions among them and with the abiotic environment.

ecosystem functioning The sum total of processes such as the cycling of matter, energy, and nutrients operating at the ecosystem level.

functional group A group of species that perform similar roles in an ecosystem process.

nutrient cycle (or biogeochemical cycle) The repeated pathway of mineral elements, such as carbon, nitrogen, phosphorus, and water, from the environment through organisms and back into the environment.

succession The predictable change in species that occupy an area over time caused by a change in biotic or abiotic factors benefiting some species but at the expense of others.

ECOSYSTEMS ARE COMPOSED OF COMMUNITIES of organisms that interact with one another and the abiotic environment. The interactions of organisms and their environment are represented in processes that are called ecosystem functions. The capture of solar energy (photosynthesis), the cycling of nutrients, and the stability of ecosystem functioning are influenced by biodiversity. An understanding of how biodiversity and ecosystem functioning are related is necessary for determining how to sustain human populations in the future.

I. DEVELOPMENT OF THE ECOSYSTEM CONCEPT

The concept of the ecosystem as a functioning unit in the natural world is a relatively recent one. The term ecosystem was coined by the British ecologist Tansley in 1935 and has since become a common word in science and with the public. An ecosystem encompasses all the organisms of a given area and their relationships with one another and the physical or abiotic environment. The ecosystem contains the linkages and dynamic interactions between life and the environment, many of which are essential to society. A focus on the ecosystem as the unit of study represents a shift from studying the ecology and behavior of individual organisms and species (natural history) to the study of processes and how they influence or are influenced by organisms and their interactions with the environment.

Dividing the complexity of nature into convenient units of study is required for scientific investigation but can present problems. Ecological systems can be

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organized in a hierarchy of increasing levels of organization and complexity: individual, population, species, community, ecosystem, landscape, and biome. The size (scale) of an ecosystem is defined by the purposes of the study. Ecosystems may have distinct boundaries as in the case of a lake or a watershed. More often, the boundaries of one ecosystem (a forest) may grade gradually into another (a meadow) across an intermediate area called an ecotone. The ecotone is often a zone of higher diversity because it may be a suitable habitat for species from each of the adjoining ecosystems. At one extreme of scale, the earth is sometimes treated as an ecosystem. At the other extreme, the complex symbiotic community of organisms inhabiting the gut of a termite has all the functional properties of an ecosystem. The definition and delineation of an ecosystem has practical importance because ecosystems are increasingly seen as a functional unit for resource and conservation management purposes. It has become evident that the management of lands for sustained levels of ecosystem services and natural resources requires an understanding of how ecosystems function, how they respond to disturbance, and how the role of biodiversity is regulating their function and stability.

TABLE I

Examples of the Biological and Physical Processes or Interactions That Contribute to Important Ecosystems Functions

Process	Ecosystem function
Photosynthesis	Primary production
Plant nutrient uptake	
Microbial respiration	Decomposition
Soil and sediment food web dynamics	
Nitrification	Nitrogen cycling
Denitrification	
Nitrogen fixation	
Plant transpiration	Hydrologic cycle
Root activity	
Mineral weathering	Soil formation
Soil bioturbation	
Vegetation succession	
Predator–prey interactions	Biological control

II. ECOSYSTEM FUNCTIONING AND ECOSYSTEM SERVICES

Society depends on the functioning of ecosystems for many essential ecosystem services on which we place economic and aesthetic value (Daily, 1997). Ecosystem functioning results from the collective activities of organisms and their life processes (production, consumption, and excretion) and the effects of these activities on the condition of the environment. These functions (services when they provide utility to humans) include production of food, fuel, and fiber, the cycling and purification of water, and the maintenance of organisms that have a role in ecosystem functioning or that provide products for human use (Table I). Humans are rapidly changing the earth's ecosystems and their services by altering land use or by harvesting biological resources (forest cutting and fisheries) (Vitousek *et al.*, 1997). Approximately 40% of the earth's primary production is diverted to human use. One consequence of these economic activities is an abrupt increase in the rate of change in biological diversity leading to species extinction, replacement of high-biodiversity ecosystems with less diverse managed systems, and invasions of natural ecosystems by exotic species. This pattern of ecosystem change has raised serious concern that the functioning and stability of our global ecosystem are threatened by the loss of biodiversity.

A. What Do Ecosystem Scientists Study?

Ecosystems share certain characteristics and functions that allow scientists to study ecosystem types (e.g., deciduous forest, temperate grassland, arctic tundra, coral reef, and deep-ocean hydrothermal vents) that vary greatly in structure, biodiversity, and spatial extent. For example, all ecosystems require inputs of energy (usually solar) and a supply of the mineral elements (nutrients) essential for life. These inputs support many ecological processes operating at multiple scales. For example, sunlight, carbon dioxide, and water are inputs for the process of photosynthesis, which can be measured and studied at the scale of individual cells, a leaf, the plant canopy, or an entire ecosystem. Photosynthesis acting with other processes such as mineral uptake by roots combine to create an ecosystem function—primary productivity.

Scientists can discover basic principles about the behavior of ecosystems by studying the functions that very different ecosystems, such as the polar desert of Antarctica and the rangelands of the southwestern United States, share in common (Virginia and Wall, 1999). The movement of energy and materials within and between ecosystems and the role of organisms in mediating these processes are the parameters used by

TABLE II

Examples of Ecosystem Services That Would Be Affected by a Decline in Ecosystem Function[a]

Pest control
Insect pollination
Fisheries
Climate regulation
Soil retention
Flood control
Soil formation and maintenance of soil fertility
Cycling of matter
Composition of the atmosphere
Maintenance of genetic diversity

[a] Based on Daily (1997).

ecosystem scientists to compare the functioning of ecosystems and their responses to disturbance. Some of the important processes and functions central to the integrity and sustained activity of an ecosystem are summarized in Table II. Ecosystem scientists study the rate at which ecosystems remove carbon from the atmosphere by photosynthesis, store it in the soil as organic matter, and then return the stored carbon to the atmosphere during decomposition. They study how nitrogen is cycled through ecosystems to sustain continued plant productivity. Our knowledge of how carbon and nitrogen move in the ecosystem helps us to understand when an ecosystem has been seriously altered by humans, for example, by adding nitrogen in the form of air pollution (acid rain) and fertilizers.

Many basic principles provide insight into the functioning of ecosystems and their response to human use and disturbance. Here, we will consider some of the essential functions of ecosystems and examine the principles that govern their operation, with an emphasis on the role of organisms (biodiversity) in determining ecosystem functioning.

III. IMPORTANT ECOSYSTEM FUNCTIONS

A. Ecosystem Productivity

A central process of most ecosystems is photosynthesis, the capture of solar radiation and its conversion to stored chemical forms (biomass). Plants require sunlight, water, and essential nutrients for the processes of photosynthesis. Photosynthesis is coupled with other plant processes that result in plant growth, i.e., the accumulation of biomass. Primary productivity, the change in plant biomass per unit area and time, is an important index of ecosystem function. Primary productivity (often referred to as ecosystem productivity) has been related to plant species diversity as well as the diversity of organisms (soil biota) that influence the availability of limiting resources. Humans depend on ecosystem productivity as the basis of our agriculture and forestry and fisheries. Thus, factors that alter ecosystem productivity (e.g., climate change and biodiversity loss) affect us directly.

Ecosystems with high rates of primary productivity have favorable amounts of the resources required for plant growth and optimal climate. These systems also tend to have higher diversity (Table III). The highest rates of terrestrial ecosystem productivity are seen in the tropics, where temperature and moisture are favorable for plant growth throughout the year. In contrast, water-limited hot and cold deserts have much lower productivity, averaging less than 10% of that of tropical systems.

1. Limits to Ecosystem Productivity

A basic principle invoked to explain variation among ecosystems in their productivity is Liebig's Law of Minimum. Justus Liebig formulated this concept during pioneering studies of the mineral nutrition of plants in the early 1800s. He found that addition of a single "limiting element" to a soil would increase plant growth. Once this element was in sufficient supply, another mineral element would have to be supplied in increased amounts to stimulate additional increases in plant growth. From these observations, he proposed that a limiting factor was responsible for limiting the growth or reproduction of an organism or population. This

TABLE III

Typical Values for the Net Primary Productivity of Major Ecosystems[a]

Ecosystem type	Net primary production (g C/m^2/year)	Relative species diversity
Tropical rain forest	900	Highest
Temperate forest	540	Intermediate
Grassland	315	Intermediate
Desert	32	Low
Extreme desert	1.5	Lowest

[a] Ecosystem productivity and biodiversity are often positively related.

factor might be a chemical factor (a growth-stimulating nutrient such as nitrogen), a physical factor such as moisture, or a biological factor such as the presence of a competing species. Thus, any change in a limiting factor is expected to have large effects on ecosystem functioning.

There are many examples in which a change in a limiting factor alters ecosystem function. The large increase in the amount of nitrogen cycling in the environment from fertilizers and fossil fuel should have significant effects on rates of ecosystem functions since nitrogen frequently is the primary limiting element for plant growth in terrestrial ecosystems. Humans have doubled the rate of nitrogen inputs to ecosystems with increases in carbon storage and declines in biodiversity (Vitousek *et al.*, 1997). In fact, the forests of the northeastern United States may have reached "saturation" in their ability to absorb and retain anthropogenic inputs of nitrogen.

Are plant species diversity and primary production related? Ecologists are accumulating evidence from experiments in controlled growth facilities and in the field that ecosystem primary productivity increases with increasing plant species diversity. The theoretical basis for the expectation that productivity and diversity should be related derives from an understanding of how limiting resources (water and nutrients) are distributed in ecosystems and an appreciation for the diversity of physiological or "functional" traits that organisms have evolved to capture and utilize these resources for growth. Differences between plant species in rooting depth, phenology (seasonality of growth), photosynthetic rates, and other physiological traits allow multispecies communities to more fully utilize the available resources.

The ability of diverse plant communities to obtain higher productivity than low-diversity systems is demonstrated in traditional (low-input) agriculture in which polycultures (multiple-species plantings) often have higher yields than single-species plantings (monocultures) (Gliessman, 1998). For example, corn (*Zea mays*) yields at comparable densities are higher when corn is grown in the presence of nitrogen-fixing beans (*Vicia* spp.). The bean crop forms a symbiotic association with bacteria that "fix" atmospheric nitrogen (N_2) to other inorganic forms (ammonia and NH_3) useable by plants. The nitrogen fixed by the bean crop improves the overall supply of this limiting element in the soil and increases the growth of the interplanted corn. The functioning provided by the diverse corn–bean–nitrogen-fixing bacteria association is often replaced in intensive agriculture by applying inorganic nitrogen fertilizers. With external inputs (fertilizers) the corn monoculture can produce higher yields than can the polyculture. Substituting an industrial source of nitrogen for a biological source has environmental costs resulting from the production and combustion of fossil fuels used to produce fertilizers. In addition, overapplication of fertilizers is a major source of water pollution in surface and groundwaters.

There are similar examples of diversity influencing productivity in natural ecosystems. In a California grassland ecosystem, Hooper and Vitousek (1997) manipulated the number of plant functional groups in a community (early vs late-season forbs, perennial grasses, and nitrogen-fixing plants) in combinations of one to four groups in a given plot. They found that the number of plant functional groups was not the main factor that determined productivity. Rather, certain functional characteristics of individual species within functional groups contributed more to ecosystem productivity than overall diversity of the plot. This study points to the complexity of trying to simply relate species diversity to function. As a general principle, ecologists recognize that some species play particularly important roles in regulating important ecosystem functions such as productivity and nutrient cycling.

B. Keystone Species

Certain species, termed keystone species, have a disproportionate influence (relative to their biomass) on ecosystem functioning. The loss of a keystone species will produce a cascade of effects on the diversity and function of the remainder of the ecosystem (Bond, 1993). Consequently, since keystone species can control ecosystem diversity and associated ecosystem functions, they and the habitats they live in often receive high priority in conservation management plans. There are many well-documented studies of keystone species and how they interact with ecosystem functioning, e.g., the North Pacific sea otter preys on sea urchins, which consume kelp. In the absence of the keystone predator, sea urchin populations increase and create areas devoid of kelp and, consequently, the myriad of fish and other species that depend on the kelp forest (Fig. 1). This is an example of a food web—the representation of trophic (feeding) relationships between species in an ecosystem.

There are many examples of keystone species in terrestrial ecosystems. A large change in African elephant numbers has dramatic effects on the diversity

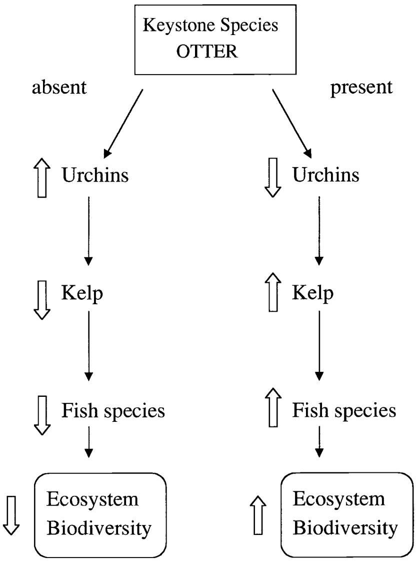

FIGURE 1 The influence of a keystone species on the biodiversity of an entire ecosystem can be large. Arrows indicate an increase or decrease in population size or species diversity in response to the presence or absence of the keystone species. The removal of the Pacific sea otter from California coastal ecosystems leads to the loss of the kelp community and many fish species.

and structure of the vegetation types (savanna woodlands and forests) they consume, altering ecosystem productivity, soil nutrient cycles, and plant community diversity. The much smaller tsetse fly shares the elephant's habitat and also has the attributes of a keystone species. The tsetse fly is the vector for the human disease sleeping sickness (African trypanosomiasis). This biting fly also influences the behavior of large herbivores that tend to avoid heavily infested areas. Consequently, herbivore-related impacts on plant communities and associated ecosystem functions are altered in tsetse-occupied ecosystems. This small insect may control the biodiversity of large tracts of Africa through another mechanism. Diverse native ecosystems have been "protected" from agricultural development and species loss because humans avoid regions where the tsetse and therefore sleeping sickness are endemic.

C. Nutrient Cycling

The sustained functioning of any ecosystem requires a minimum number of species to develop the intricate relationships between producers, consumers, and decomposers that regulate the flow of energy and nutrients. The productivity of all ecosystems is dependent on the cycling of essential elements. The movement and biological transformations of organic matter and nutrients are mediated by biota, especially those found in soil and sediments (Wall and Virginia, 1999). Therefore, changes in the biodiversity of ecosystems can alter biogeochemical processes.

1. Succession

Scientists study the process of ecological succession (ecosystem change with time, often in response to disturbance) in part to untangle relationships between biodiversity and function. Although not all ecosystems follow a predictable pathway as they develop in time, examples of succession highlight the linkage between organisms and diversity and ecosystem function. They include the recovery of a forest after harvest or following damage by a hurricane, the reestablishment of grassland following fire, and the old-field succession of natural vegetation reclaiming abandoned agricultural land. During succession, ecosystems change in generally predictable ways as they accumulate species, increase in biomass, and gain structural complexity. Odum (1969) proposed a model of ecological succession (development) that relates ecosystem diversity, structure, and functioning as ecosystems redevelop and "mature" following disturbance (Table IV). Odum's model related the stability (constancy) of function and the conservation of nutrients to increasing diversity—themes that are at the center of biodiversity and ecosystem research today.

TABLE IV

A Model of Ecological Succession Showing Relative Changes in Energy Flow, Nutrient Cycling, and Diversity over Time[a]

	Ecosystem status	
Ecosystem trait	Developing	Mature
Energetics		
Net primary production	High	Low
Food chains	Linear	Web-like
Communities		
Species diversity	Low	High
Nutrient cycling		
Mineral cycles	Open	Closed
Nutrient conservation	Poor	Good
System dynamics		
Stability	Poor	Good

[a] Based on Odum (1969).

The relationships represented in Odum's (1969) model between ecosystem function and diversity are elucidated in the Hubbard Brook watershed experiment (Likens and Bormann, 1995). One of the first long-term ecosystem studies, the Hubbard Brook project began in 1963 in the White Mountains of New Hampshire. The study was designed to understand the process of forest recovery following harvest with a focus on ecosystem functions related to production, nutrient cycling, and nutrient loss. Measurements of the mature intact deciduous forest showed that less than 0.1% of the nitrogen contained in living forest biomass and dead organic matter in the soil and litter left the site in stream flow. A nutrient cycle in which outputs are low and internal recycling of nutrients is high (the loop from soil to vegetation and back to soil) is called a closed nutrient cycle.

After the unperturbed patterns of growth and nutrient cycling were known, an entire Hubbard Brook watershed was clear-cut. What followed was a dramatic change in ecosystem functioning. Stream flow increased by approximately 40% because water use by plants had been nearly eliminated by the forest harvest. The previously "closed" nutrient cycle of this forest became "open." After clear-cut the concentrations of nitrogen (nitrate) in the stream water draining the watershed increased approximately 60-fold. Concentrations of elements that are important to the biology of the ecosystem leaked into the streams and were exported from the ecosystem. Elements not essential to plant growth or required in very small amounts (e.g., sodium) were not lost to the same degree, indicating their cycling was not regulated by biotic activity of the forest. Odum (1969) predicted that nutrient losses would decline with increasing plant biomass and function. After the Hubbard Brook forest was allowed to regrow (undergo succession), nutrients resumed being absorbed by plants and nutrient losses to streams declined to near baseline levels. The Hubbard Brook ecosystem experiment informed forest management practices by providing a better understanding of how forest removal and regrowth affect the retention of soil nutrients and therefore the long-term productivity and diversity of the ecosystem.

D. Ecosystem Stability

Ecosystems are dynamic. They experience change in species composition and function in response to variations in climate and an array of disturbances. Fire, flood, drought, frost, and biological events such as the outbreak of pathogens and pests can "stress" ecosystems and alter their condition. Ecosystems vary widely in their responses to disturbance. The ability of an ecosystem to withstand stress without a loss of function (resistance) or to recover rapidly from disturbance (resilience) is an important ecosystem trait. Some ecosystems, such as tropical forests, appear very stable (high resistance and resilience) and their functioning is little affected by variations in factors external to the system (e.g., weather). Ecosystems with high resilience are buffered against perturbation. Many ecosystems, however, show large decreases in productivity and biodiversity when disturbed. These ecosystems are "fragile" and have low resistance.

The relationship between ecosystem stability and diversity has been the subject of many field studies and theoretical tests using mathematical modeling. Ecologists have hypothesized that ecosystems with high biodiversity are more resistant (will experience less change) in response to a given level of disturbance and will also exhibit resilience—a high rate of recovery to predisturbance functioning (Folke *et al.*, 1996).

Does diversity influence the stability of ecosystem functioning? There is experimental evidence that it can do so (Chapin *et al.*, 1997). Several mechanisms have been proposed and tested to varying degrees to examine this relationship (Chapin *et al.*, 1997). Higher species diversity means that the trophic structure (feeding relationships among species) of the ecosystem is more complex, providing alternate pathways for energy flow within and between trophic levels (producers, consumers, and decomposers). Alternative pathways for energy transfers within the ecosystem could increase resistance to disturbance (species loss). Naeem and Li (1997) tested the hypothesis that redundancy (multiple species with similar functions in a food web) would stabilize ecosystem functioning by creating experimental microcosms with a varying number of species in each functional group. The simple systems contained producers (algae), decomposers (bacteria), and a primary and secondary consumer trophic level (protists)—the trophic structure of a typical aquatic ecosystem. Nutrient levels, light, and the number of species per trophic level were manipulated, and the biomass and density of the producers and decomposers were measured as an indicator of ecosystem functioning. As the number of species in a trophic level increased, the biomass and density of replicate communities were more consistent. Thus, the communities with more species were more predictable in function (biomass production) and had higher reliability, i.e., the probability that an ecosystem will provide a given level of performance over a specified period of time.

Higher species diversity may ensure functioning by reducing the risk of invasion by species that have the capacity to alter the structure or function of the ecosystem. An example is the higher resistance of species-rich natural systems to pest outbreaks compared to low-diversity agricultural ecosystems growing under the same environmental conditions. The spatial arrangement of individuals in an ecosystem can affect their risk to disease, predation, or consumption. In higher diversity systems the mean distance between individuals of the same species is on average greater than that of low-diversity systems. The wider spacing of individuals acts to slow the movement of pathogenic organisms, which should limit the occurrence of pest outbreaks that alter the performance of the ecosystem. These and other observations lead to the general expectation that diversity increases the resistance of ecosystems to disturbance.

The benefits of biodiversity to ecosystem functioning should be multiple since the processes of production and nutrient cycling are coupled by the biological interactions of organisms. The response of a Minnesota grassland to a severe drought (disturbance) illustrates this principle (Tilman *et al.*, 1996). In 1987 and 1988, a drought decreased productivity of the grassland. The species diversity of experimental plots prior to the drought explained the degree of productivity loss. Diverse plots experienced about a 50% decline in productivity, whereas productivity in the least diverse plots declined by more than 90%. The greater resistance of the higher diversity plots resulted from compensatory increases in productivity shown by drought-resistant species. The more diverse plots also had lower concentrations of nitrate in the rooting zone, indicating a more efficient use of this limiting resource.

This experiment demonstrates that species diversity has an effect on productivity and nutrient cycling and that declining species diversity influences these functions. However, we lack an understanding of the mechanisms producing these patterns of ecosystem response to disturbance and biodiversity change. Increasing diversity may increase the chance that a single drought-adapted and productive species will be present in the community, ensuring relatively high productivity. Alternatively, higher diversity may provide for a more efficient utilization of limiting resources, as suggested by the lower soil nitrate in more diverse plots. Before the basic relationships between biodiversity and ecosystem functioning can be more fully formalized, we need more detailed information on the critical levels (thresholds) of diversity associated with specific ecosystem functions and how environmental conditions operating over time alter their relationship (Folke *et al.*, 1996).

IV. CONCLUSIONS

Humans have become major agents of environmental change and influence the biodiversity and structure of ecosystems in many ways. Air pollution, clearing of natural systems for agriculture, forestry and urban development, the spread of exotic species, changes in the composition of the atmosphere, and other anthropogenic influences are altering ecosystem functioning. By changing ecosystem biodiversity and altering the processes that biota mediate, we significantly decrease the ability of ecosystems to provide services and resources for our use. The management of ecosystems for sustained levels of services and the restoration of damaged ecosystems will require greater knowledge about the role that species play in ecosystems functions related to production and nutrient cycling. Although we cannot know with certainty the roles of most species in ecosystems, it is prudent to assume that all biodiversity is essential to ecosystem function and stability and should be valued and protected.

See Also the Following Articles

ECOSYSTEM, CONCEPT OF • ECOSYSTEM SERVICES, CONCEPT OF • ENERGY FLOW AND ECOSYSTEMS • KEYSTONE SPECIES • NITROGEN CYCLE

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