The Ecosystem Concept

1

Ecosystem ecology studies the links between organisms and their physical environment within an Earth-System context. This chapter provides background on the conceptual framework and history of ecosystem ecology.

Introduction

Ecosystem ecology addresses the interactions between organisms and their environment as an integrated system. The ecosystem approach is fundamental to managing Earth's resources because it addresses the interactions that link biotic systems, of which people are an integral part, with the physical systems on which they depend. The approach applies at the scale of Earth as a whole, the Amazon River basin, or a farmer's field. An ecosystem approach is critical to the sustainable management and use of resources in an era of increasing human population and consumption and large, rapid changes in the global environment.

The ecosystem approach has grown in importance in many areas. The United Nations Convention on Biodiversity of 1992, for example, promoted an ecosystem approach, including humans, for conserving biodiversity rather than the more species-based approaches that predominated previously. There is growing appreciation for the role that species interactions play in the functioning of ecosystems (Díaz et al. 2006). Important shifts in thinking have occurred about how to manage more sustainably the ecosystems on which we depend for food and fiber. The supply of fish from the sea is now declining because fisheries management depended on species-based stock assessments that did not adequately consider the resources on which commercial fish depend (Walters and Martell 2004). A more holistic view of managed systems can account for the complex interactions that prevail in even the simplest ecosystems. There is also a growing appreciation that a thorough understanding of ecosystems is critical to managing the quality and quantity of our water supplies and in regulating the composition of the atmosphere that determines Earth's climate (Postel and Richter 2003).

A Focal Issue

Human exploitation of Earth's ecosystems has increased more in the last half-century than in the entire previous history of the planet (Steffen et al. 2004), often with unintended detrimental effects. Forest harvest, for example, provides essential wood and paper products (Fig. 1.1). The amount and location of harvest, however, influences other benefits that society receives from forests, including the quantity and quality of water in headwater streams; the recreational and aesthetic benefits of forests; the probability of landslides, insect outbreaks, and forest fires; and the potential of forests to release or sequester carbon dioxide (CO_2), which influences climatic change. How can ecosystems be managed to meet these multiple (and often conflicting) needs? In the Northwestern

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Fig. 1.1 Patch clear-cutting leads to single-species patches in a mosaic of 100 to 500-year native Douglas-fir forests in the Northwestern U.S. The nature and extent of forest clearing influences ecosystem processes at scales ranging from single patches (e.g., productivity and species diversity) to regions (e.g., water supply and fire risk) or even the entire planet (climatic change). Photograph by Al Levno, U.S. Forest Service

U.S., for example, timber was harvested in the second half of the twentieth century more rapidly that it regenerated. Concern about loss of old-growth forest habitat for endangered species such as the spotted owl led to the development of ecosystem management in the 1990s to address the multiple functions and uses of forests (Christensen et al. 1996; Szaro et al. 1999). Ecosystem ecology draws on a breadth of disciplines to provide the principles needed to understand the consequences of society's choices.

Overview of Ecosystem Ecology

The flow of energy and materials through organisms and the physical environment provides a framework for understanding the diversity of form and functioning of Earth's physical and biological processes. Why do tropical forests have large trees but accumulate only a thin layer of dead leaves on the soil surface, whereas tundra supports small plants but an abundance of organic matter at the soil surface? Why does the concentration of carbon dioxide in the atmosphere decrease in summer and increase in winter? What happens to nitrogen fertilizer that farmers add to their fields but do not harvest with the crop? Why has the introduction of exotic grasses to pastures caused adjacent forests to burn? These are representative of the questions addressed by ecosystem ecology. Answers to these questions require an understanding of the interactions between organisms and their physical environments – both the response of organisms to environment and the effects of organisms on their environment. These questions also require a focus on integrated ecological systems rather than individual organisms or physical components.

Ecosystem analysis seeks to understand the factors that regulate the **pools** (quantities) and **fluxes** (flows) of materials and energy through ecological systems. These materials include carbon, water, nitrogen, rock-derived elements such as phosphorus, and novel chemicals such as pesticides or radionuclides that people have added to the environment. These materials are found in

abiotic (nonbiological) pools such as soils, rocks, water, and the atmosphere and in **biotic** pools such as plants, animals, and soil microorganisms (microbes).

An **ecosystem** consists of all the organisms and the abiotic pools with which they interact. **Ecosystem processes** are the transfers of energy and materials from one pool to another. Energy enters an ecosystem when light energy drives the reduction of carbon dioxide (CO_2) to form sugars during photosynthesis. Organic matter and energy are tightly linked as they move through ecosystems. The energy is lost from the ecosystem when organic matter is oxidized back to CO_2 by combustion or by the respiration of plants, animals, and microbes. Materials move among abiotic components of the system through a variety of processes, including the weathering of rocks, the evaporation of water, and the dissolution of materials in water. Fluxes involving biotic components include the absorption of minerals by plants, the fall of autumn leaves, the decomposition of dead organic matter by soil microbes, the consumption of plants by herbivores, and the consumption of herbivores by predators. Most of these fluxes are sensitive to environmental factors such as temperature and moisture, and to biological factors regulating the population dynamics and species interactions in communities. The unique contribution of ecosystem ecology is its focus on biotic and abiotic factors as interacting components of a single integrated system.

Ecosystem processes can be studied at many spatial scales. How big is an ecosystem? Ecosystem processes take place at a wide range of scales, but the appropriate scale of study depends on the question asked (Fig. 1.2). The impact of zooplankton on their algal food might be studied in small bottles in the laboratory. The controls over productivity might be studied in relatively homogeneous patches of a lake, forest, or agricultural field. Questions that involve exchanges occurring over very broad areas might best be addressed at the global scale. The concentration of atmospheric CO_2, for example, depends on global patterns of biotic exchanges of CO_2 and the burning of fossil fuels, which are spatially variable across the planet. The rapid mixing of CO_2 in the atmosphere averages across this variability, facilitating estimates of long-term changes in the total global flux of carbon between Earth and the atmosphere (see Chap. 14).

Some questions require careful measurements of lateral transfers of materials. A watershed is a logical unit to study the impacts of forests on the quantity and quality of the water that supplies a town reservoir. A **drainage basin**, also known as a catchment or watershed, consists of a stream or river and all the terrestrial surfaces that drain into it. By studying a drainage basin, we can compare the quantities of materials that enter from the air and rocks with the amounts that leave in stream water, just as you balance your checkbook. Studies of input–output budgets of drainage basins have improved our understanding of the interactions between rock weathering, which supplies nutrients, and plant and microbial growth, which retains nutrients in ecosystems (Vitousek and Reiners 1975; Bormann and Likens 1979; Driscoll et al. 2001; Falkenmark and Rockström 2004).

The upper and lower boundaries of an ecosystem also depend on the question asked and the scale that is appropriate to the question. The atmosphere, for example, extends from the gases between soil particles to the edge of outer space. The exchange of CO_2 between a forest and the atmosphere might be measured a few meters above the top of the canopy where variation in CO_2 concentration largely reflects processes occurring within the forest rather than in upwind ecosystems. The *regional* impact of grasslands on the moisture content of the atmosphere might, however, be measured at a height of several kilometers above the ground, where the moisture released by the ecosystem condenses and returns as precipitation (see Chap. 2). For questions that address plant effects on water and nutrient cycling, the bottom of the ecosystem might be the maximum depth to which roots extend because soil water or nutrients below this depth are inaccessible to plants. Studies of long-term soil development, in contrast, must also consider rocks deep in the soil, which constitute the long-term reservoir of many nutrients that gradually become incorporated into surface soils (see Chap. 3).

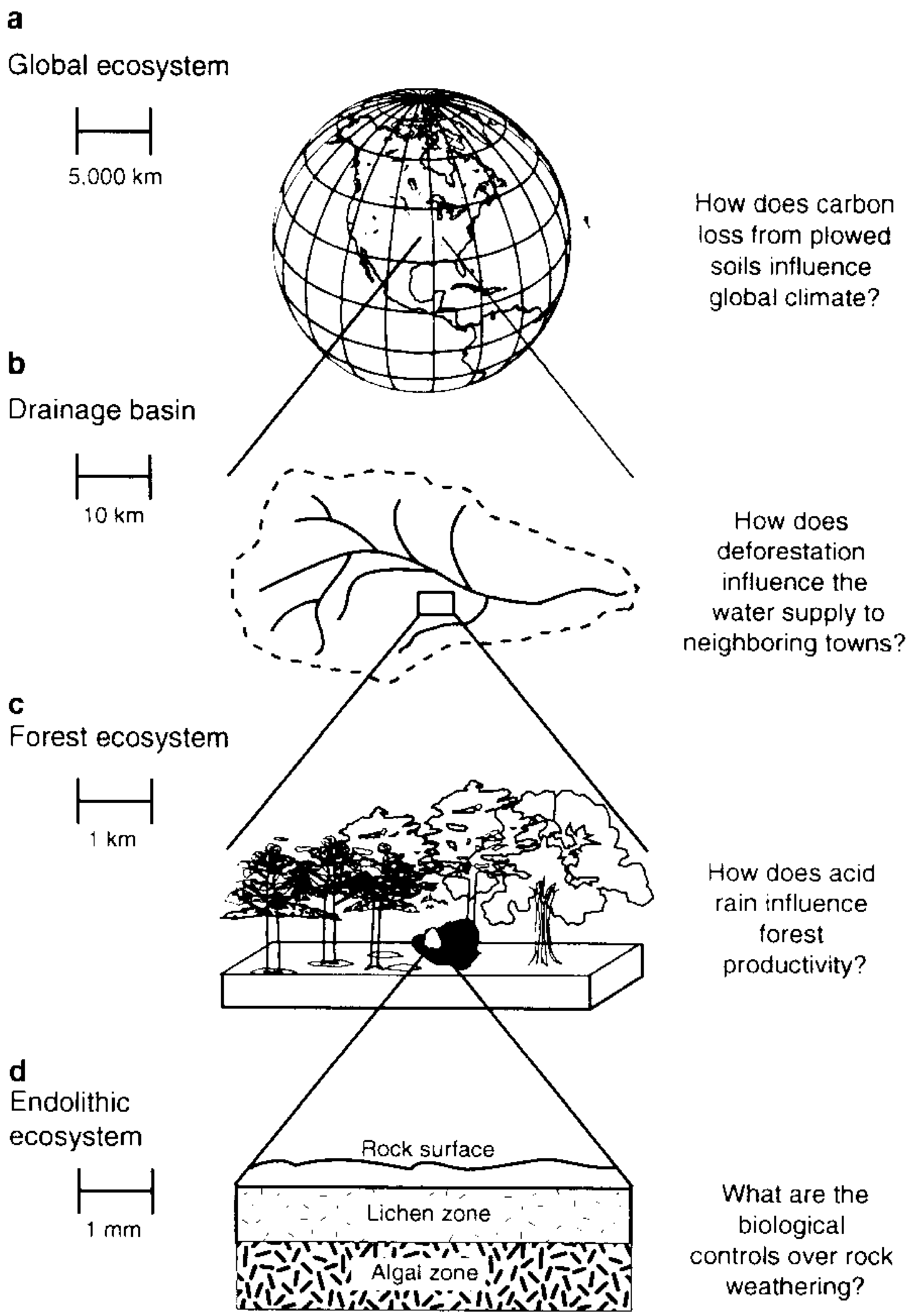

Fig. 1.2 Examples of ecosystems that range in size by ten orders of magnitude: an endolithic ecosystem in the surface layers of rocks (1×10^{-3} m in height), a forest 1×10^{3} m in diameter, a drainage basin (1×10^{5} m in length), and Earth (4×10^{7} m in circumference). Also shown are examples of questions appropriate to each scale

Ecosystem dynamics are a product of many temporal scales. The rates of ecosystem processes are constantly changing due to fluctuations in environment and activities of organisms on time scales ranging from microseconds to millions of years (see Chap. 12). Light capture during photosynthesis responds almost instantaneously to fluctuations in the light that strikes a leaf. At the opposite extreme, the evolution of photosynthesis two billion years ago added oxygen to the atmosphere over millions of years, causing the prevailing geochemistry of Earth's surface to change from chemical reduction to chemical oxidation (Schlesinger 1997). Microorganisms in the group Archaea evolved in the early reducing atmosphere of Earth. These microbes are still the only organisms that produce methane. They now function in anaerobic environments such as wetland soils or the anaerobic interiors of soil aggregates or animal intestines. Episodes of mountain building and erosion strongly influence the availability of minerals to support plant growth. Vegetation is still migrating in response to the retreat of Pleistocene glaciers 10,000 to 20,000 years ago. After disturbances such as fire or treefall, plant, animal, and microbial communities change gradually over years to centuries. Rates of carbon input to an ecosystem through photosynthesis change over time scales of seconds to decades due to variations in light, temperature, and leaf area.

Many early studies in ecosystem ecology made the simplifying assumption that some ecosystems are in **equilibrium** with their environment. In this perspective, relatively undisturbed ecosystems were thought to have properties that reflected (1) largely closed systems dominated by internal recycling of elements, (2) self-regulation and deterministic dynamics, (3) stable endpoints or cycles, and (4) absence of disturbance and human influence (Pickett et al. 1994; Turner et al. 2001). One of the most important conceptual advances in ecosystem ecology has been the increasing recognition of the importance of past events and external forces in shaping the functioning of ecosystems. In this nonequilibrium perspective, we recognize that most ecosystems exhibit unbalanced inputs and losses; their dynamics are influenced by varying external and internal factors; they exhibit no single stable equilibrium; disturbance is a natural component of their dynamics; and human activities exert a pervasive influence. The complications associated with the current nonequilibrium view require a more dynamic and stochastic perspective on controls over ecosystem processes.

Ecosystems are considered to be at **steady state**, if the balance between inputs and outputs to the system shows no trend with time (Bormann and Likens 1979). Steady state assumptions differ from equilibrium assumptions because they accept temporal and spatial variation as a normal aspect of ecosystem dynamics. Even at steady state, for example, plant growth changes from summer to winter and between wet and dry years (see Chap. 6). At a stand scale, younger individuals replace plants that die from old age or pathogen attack. At a landscape scale, some patches may be altered by fire or other disturbances, and other patches are in various stages of recovery. These ecosystems or landscapes are in steady state if there is no long-term directional trend in their properties or in the balance between inputs and outputs over the time scale considered.

Ecosystem ecology depends on information and principles developed in physiological, evolutionary, population, and community ecology (Fig. 1.3). The biologically mediated movement of carbon and nitrogen through ecosystems depends on the physiological properties of plants, animals, and soil microbes. The traits of these organisms are the products of their evolutionary histories and the competitive interactions that sort species into communities where they successfully grow, survive, and reproduce (Vrba and Gould 1986). Ecosystem fluxes also depend on the population processes that govern plant, animal, and microbial densities and age structures and on community processes such as competition and predation that determine which species are present and their rates of resource consumption.

The supply of water and minerals from soils to plants depends not only on the activities of soil microbes but also on physical and chemical interactions among rocks, soils, and the atmosphere. The low availability of phosphorus due to the extensive weathering and loss of nutrients in the ancient soils of western Australia, for example, strongly constrains plant growth and the quantity and types of plants and animals that can be supported. Principles of ecosystem ecology must therefore also incorporate the concepts and understanding of disciplines such as geochemistry, hydrology, and climatology that focus on the physical environment (Fig. 1.3).

People interact with ecosystems through both their impacts on ecosystems and their use of **ecosystem services** – the benefits that people derive from ecosystems. The patterns of human engagement with ecosystems reflect a complex suite of social processes operating at many temporal and spatial scales. Ecosystem ecology therefore informs and depends on concepts in the emerging field of **social–ecological stewardship**

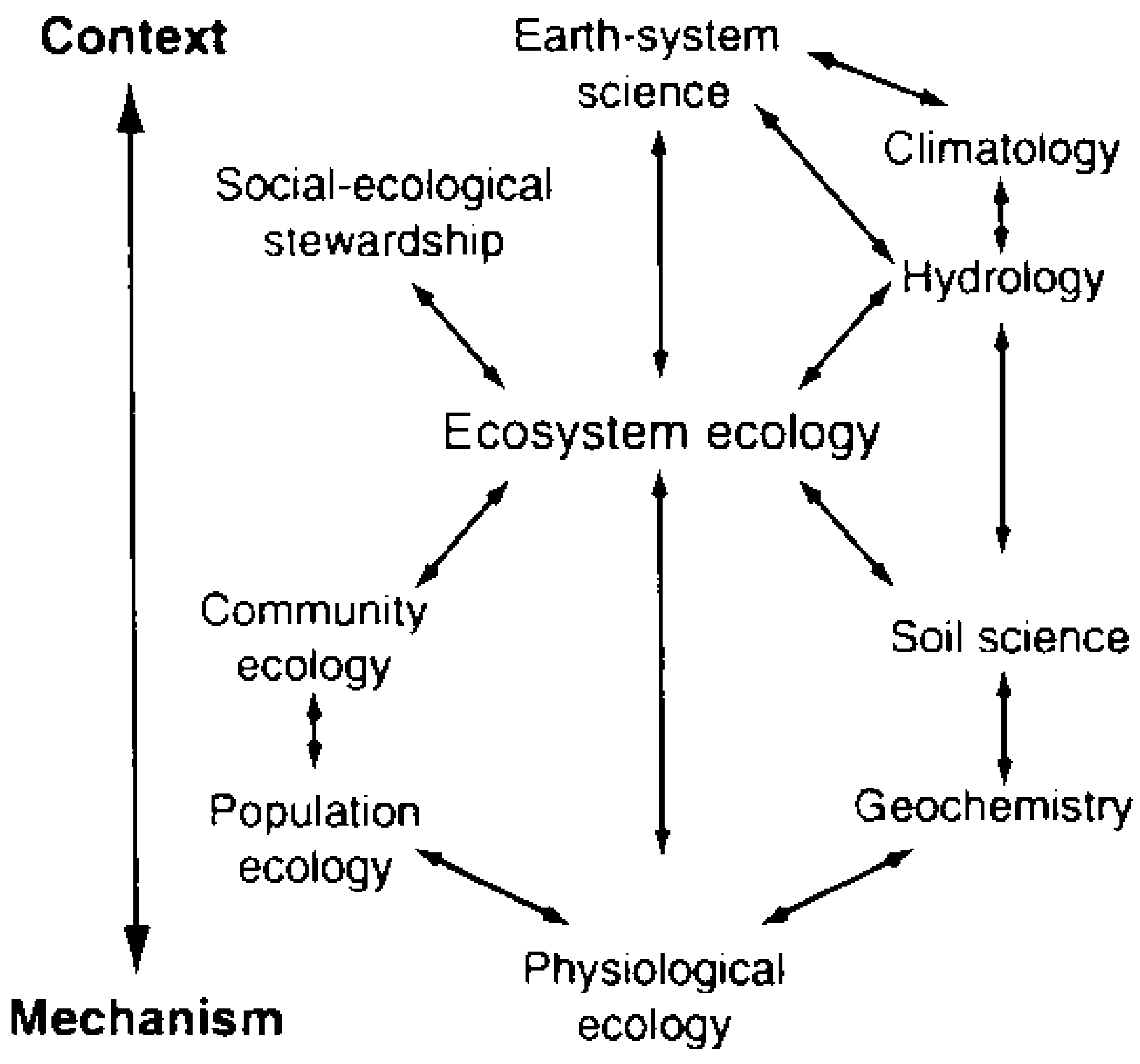

Fig. 1.3 Relationships between ecosystem ecology and other disciplines. Ecosystem ecology integrates the principles of several biological and physical disciplines, determines the resources available to society, and provides the mechanistic basis for Earth-System science

that enables people to shape the trajectory of social–ecological change to enhance ecosystem resilience and human well-being (Fig. 1.3).

Ecosystem ecology provides the mechanistic basis for understanding processes that occur at global scales. Study of Earth as a physical system relies on information about the rates and pathways by which land and water surfaces interact with the atmosphere, rocks, and waters of Earth (Fig. 1.3). Conversely, the global budgets of materials that cycle between the atmosphere, land, and the ocean provide a context for understanding the broader significance of processes studied in a particular ecosystem. Latitudinal and seasonal patterns of atmospheric CO_2 concentration, for example, help define the locations where carbon is absorbed or released from the land and ocean (see Chap. 14).

History of Ecosystem Ecology

Many early discoveries of biology were motivated by questions about the integrated nature of ecological systems. In the seventeenth century, European scientists were still uncertain about the source of materials found in plants. Plattes, Hooke, and others advanced the novel idea that plants derive nourishment from both air and water (Gorham 1991). Priestley extended this idea in the eighteenth century by showing that plants produce a substance that is essential to support the breathing of animals. At about the same time, MacBride and Priestley showed that breakdown of organic matter caused production of "fixed air" (carbon dioxide) that did not support animal life. In the nineteenth century, De Saussure, Liebig, and others clarified the explicit roles of carbon dioxide, oxygen, and mineral nutrients in these cycles. For example, in 1843, Liebig described the first nitrogen cycle, postulating that nitrogen was fixed by volcanoes, absorbed by plants, and then released to the atmosphere as NH_3 during decomposition, only later to reenter ecosystems with precipitation. Much of the biological research during the nineteenth and twentieth centuries explored the detailed mechanisms of biochemistry, physiology, behavior, and evolution that explain how life functions. Only in recent decades have we returned to the question that originally motivated this research: How are biogeochemical processes integrated in the functioning of natural ecosystems?

Many threads of ecological thought have contributed to the development of ecosystem ecology (Hagen 1992), including ideas relating to **trophic interactions** (the feeding relationships among organisms) and **biogeochemistry** (biological interactions with chemical processes in ecosystems). Early research on trophic interactions emphasized the transfer of energy among organisms. Elton, an English zoologist interested in natural history, described the role that an animal plays in a community (its **niche**) in terms of what it eats and is eaten by (Elton 1927). He viewed each animal species as a link in a **food chain** that describes the movement of matter from one organism to another. Elton's concepts of trophic structure provide a framework for understanding the flow of materials through ecosystems (see Chap. 10).

Hutchinson, an American limnologist, was strongly influenced by the ideas of Elton and the Russian geochemist Vernadsky who described the movement of minerals from soil into vegetation and back to soil. Hutchinson suggested that the resources available in a lake must limit the productivity of algae and that algal productivity, in turn, must limit the abundance of algae-eating animals. Meanwhile, Tansley, a British terrestrial plant ecologist, was also concerned that ecologists focused their studies so strongly on organisms that they failed to recognize the importance of exchange of materials between organisms and their abiotic environment. He coined the term **ecosystem** to emphasize the importance of interchanges of materials between organisms and their environment (Tansley 1935).

Lindeman, another limnologist, was strongly influenced by all these threads of ecological theory. He suggested that energy flow through an ecosystem could be used as a currency to quantify the roles that groups of organisms play in trophic dynamics. Green plants (**primary producers**) capture energy and transfer it to animals (**consumers**) and **decomposers**. At each transfer, some energy is lost from the ecosystem through respiration. Therefore, the productivity of plants constrains the quantity of consumers that an ecosystem can support (see Chap. 10). The energy flow through an ecosystem maps closely to carbon flow in the processes of photosynthesis, trophic transfers, and respiratory release of carbon. Lindeman's dissertation research on "The trophic-dynamic aspect of ecology" was initially rejected for publication because reviewers felt that there were insufficient data to draw such broad conclusions and that it was inappropriate to use mathematical models to infer general relationships based on observations from a single lake. After Lindeman's death, his postdoctoral advisor Hutchinson persuaded the editor to publish this paper, which has been the springboard for many of the basic concepts in ecosystem theory (Lindeman 1942).

H.T. Odum, also trained by Hutchinson, and his brother E.P. Odum further developed the "**systems approach**" to studying ecosystems, emphasizing the general properties of ecosystems without documenting all the underlying mechanisms and interactions. The Odum brothers used radioactive tracers to measure the movement of energy and materials through a coral reef and other systems, enabling them to document the patterns of energy flow and metabolism of whole ecosystems and to suggest generalizations about how ecosystems function (Odum 1969). Ecosystem budgets of energy and materials have since been developed for many freshwater and terrestrial ecosystems (Ovington 1962; Golley 1993), providing information that is essential to generalize about global patterns of processes such as productivity (Saugier et al. 2001; Luyssaert et al. 2007). Some of the questions addressed by systems ecology include information transfer (Margalef 1968), the structure of food webs (Polis 1991), the hierarchical changes in ecosystem controls at different temporal and spatial scales (O'Neill et al. 1986; Peterson et al. 1998; Enquist et al. 2007), and the resilience of ecosystem properties after disturbance (Holling 1973).

We now recognize that element cycles interact in important ways and cannot be understood in isolation. The availability of water and nitrogen are important determinants of the rate at which carbon cycles through the ecosystem. Conversely, the productivity of vegetation strongly influences the cycling rates of nitrogen and water. This **coupling** of biogeochemical cycles is critical to understanding processes ranging from the interactions of plants and fungi on root tips to the responses of terrestrial productivity to human-induced increases in atmospheric CO_2 concentration or nitrogen deposition (see Chap. 9).

Additionally, regional and global changes in the environment have increased ecologists' awareness of the effects of disturbance and other environmental changes on ecosystem processes. **Succession**, the directional change in ecosystem structure and functioning that follows disturbance, is an important framework for understanding these transient dynamics of ecosystems. Early American ecologists such as Cowles and Clements were struck by the relatively predictable patterns of vegetation development after exposure of unvegetated land surfaces. Sand dunes on Lake Michigan, for example, are initially colonized by drought-resistant herbaceous plants that give way to shrubs, then small trees, and eventually forests (Cowles 1899). Clements advanced a theory of community development, suggesting that this vegetation succession is a predictable process that eventually leads, in the absence of disturbance, to a stable community-type characteristic of a particular climate (the **climatic climax**; Clements 1916). He suggested that a community is like an organism made of interacting parts (species) and that successional development toward a climax community is analogous to the development of an organism to adulthood. Clements' ideas were controversial from the outset; other ecologists, such as Gleason (1926), believed that vegetation change was not as predictable as Clements had implied. Instead, chance dispersal events could explain much of the vegetation pattern on the landscape. This debate led to a century of research on the mechanisms responsible for vegetation change (see Chap. 12). Nevertheless, the analogy between an ecological community and an organism laid the groundwork for concepts of ecosystem physiology (e.g., the net exchange of CO_2 and water vapor between the ecosystem and the atmosphere). These measurements of net ecosystem exchange are still an active area of research in ecosystem ecology, although they are now motivated by different questions than those posed by Clements.

Ecosystem ecologists study ecosystems through comparative observations and experiments. The comparative approach originated from studies by plant geographers and soil scientists who described general patterns of variation with respect to climate and geological substrate (Schimper 1898). These studies showed that many of the global patterns of plant production and soil development vary predictably with climate (Jenny 1941; Rodin and Bazilevich 1967; Lieth 1975). The studies also showed that, in a given climatic regime, the properties of vegetation depended strongly on soils and vice versa (Dokuchaev 1879; Jenny 1941; Ellenberg 1978). Process-based studies of organisms and soils provided insight into many of the mechanisms underlying the distributions of organisms and soils along these gradients (Billings and Mooney 1968; Mooney 1972; Paul and Clark 1996; Larcher 2003), providing a basis for extrapolation of processes across complex landscapes to characterize large regions (Woodward 1987; Turner et al. 2001). These studies often relied on field or laboratory experiments that manipulate some ecosystem property (e.g., litter quality or nutrient supply) or process, or on comparative studies across environmental gradients (Vitousek 2004; Turner 2010). Comparative studies have shown, for example, that ecosystems differ substantially in their average productivity and water flux, but that under dry conditions ecosystem are similar in the efficiency with which they use precipitation inputs to support production (Knapp and Smith 2001; Huxman et al. 2004). Paleoecological studies can extend these observations over long time scales and under conditions that do not exist today, using records stored in ice cores, sediments, and tree rings (Webb and Bartlein 1992; Petit et al. 1999).

Manipulations of entire ecosystems provide opportunities to test hypotheses that are suggested by observations (Likens et al. 1977; Schindler 1985; Chapin et al. 1995). These experiments often provide insights that are useful in management. The clear-cutting of an experimental watershed (drainage basin) at Hubbard Brook in the Northeastern U.S., for example, caused a 2–3-fold increase in streamflow and more than 50-fold increase in stream nitrate concentration – to levels exceeding health standards for drinking water (Bormann and Likens 1979). These dramatic results demonstrated the key role of vegetation in regulating the cycling of water and nutrients in forests. The results halted plans for large-scale deforestation that had been planned in order to increase water supplies during a long-term drought. Nutrient addition experiments in the Experimental Lakes Area of southern Canada showed that phosphorus limits the productivity of many lakes (Schindler 1985) and that phosphorus pollution was responsible for algal blooms and fish kills that were common in lakes near densely populated areas in the 1960s. This research provided the basis for regulations that removed phosphorus from detergents and regulated the outflow of sewage effluent.

Changes in the Earth System have led to studies of the interactions among terrestrial ecosystems, the atmosphere, and the ocean.

The dramatic impact of human activities on the Earth System (Steffen et al. 2004; MEA 2005; Ellis and Ramankutty 2008; Rockström et al. 2009) has lent urgency to the need to understand how terrestrial ecosystem processes affect the atmosphere and the ocean. The scale at which these ecosystem impacts are occurring is so large that the traditional tools of ecologists are insufficient. Satellite-based remote sensing of ecosystem properties, global networks of atmospheric sampling sites, and the development of global models are important new tools to address global issues (Goetz et al. 2005; Field et al. 2007; Waring and Running 2007; Bonan 2008). Information on global patterns of CO_2 and pollutants in the atmosphere, for example, provide telltale evidence of the major locations and causes of global problems (Field et al. 2007). This information provides hints about which ecosystems and processes have the greatest impact on the Earth System and therefore where research and management should focus efforts to understand and solve these problems.

The intersection of systems approaches, process understanding, and global analysis is an exciting frontier of ecosystem ecology. How do changes in the global environment alter controls over ecosystem processes? What are the integrated system consequences of these changes? How do these changes in ecosystem properties influence the Earth System? Understanding the rapid changes that are occurring in ecosystems blurs any previous distinction between basic and applied research (Stokes 1997). There is an urgent need to understand how and why the ecosystems of Earth are changing.

Ecosystem Structure and Functioning

Ecosystem Processes

Most ecosystems gain energy from the sun and materials from the air or rocks, transfer these among components within the ecosystem, then release energy and materials to the environment. The essential biological components of ecosystems are plants, animals, and decomposers. The essential abiotic components of a terrestrial ecosystem are **water**, the **atmosphere**, which supplies carbon and nitrogen, and **soil**, which provides support, storage, and other nutrients required by organisms. **Plants** capture solar energy in the process of bringing carbon into the ecosystem. A few ecosystems, such as deep-sea hydrothermal vents, have no plants but instead have bacteria that derive energy from the oxidation of hydrogen sulfide (H_2S) to produce organic matter. Plants use solar energy to acquire nutrients and assemble organic material.

Decomposer microorganisms (microbes) break down dead organic material, releasing CO_2 to the atmosphere and nutrients in forms that are available to other microbes and plants. If decomposition did not occur, large accumulations of dead organic matter would sequester the nutrients required to support plant growth. **Animals** transfer energy and materials and can regulate the quantity and activities of plants and soil microbes.

An **ecosystem model** describes the major pools and fluxes in an ecosystem and the factors that regulate these fluxes. Carbon, water, and nutrients differ from one another in the relative importance of ecosystem inputs and outputs vs. internal recycling (see Chaps. 4–9). Plants, for example, acquire carbon primarily from the atmosphere, and most carbon released by respiration returns to the atmosphere. Carbon cycling through ecosystems is therefore quite open, with large inputs to, and losses from, the system (see Fig. 6.1). Despite these large carbon inputs and losses, the large quantities of carbon stored in plants and soils of ecosystems buffer the activities of animals and microbes from temporal variations in carbon absorption by plants. The water cycle of ecosystems is also relatively open, with most water entering as precipitation and leaving by evaporation, transpiration, and drainage to groundwater and streams (see Fig. 4.4). In contrast to carbon, most terrestrial ecosystems have a limited capacity to store water in plants and soil, so the activity of organisms is closely linked to water inputs. In contrast to carbon and water, mineral elements, such as nitrogen and phosphorus, are recycled rather tightly within ecosystems, with annual inputs and losses that are small relative to the quantities that annually recycle within the ecosystem (see Fig. 9.17). These differences in the "openness" and "buffering" of cycles fundamentally influence the controls over rates and patterns of cycling of materials through ecosystems.

The pool sizes and rates of cycling of carbon, water, and nutrients differ substantially among ecosystems. Tropical forests have much larger pools of carbon and nutrients in plants than do deserts or tundra. Peat bogs, in contrast, have large pools of soil carbon rather than plant carbon. Ecosystems also differ substantially in annual fluxes of materials among pools, for reasons that we explore in later chapters.

Ecosystem Structure and Constraints

The differences in physical properties between water and air lead to fundamental structural differences between aquatic and terrestrial ecosystems. Due to its greater density, water offers greater physical support for photosynthetic organisms than does the air that bathes terrestrial ecosystems (Table 1.1). The primary producers in **pelagic** (open-water) ecosystems are therefore microscopic photosynthetic organisms (**phytoplankton**) that float near the water surface, where light availability is greatest, whereas terrestrial plants produce elaborate support structures to raise their leaves above neighbors. Plants are often the major habitat-structuring feature on land. Their physical structure governs the patterns of physical environment, organism activity, and ecosystem processes. In the ocean and lakes, however, the environment is physically structured by vertical gradients in light, temperature, oxygen, and salinity. In small lakes and clearwater streams, **benthic** (bottom-dwelling) algae account for most primary production (Vander Zanden et al. 2005; Allan and Castillo 2007). Vascular plants are also important primary producers on edges of lakes, streams, rivers, estuaries, and lagoons.

The size of aquatic organisms determines their locomotion strategies. Water is a polar molecule that sticks to the surface of organisms. These viscous forces impede the movement of small organisms and particles. Large organisms, in contrast, can swim, and their speed is largely determined by inertia. The Reynolds' number (*Re*) is the ratio of inertial to viscous forces and is a measure of the ease with which organisms can move through a viscous fluid like water.

$$Re = \frac{lv}{V_k} \qquad (1.1)$$

The movement of organisms through water is not strongly impeded for organisms with a large length (l) and velocity (v) under conditions of low kinematic viscosity (V_k; Fig. 1.4). Small bacteria and photosynthetic plankton, however, must deal with life at a low Reynolds' number, where viscous forces are much stronger than inertial forces. At these small sizes, diffusion is the main process that moves nutrients to the cell surface, just as with fine roots on land. At slightly larger sizes, zooplankton actively filter feed or swim to acquire their food.

Oxygen and other gases diffuse about 10,000 times more rapidly in air than water, with turbulence and lateral flow enhancing this movement in both air and water. The surface ocean water, for example, has an oxygen concentration 30-fold lower than in air (Table 1.1), and aquatic sediments are much more likely to be anaerobic than are

Table 1.1 Basic properties of water and air at 20°C at sea level that influence ecosystem processes

Property[a]	Water	Air	Ratio (water:air)
Oxygen concentration (ml L^{-1}) at 25°C	7.0	209.0	1:30
Density (kg L^{-1})	1.000	0.0013	800:1
Viscosity (cP)	1.0	0.02	50:1
Heat capacity (cal L^{-1} (°C)$^{-1}$)	1000.0	0.31	3,000:1
Diffusion coefficient (mm s^{-1})			
Oxygen	0.00025	1.98	1:8,000
Carbon dioxide	0.00018	1.55	1:9,000

[a] Data from Moss (1998)

Fig. 1.4
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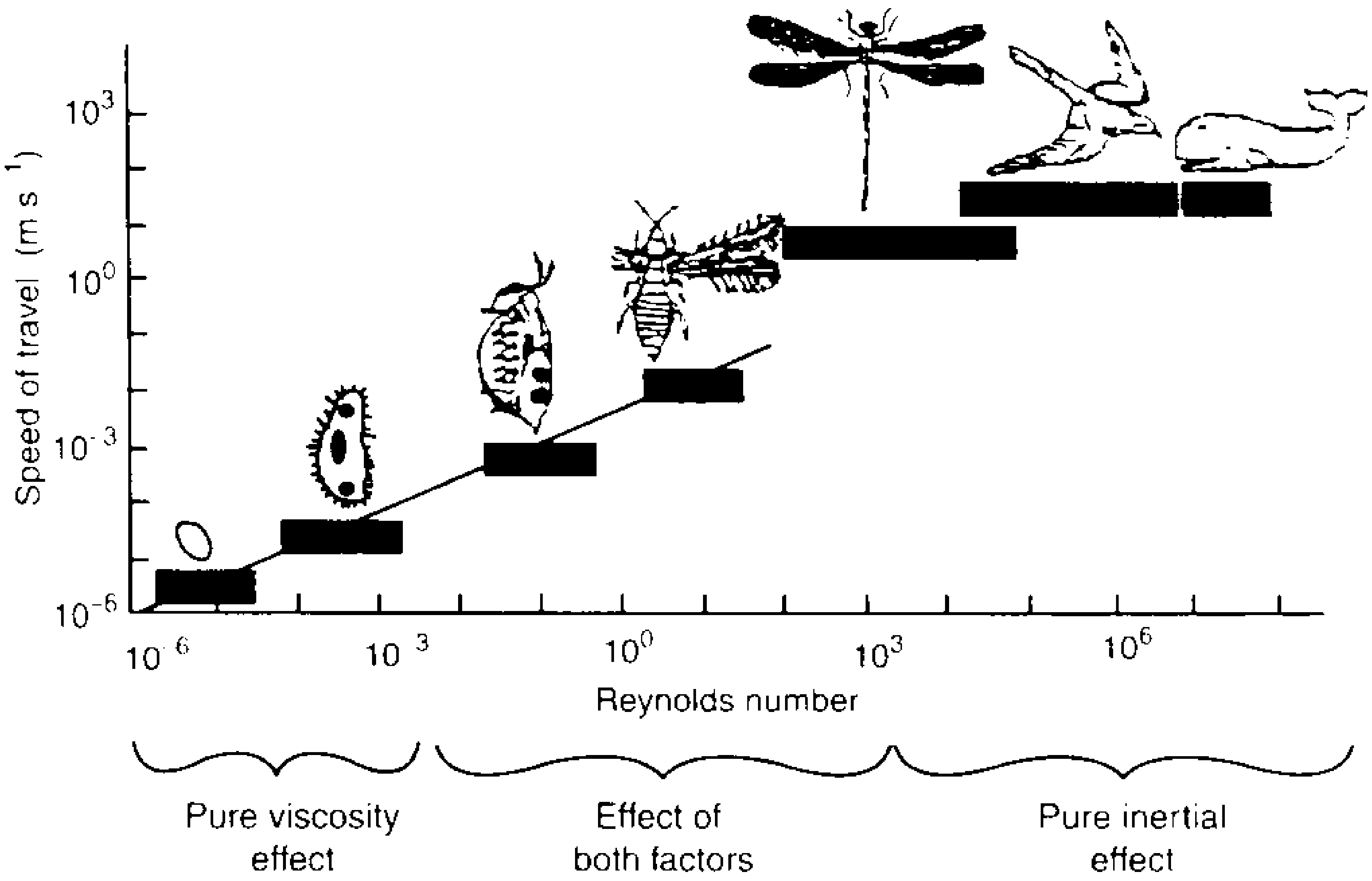

Fig. 1.4 Range of Reynolds numbers for organisms of different lengths and speeds. Small organisms like phytoplankton have small Reynolds numbers and derive their nutrition by diffusion. As size and Reynolds number increase, nutrition based on movement (filter feeding and swimming) becomes progressively more important. Redrawn from Schwoerbel (1987)

terrestrial soils. Aquatic organisms therefore exhibit a variety of adaptations to acquire oxygen and withstand anaerobic conditions. On land, in contrast, the acquisition of water and the avoidance or tolerance of desiccation are more common evolutionary themes.

Streams and rivers are structured by moving water. The physical environment and therefore the biotic structure of stream ecosystems differ dramatically from those of land, lakes, and the ocean. Water constantly moves downstream across the riverbed, bringing in new material from upstream and sweeping away anything that is not attached or able to swim vigorously. Phytoplankton are therefore unimportant in streams, except in slow-moving polluted sites and large rivers. The major primary producers of rapidly moving streams are the algal components of **periphyton**, assemblages of algae, bacteria, and invertebrates that attach to stable surfaces such as rocks and vascular plants. The slippery surfaces of rocks in a riverbed consist of periphyton in a polysaccharide matrix. Submerged or emergent vascular plants and benthic mats become relatively more important in slow-moving sections of a river. Within a given section of river, alternating pools and riffles differ in flow rate and ecosystem structure. Seasonal changes in discharge radically alter the flow regime and therefore structure of rivers and streams. Desert streams, for example, have flash floods after intense rains but may have no surface flow during dry periods (Fisher et al. 1998). Other streams have predictable discharge peaks associated with snowmelt. In general, floods and other high-discharge events are important because they scour sediments and biota from the riverbed and **riparian** (streambank) zones, redistribute logs and other material that structure aquatic habitat, and deposit new soil and create new habitats across floodplains. Some rivers flood annually, so floodplains alternate between being terrestrial and aquatic habitats. Human efforts to prevent flooding by building dams and levees therefore radically alter river and riparian ecosystem structure and dynamics.

Controls Over Ecosystem Processes

Ecosystem structure and functioning are governed by multiple independent control variables. These **state factors**, as Jenny and his

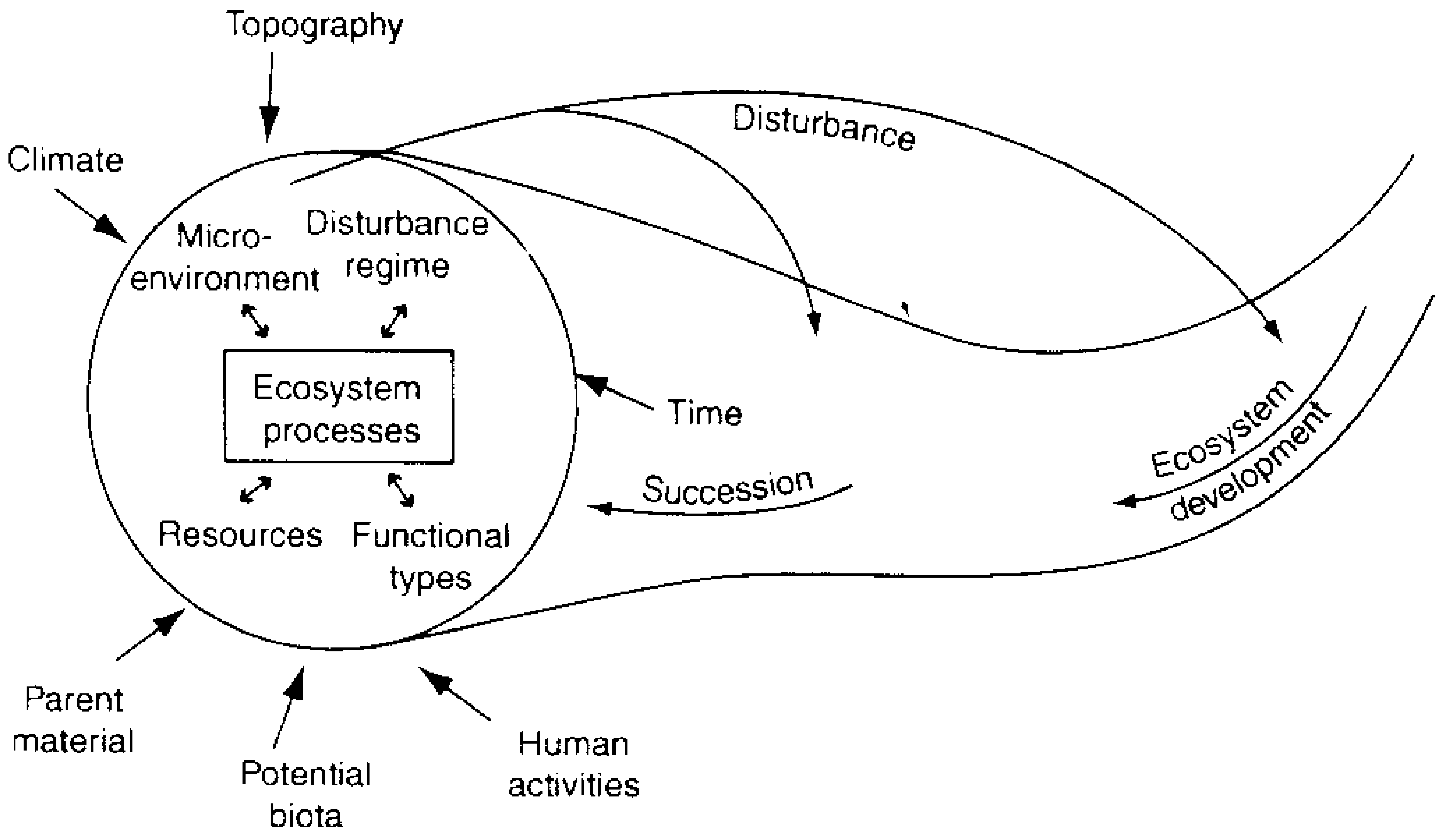

Fig. 1.5 The relationship between state factors (*outside the circle*), interactive controls (*inside the circle*), and ecosystem processes (*inside the box*). The *circle* represents the boundary of the ecosystem, whose structure and functioning respond to and affect interactive controls, which are ultimately governed by state factors. The properties of the ecosystem change through long-term development and shorter-term succession. Modified from Chapin et al. (2006b)

coworkers called them, include **climate**, **parent material** (the rocks that give rise to soils), **topography**, **potential biota** (the organisms present in the region that could potentially occupy a site), and **time** (Fig. 1.5; Jenny 1941; Amundson and Jenny 1997; Vitousek 2004). Together these five factors, among others, set the bounds for the characteristics of an ecosystem.

On broad geographic scales, climate is the state factor that most strongly determines ecosystem processes and structure. Global variations in climate explain the distribution of **biomes** (general categories of ecosystems) such as wet tropical forests, temperate grasslands, and arctic tundra (see Chap. 2). Within each biome, parent material strongly influences the types of soils that develop and explains much of the regional variation in ecosystem processes (see Chap. 3). Topographic relief influences both microclimate and soil development at a local scale. The potential biota governs the types and diversity of organisms that actually occupy a site. Island ecosystems, for example, are often less diverse than climatically similar mainland ecosystems because new species reach islands less often and are more likely to go locally extinct than on the mainland (MacArthur and Wilson 1967). Time influences the development of soil and the evolution of organisms over long time scales (Vitousek 2004). Time also incorporates the influences on ecosystem processes of past disturbances and environmental changes over a wide range of time scales. State factors are described in more detail in Chap. 3 in the context of soil development.

Late in his life, Jenny (1980) suggested that human activity was becoming so pervasive as to represent a sixth major state factor. Human activities have an increasing impact on virtually all the processes that govern ecosystem properties (MEA 2005). Humans have been a natural component of most ecosystems for thousands of years. Since the beginning of the industrial revolution, however, the magnitude of human impact has been so great and so distinct from that of other organisms that the modern impacts of human activities warrant particular attention (Vitousek et al. 1997b; Steffen et al. 2004). The cumulative impact of human activities extends well beyond an individual ecosystem and affects state factors such as climate (through changes in atmospheric composition) and potential biota (through the introduction and extinction of species; Fig. 1.5). Human activities are causing major changes in the structure and functioning of all ecosystems, resulting in novel conditions that lead to new types of ecosystems (Foley et al. 2005; Ellis and Ramankutty 2008). The major categories of human impact are summarized in the next section.

Jenny's state-factor approach was a major conceptual contribution to ecosystem ecology. First, it emphasized the controls over *processes* rather than simply descriptions of patterns. Second, it suggested a study design to test the importance and mode of action of each control. A logical way to study the role of each state factor is to compare sites that are as similar as possible with respect to all but one factor. A **chronosequence**, for example, is a series of sites of different ages with similar climate, parent material, topography, and potential to be colonized by the same organisms (see Chap. 12). In a **toposequence**, ecosystems differ mainly in their topographic position (Shaver et al. 1991). Sites that differ primarily with respect to climate or parent material allow us to study the impacts of these state factors on ecosystem processes (Vitousek 2004). Finally, a comparison of ecosystems that differ primarily in potential biota, such as the Mediterranean shrublands that have developed on west coasts of California, Chile, Portugal, South Africa, and Australia, illustrates the importance of evolutionary history in shaping ecosystem processes (Mooney and Dunn 1970; Cody and Mooney 1978).

Ecosystem processes both respond to and control the factors that directly govern their activity. Interactive controls are factors that operate at the ecosystem scale and both *control* and *respond to* ecosystem characteristics (Fig. 1.5; Chapin et al. 1996). Important interactive controls include the supply of **resources** to support the growth and maintenance of organisms, **microenvironment** (e.g., temperature, pH) that influences the rates of ecosystem processes, **disturbance regime**, and the **biotic community**.

Resources are the energy and materials in the environment that are used by organisms to support their growth and maintenance (Field et al. 1992). The acquisition of resources by organisms generally depletes their abundance in the environment and availability to other organisms, although some resources (e.g., atmospheric carbon dioxide) mix so rapidly that they can be considered nondepletable (Rastetter and Shaver 1992). Energy resources can either be chemical energy stored in matter, or incoming solar radiation. Material resources include carbon, oxygen, water, and the other elements that are required for life, which we generically refer to as **nutrients**. In terrestrial ecosystems, these resources are spatially separated, being available primarily either aboveground (light and CO_2) or belowground (water and nutrients). Resource supply is governed by state factors such as climate, parent material, and topography. It is also sensitive to processes occurring within the ecosystem. Light availability, for example, depends on climatic elements such as cloudiness and on topographic aspect but is also sensitive to the degree of shading by vegetation. Similarly, soil fertility depends on parent material and climate, but is also sensitive to ecosystem processes such as erosional loss of soils after overgrazing and inputs of nitrogen from invading nitrogen-fixing species. Soil water availability strongly influences species composition in dry climates. Soil water availability also depends on other interactive controls such as disturbance regime (e.g., compaction by animals) and the types of organisms that are present (e.g., the presence or absence of deep-rooted trees such as mesquite that tap deep groundwater). In aquatic ecosystems, water seldom directly limits the activity of organisms, but light and nutrients are at least as important as on land. Oxygen is a particularly critical resource in aquatic ecosystems because of its low solubility and slow rate of diffusion through water.

The **microenvironment** includes physical and chemical properties like temperature and pH that affect the activity of organisms but, unlike resources, are neither consumed nor depleted by organisms (Field et al. 1992). Microenvironmental factors like temperature vary with climate (a state factor) but are sensitive to ecosystem processes, such as shading and evaporation. Soil pH depends on parent material and time, but also responds to vegetation composition.

Landscape-scale **disturbance** by fire, wind, floods, insect outbreaks, and hurricanes is a critical determinant of the natural structure and process rates in ecosystems (Pickett and White 1985; Peters et al. 2011). Like other interactive controls, disturbance regime depends on both state factors and ecosystem processes. Fire probability and spread, for example, depends on both climate and the quantity and flammability of plants and dead organic matter. Deposition and erosion during floods shape river channels and influence the probability of future floods. Change in either the intensity or frequency of disturbance can cause long-term ecosystem change. Woody plants, for example, often invade grasslands when fire suppression reduces fire frequency.

The nature of the biotic community – i.e., the types of species present, their relative abundances, and the nature of their interactions, can influence ecosystem processes just as strongly as do differences in climate or parent material (see Chap. 11). These species effects can often be generalized at the level of **functional types**, which are groups of species that are similar to one another in their role in a specific community or ecosystem process. Most evergreen tree species, for example, produce leaves that have low rates of photosynthesis and a chemical composition that deters herbivores and slows down decomposition. A shift from one evergreen tree species to another usually has less influence on an ecosystem process than a shift to a deciduous tree species. A gain or loss of key functional types, for example through introduction or removal of species with large ecosystem effects, can permanently change the character of an ecosystem through changes in resource supply or disturbance regime. Introduction of nitrogen-fixing trees onto British mine wastes, for example, substantially increases nitrogen supply, productivity, and rates of vegetation development (Bradshaw 1983). Invasion of grasslands by exotic grasses can alter fire frequency, resource supply, trophic interactions, and rates of most ecosystem processes (D'Antonio and Vitousek 1992; Mack et al. 2001). Elimination of predators can cause an outbreak of deer that overbrowse their food supply (Beschta and Ripple 2009) or move disease-bearing ticks around the landscape (Ostfeld and Keesing 2000). The types of species present in an ecosystem depend strongly on other interactive controls (see Chap. 11), so functional types respond to and affect most interactive controls and ecosystem processes.

Feedbacks regulate the internal dynamics of ecosystems. A thermostat, for example, causes a furnace to switch on when a house gets cold and to switch off when the house warms to the desired temperature. Natural ecosystems are complex networks of interacting feedbacks (DeAngelis and Post 1991). **Stabilizing feedbacks** (termed negative feedbacks in the systems literature) occur when two components of a system have opposite effects on one another (Fig. 1.6). Consumption of prey by a predator, for example, has a positive effect on the consumer but a negative effect on the prey. The negative effect of predators on prey prevents uncontrolled growth of a prey's population, thereby stabilizing the

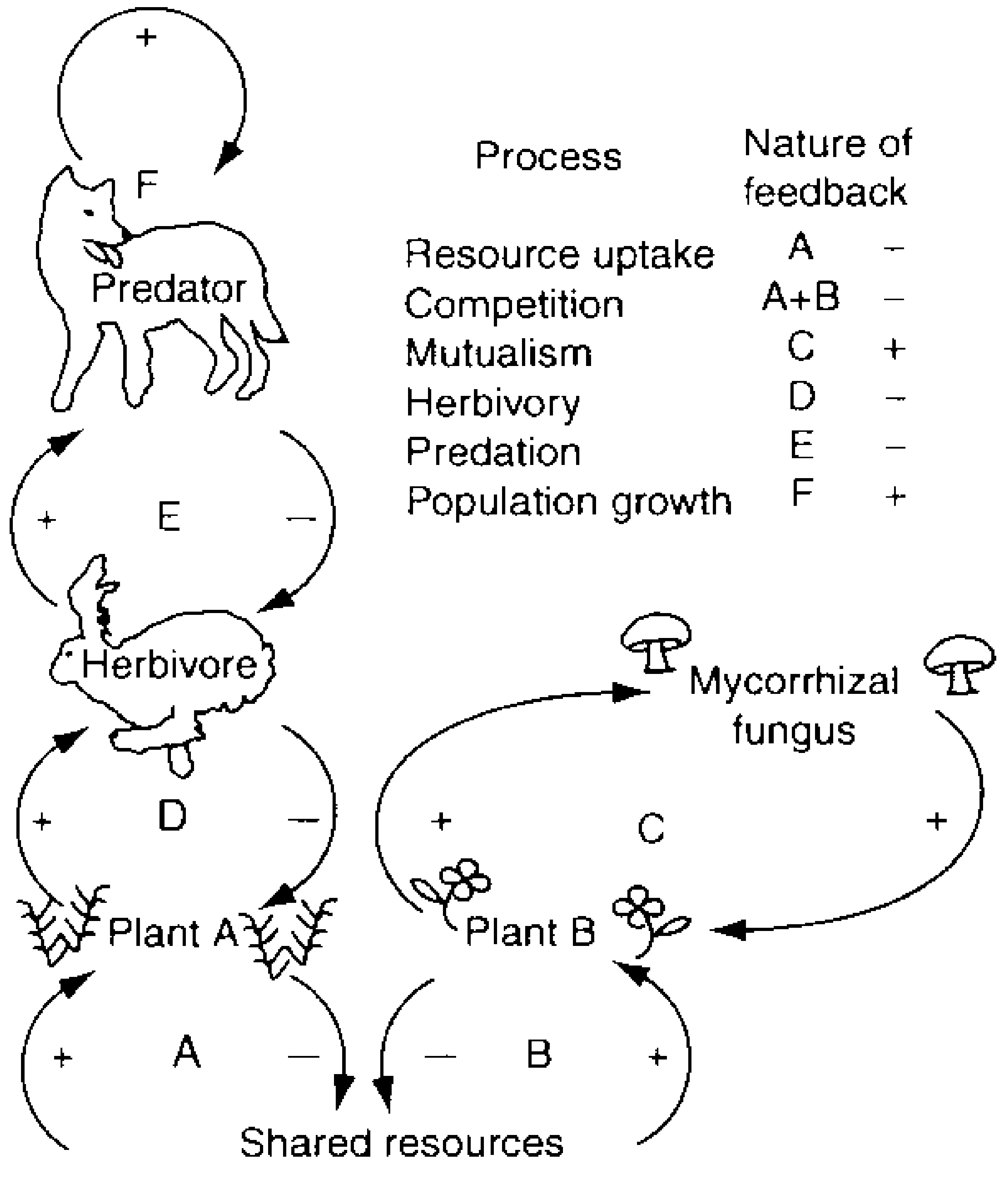

Fig. 1.6 Examples of linked amplifying and stabilizing feedbacks in ecosystems. The effect of each organism (or resource) on other organisms can be positive (+) or negative (–). Feedbacks are amplifying (positive feedbacks) when the reciprocal effects of each organism (or resource) have the same sign (both positive or both negative). Feedbacks are stabilizing (negative feedbacks) when reciprocal effects differ in sign. Stabilizing feedbacks resist tendencies for ecosystems to change, whereas amplifying feedbacks reinforce tendencies to change. Redrawn from Chapin et al. (1996)

population sizes of both predator and prey. There are also **amplifying feedbacks** (termed positive feedbacks in the systems literature) in ecosystems in which both components of a system have a positive effect on one other, or both have a negative effect on one another. Plants, for example, provide their mycorrhizal fungi with carbohydrates in return for nutrients. This exchange of growth-limiting resources between plants and fungi promotes the growth of both components of the symbiosis until they become constrained by other factors.

Stabilizing feedbacks provide resistance to changes in interactive controls and maintain the characteristics of ecosystems in their current state, whereas amplifying feedbacks accentuate changes. The acquisition of water, nutrients, and light to support growth of one plant, for example, reduces availability of these resources to other plants, thereby constraining community productivity (Fig. 1.6). Similarly, animal populations cannot sustain exponential population growth indefinitely because declining food supply and increasing predation reduce the rate of population increase. On the other hand, succession often involves a series of amplifying feedbacks, as plant growth and soil fertility reinforce each other, until another disturbance resets the successional clock. If stabilizing feedbacks are weak or absent (e.g., a low predation rate due to predator control), population cycles can amplify, causing extinction of one or both of the interacting species. Community dynamics, which operate within a single ecosystem patch, primarily involve feedbacks among soil resources and functional types of organisms.

Landscape dynamics, which govern changes in ecosystems through cycles of disturbance and recovery, involve additional feedbacks with microclimate and disturbance regime that link ecosystems across landscapes (see Chap. 13). Post-disturbance vegetation development, for example, is driven by amplifying feedbacks at the ecosystem scale, but also contributes to stabilizing feedbacks in landscapes over longer time periods by maintaining a diversity of successional stages and reducing risks of large-scale spread of disturbances like wildfire or insect outbreaks.

Human-Induced Ecosystem Change

Human Impacts on Ecosystems

Human activities have transformed the land surface, species composition, and biogeochemical cycles at scales that have altered the biogeochemistry and climate of the planet. These **anthropogenic** (human-caused) effects are so profound that the beginning of the industrial revolution (about 1,750) is widely recognized as the start of a new geologic epoch – the **Anthropocene** (see Fig. 2.15; Crutzen 2002).

The most direct and substantial human alteration of ecosystems is through the transformation of land for production of food, fiber, and other goods used by people (Fig. 1.7). People inhabit more than 75% of Earth's ice-free land surface. These inhabited areas include cities and villages (7%), croplands (20%), rangelands (30%), and forests (20%; Fig. 1.8; Foley et al. 2005; Ellis and Ramankutty 2008). The 25% uninhabited lands are primarily barren lands as well as additional forest lands. From inhabited landscapes, people appropriate 25–40% of terrestrial aboveground productivity through human harvest (53% of the human appropriation), land-use change and altered productivity (40%), and human-induced fires (7%; Vitousek et al. 1997b; Haberl et al. 2007).

Human activities have also altered freshwater and marine ecosystems. People currently use about 25% of the runoff from land to the ocean (see Chap. 14; Postel et al. 1996; Vörösmarty et al. 2005). We use about 8% of marine primary production (Pauly and Christensen 1995). Commercial fishing reduces the size and abundance of target species and alters the population characteristics of species that are incidentally caught in the fishery. About 70% of marine fisheries are overexploited, including 25% that have collapsed (defined as greater than 90% reduction in biomass; Mullon et al. 2005). A large proportion of the human population resides within 100 km of a coast, so the coastal margins of the ocean are strongly influenced by human activities. For example, nutrient enrichment of many coastal waters from agricultural runoff and from human and livestock sewage has increased algal production. Decomposition of

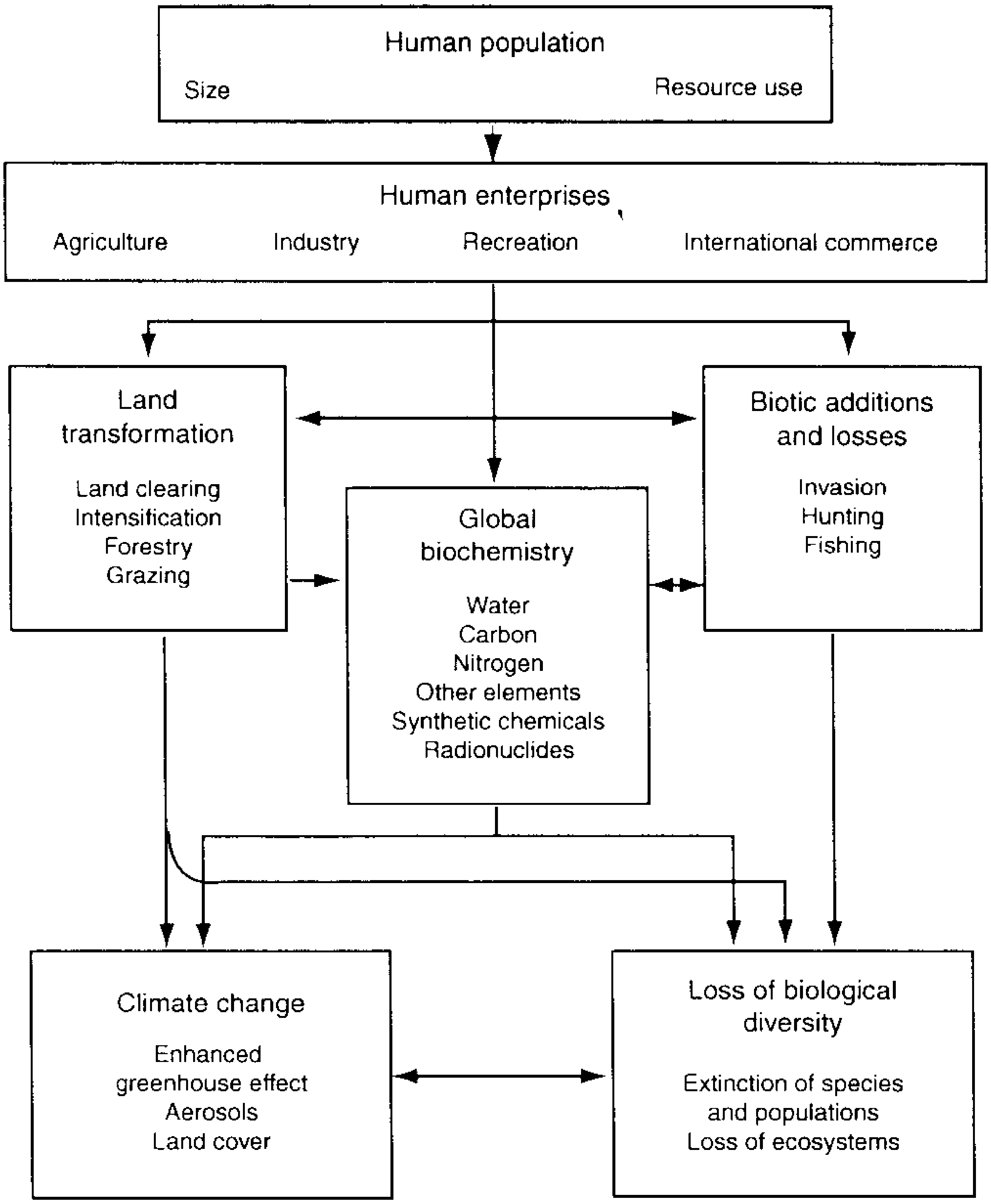

Fig. 1.7 Direct and indirect impacts of human activities on Earth's ecosystems. Redrawn from Vitousek et al. (1997b)

this material depletes oxygen within the water column, creating dead zones where anaerobic conditions kill fish and other animals (see Fig. 9.1; Rabalais et al. 2002).

Land-use change and the resulting loss of habitat are the primary driving forces causing species extinctions and loss of biological diversity (see Chap. 11; Mace et al. 2005). In addition, transport of species around the world increases the frequency of biological invasions, due to the globalization of the economy and increased international transport of people and products. Nonindigenous species now account for 20% or more of the plant species in many continental areas and 50% or more of the plant species on many islands (Vitousek et al. 1997b). International commerce breaks down biogeographic barriers through both inadvertent introductions and the purposeful selection of species that are intended to grow and reproduce well in their new environment. Many of these introductions, such as agricultural crops and pasture grasses, increase certain ecosystem services, such as food for human consumption. Yet, the addition of new species can also degrade human health (e.g., rinderpest in Africa; Sinclair and Norton-Griffiths 1979) and cause large

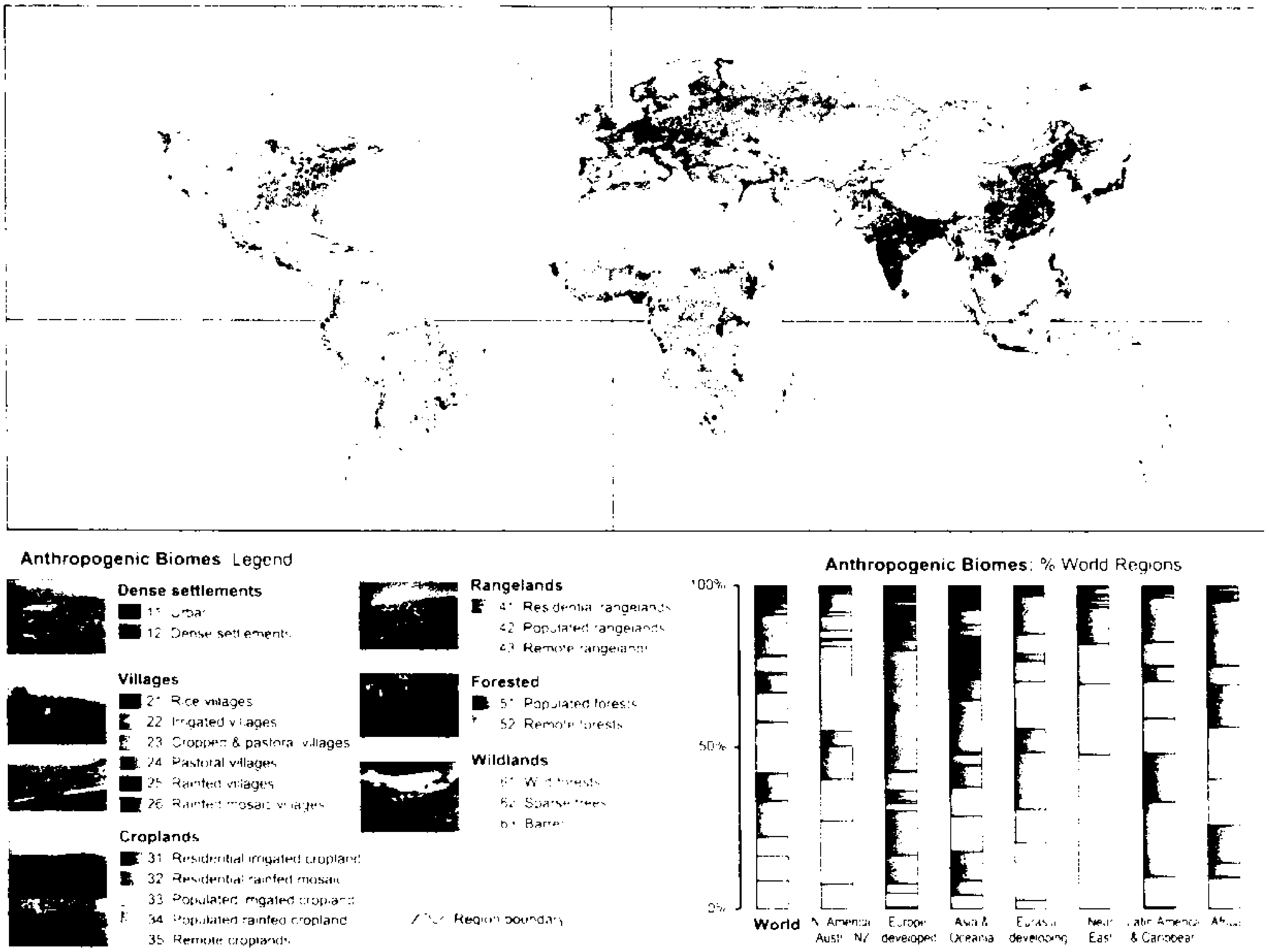

Fig. 1.8 Anthropogenic ecosystems of the world. Human activity has fundamentally altered both the nature of Earth's ecosystems and the way they are conceptualized. Reprinted from Ellis and Ramankutty (2008)

economic losses (e.g., introduction of fire-prone cheatgrass to North American rangelands; Bradley and Mustard 2005). Others alter the structure and functioning of ecosystems, leading to further loss of species diversity. Many biological invasions are irreversible because it is difficult or prohibitively expensive to remove invasive species once they establish.

Human activities have influenced biogeochemical cycles in many ways. Extensive use of fossil fuels and the expansion and intensification of agriculture have increased the concentrations of atmospheric gases, altering global cycles of carbon, nitrogen, phosphorus, sulfur, and water (see Chap. 14). Biogeochemical changes also alter the internal dynamics of ecosystems, as well as downwind ecosystems through atmospheric transport and downstream ecosystems through runoff to lakes, rivers, and the coastal zone of the ocean.

Human activities introduce novel chemicals into the environment. Some apparently harmless anthropogenic gases have had drastic impacts on the atmosphere and ecosystems. Chlorofluorocarbons (CFCs), for example, were first produced in the 1950s as refrigerants, propellants, and solvents. In the upper atmosphere, however, CFCs react with and deplete ozone, which shields Earth's surface from high-energy UV radiation. Ozone depletion was first detected as a dramatic **ozone hole** near the South Pole, but it now occurs at lower latitudes in the southern hemisphere and at high Northern latitudes. Other synthetic organic chemicals include DDT (an insecticide) and PCBs (polychlorinated biphenyls, industrial compounds) that were used extensively in the developed world in the 1960s before their ecological impacts were widely recognized. They are mobile and degrade slowly, causing long-term persistence and transport to ecosystems across the globe. Many of these compounds are fat soluble, so they accumulate in organisms and increase in concentration as they move up food chains (see Chap. 10). When these compounds reach critical concentrations, they can cause reproductive failure (Carson 1962), particularly in higher trophic levels and in animals that feed on fat-rich species. Some processes, such as eggshell formation in birds, are particularly sensitive to pesticide accumulations and have caused population declines in predatory birds like the peregrine falcon, even in regions far removed from the locations of pesticide use.

Atmospheric testing of atomic weapons in the 1950s and 1960s increased atmospheric concentrations of radioactive forms of many elements. Explosions and leaks in nuclear reactors used to generate electricity have also released radioactivity at local to regional scales. The explosion of a power-generating plant in 1986 at Chernobyl in the Ukraine, for example, released radioactivity that directly affected human health in the region and increased the atmospheric deposition of radioactive materials across Eastern Europe and Scandinavia. Some radioactive isotopes of elements such as strontium and cesium, which are chemically similar to calcium and potassium, respectively, are actively accumulated and retained by organisms. Lichens, for example, acquire minerals primarily from the atmosphere and actively accumulate strontium and cesium. Reindeer feeding on lichens further concentrate these minerals, as do people who eat reindeer. For this reason, the input of radioisotopes to the atmosphere or water has had impacts that extend far beyond the regions where they were used.

In other cases, the chemicals that people introduce to ecosystems are much more targeted as in the case of BT-corn, a genetically modified corn variety carrying bacterial genes that cause production of a compound that is toxic to European corn borer. Any introduction of novel chemicals raises questions of toxicity to non-target organisms or the evolution of resistance in target species (Marvier et al. 2007). These questions are amenable to study by ecosystem ecologists.

The growing scale and extent of human activities suggest that *all* ecosystems are being influenced, directly or indirectly, by human actions. No ecosystem functions in isolation, and all are influenced by human activities taking place in adjacent communities and around the world. Human activities are leading to global changes in most major ecosystem controls: climate (global warming), soil and water resources (nitrogen deposition, erosion, diversions), disturbance regime (land-use change, fire suppression), and functional types of organisms (species introductions and extinctions). Many of these global changes interact with one another at regional and local scales (Rockström et al. 2009). All ecosystems are therefore experiencing directional changes in ecosystem controls, creating novel conditions and, in some cases, amplifying feedbacks that lead to novel ecosystems. These changes in interactive controls inevitably alter ecosystem dynamics.

Resilience and Threshold Changes

Despite pervasive human impacts on state factors and interactive controls, ecosystems exhibit a wide range of responses, ranging from substantial resilience to threshold changes. **Resilience** is the capacity of a social–ecological system to maintain similar structure, functioning, and feedbacks despite shocks and perturbations. **Thresholds** are critical levels of one or more ecosystem controls that, when crossed, cause abrupt ecosystem changes. Lakes may, for example, maintain water clarity and support desired fish stocks despite substantial nutrient inputs from agricultural runoff or local septic systems because of stabilizing (negative) feedbacks from lake sediments that bind phosphorus, removing it from the water column, and providing resilience. At some point, however, phosphorus-binding capacity becomes saturated, so sediments become a source of phosphorus to the water column, supporting the growth of nuisance algae that reduce water clarity and trigger a cascade of other events that are not easily reversed (see Chaps. 9 and 12). Biodiversity can also confer resilience because a large number of species is likely to sustain ecosystem processes over a broader range of conditions than would one or a few species (see Chap. 11; Elmqvist et al.

2003; Suding et al. 2008). Social processes that govern the role of people in ecosystems can be a source of resilience (sustainability) or can trigger threshold changes. Ecologists are only beginning to understand the factors that govern ecosystem resilience and threshold change (see Chap. 12). This is emerging as a critical research area in our increasingly human-dominated planet.

Although some pressures on ecosystems are easily observed (e.g., acid rain) or predicted (e.g., rising global temperature that was predicted decades ago and is now being observed), **surprises** that are difficult or impossible to anticipate also occur. Some processes that confer resilience are quite specific to a given driver of change (e.g., sediment sequestration of phosphorus). Others, such as biodiversity or a multiple-use management policy, may confer resilience to a variety of potential changes, some of which may occur unexpectedly.

Degradation in Ecosystem Services

Many ecosystem services have been degraded globally since the mid-twentieth century (Daily 1997; MEA 2005). Society benefits in numerous ways from ecosystems, including (1) **provisioning services** (or **ecosystem goods**), which are products of ecosystems that are directly harvested by people (e.g., food, fiber, and water); (2) **regulating services**, which are the effects of ecosystems on processes that extend beyond their boundaries (e.g., regulation of climate, water quantity and quality, disease, wildfire spread, and pollination); and (3) **cultural services**, which are nonmaterial benefits that are important to society's well-being (e.g., recreational, aesthetic, and spiritual benefits; see Fig. 15.4). Many ecosystem processes (e.g., productivity, nutrient cycling, and maintenance of biodiversity) support these ecosystem services. More than half of these ecosystem services were degraded globally over the last half of the twentieth century – not deliberately, but inadvertently as people sought to meet their material desires and needs (MEA 2005). Change creates both challenges and opportunities. People have amply demonstrated our capacity to alter the life-support system of the planet. With appropriate ecosystem stewardship, this human capacity can be mobilized to not only repair but also enhance the capacity of Earth's life-support system to support societal development. An important challenge for ecosystem ecology is to provide the scientific knowledge to meet this goal.

Summary

Ecosystem ecology addresses the interactions among organisms and their environment as an integrated system through study of the factors that regulate the pools and fluxes of materials and energy through ecological systems. The spatial scale at which we study ecosystems is chosen to facilitate the measurement of important fluxes into, within, and out of the ecosystem. The functioning of ecosystems depends not only on their current structure and environment but also on a legacy of response to past events. The study of ecosystem ecology is highly interdisciplinary, building on many aspects of ecology, hydrology, climatology, geology, and sociology and contributing to current efforts to understand Earth as an integrated system. Many unresolved problems in ecosystem ecology require an integration of systems approaches, process understanding, and global analysis.

Most ecosystems ultimately acquire their energy from the sun and their materials from the atmosphere and rock minerals. Energy and materials are transferred among components within ecosystems and are then released to the environment. The essential biotic components of ecosystems include plants, which bring carbon and energy into the ecosystem; decomposers, which break down dead organic matter and release CO_2 and nutrients; and animals, which transfer energy and materials within ecosystems and modulate the activity of plants and decomposers. The essential abiotic components of ecosystems are the atmosphere, water, and soils. Ecosystem processes are controlled by a set of relatively independent state factors (climate, parent material, topography, potential biota, time, and increasingly human activities) and by a group of interactive controls (including resource supply, microenvironment, disturbance regime, and functional types of organisms) that directly control ecosystem processes. The interactive controls both respond to and affect ecosystem processes, while state factors are considered independent of ecosystems. The stability and resilience of ecosystems depend on the strength and interactions between stabilizing (negative) feedbacks that maintain the characteristics of ecosystems in their current state and amplifying (positive) feedbacks that are sources of renewal and change.

Review Questions

1. What is an ecosystem? How does it differ from a community? What kinds of environmental questions can ecosystem ecologists address that are not easily addressed by community ecologists?
2. What is the difference between a pool and a flux? Which of the following are pools and which are fluxes: plants, plant respiration, rainfall, soil carbon, and consumption of plants by animals?
3. What are the state factors that control the structure and rates of processes in ecosystems? What are the strengths and limitations of the state-factor approach to answering this question?
4. What is the difference between state factors and interactive controls? Why would you treat a state factor and an interactive control differently in developing a management plan for a region?
5. Using a forest or a lake as an example, explain how climatic warming or harvest of trees or fish by people might change the major interactive controls, and how these changes in controls might alter the structure or processes in these ecosystems.
6. Use examples to show how amplifying and stabilizing feedbacks might affect the responses of an ecosystem to climatic change.

Additional Reading

Chapin, F.S., III, G.P. Kofinas, and C. Folke. 2009. *Principles of Ecosystem Stewardship: Resilience-Based Natural Resource Management in a Changing World*. Springer, New York.

Ellis E.C., and N. Ramankutty. 2008. Putting people on the map: Anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6:439–447.

Golley, F.B. 1993. *A History of the Ecosystem Concept in Ecology: More than the Sum of the Parts*. Yale University Press, New Haven.

Gorham, E. 1991. Biogeochemistry: Its origins and development. *Biogeochemistry* 13:199–239.

Hagen, J.B. 1992. *An Entangled Bank: The Origins of Ecosystem Ecology*. Rutgers University Press, New Brunswick, New Jersey.

Jenny, H. 1980. *The Soil Resources: Origin and Behavior*. Springer-Verlag, New York.

Lindeman, R.L. 1942. The trophic-dynamic aspects of ecology. *Ecology* 23:399–418.

MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington.

Schlesinger, W.H. 1997. *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284–307.

Vitousek, P.M. 2004. *Nutrient Cycling and Limitation: Hawai'i as a Model System*. Princeton University Press, Princeton.

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