

CHAPTER 4

ECOSYSTEMS AND TOP CONSUMERS

4.1 The trophic organization of ecosystems

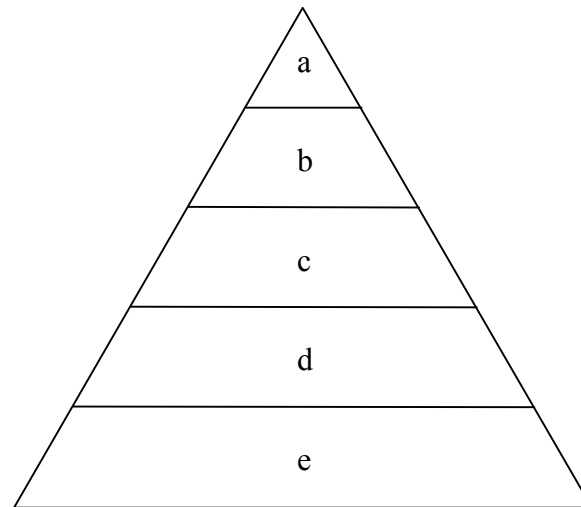
In the previous chapter, an ecosystem was characterized as a hierarchy ordered by prey and predator, bound together by a system of feedback loops. This conception of ecosystems enabled us to make some preliminary observations about the flow of energy through biological systems, including the comprehensive ecosystem consisting of the biosphere at large. We turn now for a closer look at how ecosystems are organized.

Broadly conceived, an ecosystem is a system of living and nonliving components that interact in filling the vital needs of its constituent organisms. Among their constituent organisms, ecosystems typically include (i) *producers* (plants and protozoa capable of photosynthesis), (ii) *consumers* (organisms that eat other organisms), and (iii) *decomposers* (bacteria, worms, fungi, etc.) that break down organic materials cast off by other organisms. Within the class of consumers, a further distinction is made between *primary consumers* or *herbivores* (organisms that eat only plants) and *secondary consumers*, with the latter broken down into *carnivores* (meat eaters) and *omnivores* (animals that eat both plants and other animals).

Among the nonliving components of an ecosystem are the habitats (aquatic or terrestrial) in which its organisms interact, the supplies of minerals and other materials they rely on for growth, and various physical features of the environment that affect their vital processes. There is nothing hierarchical about the arrangement of these physical components. An ecosystem owes its hierarchical structure to the interactions among its constituent organisms.

Our previous characterization of this structure in terms of prey and predator applies mainly to consumers and does not take the roles of producers and decomposers into account. Let us extend our characterization in a way that brings the nutritional (trophic¹) roles of producers,

consumers, and decomposers together in a comprehensive picture. The hierarchical arrangement of these several trophic levels is commonly depicted in some form like the following.



- (a) omnivores (humans, bears)
- (b) carnivores (lions, owls, snakes)
- (c) herbivores (deer, rabbits, mice)
- (d) producers (plants)
- (e) decomposers (bacteria, beetles, worms, fungi)

Trophic structure of an ecosystem

Figure 4.1

The hierarchy represented in this figure is one of nutritional dependency. Organisms on each level are dependent upon organisms below for nutrients essential to growth and metabolism. The obvious exception is the bottom level of decomposers, which take nutrition from organic matter left behind by organisms on the several levels above.

Needless to say, Figure 4.1 is simplified in many ways. For instance, it gives no indication that some plants are carnivores (pitcher plants feed on insects, and sometime small mammals), or that carnivores sometimes feed on omnivores (sharks eat people) or other carnivores (great horned owls eat snakes). Another simplification is that all organisms mentioned by way of example come from terrestrial ecosystems. An aquatic illustration might

have herring feeding on plankton (level d), salmon on herring, seals on salmon, and sharks on seals. It should also be noted that ecosystems have varying numbers of trophic levels, depending on the identity of their top-level consumers. An ecosystem with a population of golden eagles on top will have more levels overall than one with a colony of prairie dogs in that position.

An ecosystem supporting a population of wide-ranging omnivores (such as human beings), moreover, might contain many sequences of nutritional dependency, distributed through many trophic levels. The immediate lesson of Figure 4.1 is simply that organisms on the top level of any given ecosystem depend upon lower levels for their very existence. When an ecosystem supporting a given top-level population collapses (consider the plight of the Easter Islanders²), the population it supports goes down with it.

4.2 Energy flow in ecosystems

About 30% of the solar radiation reaching the earth's outer atmosphere is reflected back into space and another 20% is absorbed by the atmosphere. The remaining 50% reaches the ground or ocean surface where most of it is converted directly into heat. As already noted in connection with Figure 3.1, about one quarter of the solar radiation penetrating the atmosphere is in wavelengths useful for photosynthesis, of which only about one percent is actually engaged in that process. Our present concern is with this latter small portion.

From an energetic perspective, ecosystems may be viewed as means of channeling solar energy through the metabolisms of their constituent organisms. Several stages are involved in this process, the most notable for present purposes being (i) the conversion of solar energy into biomass by photosynthesis, (ii) the conversion of chemical energy in plants to more concentrated forms serving the energy needs of consumer organisms, and (iii) the discharge of low grade energy (i.e., entropy) expended in metabolic activity back into the surrounding environment.

Photosynthesis is a biochemical reaction, energized by sunlight, that converts carbon dioxide and water into carbohydrates and oxygen. A by-product of this transaction is the

formation of phosphates with high-energy bonds (primarily adenosine triphosphate, or ATP) that store energy for eventual use by consumer organisms. Photosynthesis takes place in chlorophyll-bearing plants and algae, which serve as producers in their respective ecosystems (terrestrial or aquatic). This process is the primary source of nutrients upon which other organisms in the biosphere ultimately depend.

Over half the energy fixed in photosynthesis is used by the metabolisms of producer organisms. Most of the rest is converted to forms usable by consumers. It has been estimated that between 10% and 20% of energy fixed by producers (less for aquatic than for terrestrial systems) is passed on to herbivores, that about the same proportion of this is passed on to the first level of carnivores, and so on through successive trophic levels.³ This means that in ecosystems with three or four levels of consumers (e.g., one supporting a population of grizzly bears), considerably less than one percent of the energy fixed on the producer level will reach the level of top consumer.

Despite this diminution in amount of energy passed from lower to upper trophic levels, there is a progressive concentration of energy made available to individual consumers. In the food chain from plankton to herring to salmon to grizzly bear, for instance, the salmon requires a great deal more energy than the herring, and the bear more yet than the salmon. This is one obvious reason why there are many more individual organisms at the bottom than at the top of a typical ecosystem.

The final stage in the passage of energy through an ecosystem is the discharge of the entropy which, in the words of Schroedinger (Chapter 3), an organism "cannot help producing while alive." All energy expended in the life-process takes the form of entropy, and an organism must rid itself of this entropy on a continual basis just to stay alive. A consequence of top consumers consuming more energy than organisms below them (e.g., grizzly bears than salmon) is that they produce more entropy to be discharged into the environment.

In a healthy ecosystem, some of the degraded energy produced by its constituent organisms will be transferred to neighboring ecosystems and some will be directly emitted into space as low-grade heat. Within the economy of the biosphere overall, however, even low-grade energy that is diverted from one ecosystem to another is destined eventually to leave the planet as heat radiation (see Figure 3.5).

The basic dynamics of energy flow in a typical ecosystem are represented in the following figure, which retains the hierarchical structure of Figure 4.1.

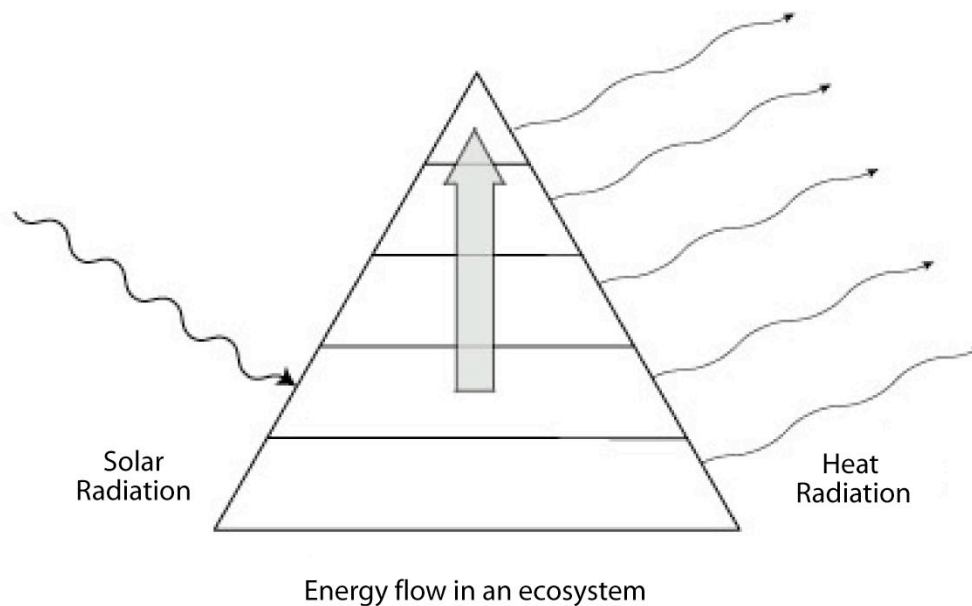


Figure 4.2

The "high frequency" arrow at the left represents incoming solar radiation, shown entering at the producer level ((d) of Figure 3.1). The broad arrow in the middle represents the flow of usable energy upward from producers to consumers. To keep things simple, there is no indication of the relatively minor counterflow of energy from the upper levels that fuels the metabolisms of the decomposers (level (e)). The "low frequency" arrows to the right represent outgoing radiation of low-grade heat. Heat leaves the ecosystem at all levels shown, inasmuch as all organisms produce metabolic heat.

Each type of arrow in this figure indicates a factor that is essential to the ecosystem's integrity. Ecosystems that lose their solar input for more than a few days stand in danger of total collapse. This effect is behind a current theory purporting to explain the sudden disappearance of dinosaurs from the fossil record about 65 million years ago.⁴ According to this theory, a giant asteroid that slammed into the earth during this period propelled enough debris into the atmosphere to destroy most of the plant life around the planet. This spelled doom not only for giant herbivores like Triceratops and Stegosaurus but also for Tyrannosaurus rex and other carnivores that preyed upon them.

The flow of usable energy from producers to consumers (the broad arrow in the middle) is the factor around which the ecosystem is organized. Anything that disrupts this upward flow will break the link between the upper and lower levels of the system. A common cause of such failure is an interruption of solar radiation needed for photosynthesis, as in the case of the vanishing dinosaurs. Another potential cause of disruption is the introduction of invasive species into the ecosystem. Purple loosestrife, for example, might crowd out other vegetation on which the herbivores of the system have come to rely. Although photosynthesis continues with the loosestrife, the plant is too coarse to eat and no longer produces biomass in forms usable by upper-level consumers.

No less essential to the vitality of an ecosystem is its ability to rid itself of the degraded energy (entropy) resulting from its interior biological activity. The "low frequency" arrows to the right of Figure 4.2 represent low-grade heat that must be cast off for this activity to continue. If for any reason this heat is retained within it, the normal operation of the system will be impeded. When this condition persists, the ecosystem's ability to supply its top consumers with needed energy will be increasingly impaired.

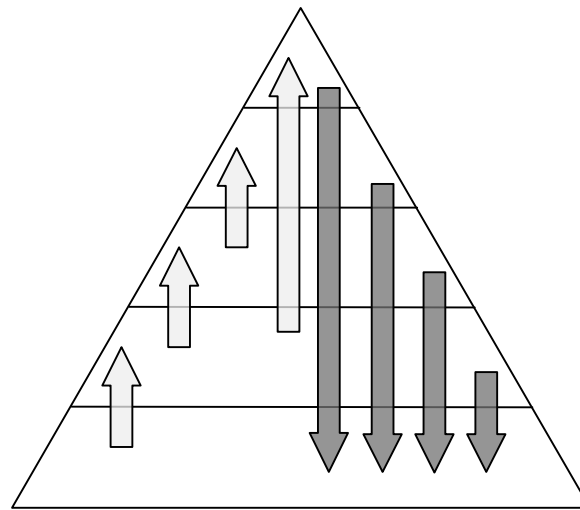
4.3 Transformations of physical structure

As energy can take the form of either disorder or degraded energy (chapter 2), so negentropy might be available as either order or high-grade energy. Although order in turn can take various forms, our present concern is with order of two specific sorts. One is order in the form of material structure. Examples of ecological significance are chemical elements (e.g., carbon, hydrogen, and nitrogen) and various compounds that remain intact as they move through the ecosystem. The other is order in the form of nonphysical structure, having to do with the functional interactions of the system's biological components. The present section deals with the ecosystem's management of physical structure.

Whereas the flow of energy in an ecosystem is primarily from lower to higher levels, physical structure moves in both upward and downward directions. Matter is passed up the food chain through successive trophic levels, and then passed down in the form of excreta, molted feathers, decaying leaves, and so forth. This corresponds to the two-way movement of matter in individual organisms, inward by way of ingesting food and outward by way of discharging waste products.

In contrast with the passage of food through the digestive systems of individual organisms, however, interchange of materials within a given ecosystem tends to be a self-contained process. Material structure is generated by an ecosystem's chlorophyll-bearing components and passed upwards for incorporation in higher-level organisms. Once degraded by use at upper trophic levels, matter is then passed downward for decomposition into forms that can contribute to further photosynthesis.

The basic patterns of structural transformation in ecosystems are depicted in the following figure.



Structural transformations in an ecosystem

Figure 4.3

The upward arrows in this figure depict the passage of material structure from lower to higher trophic levels. Chemical nutrients move upward from decomposers to producers (levels (e) and (d), respectively, of Figure 3.1), and plant materials move onward to primary consumers. Also indicated in the figure is a movement of biomass from herbivores to carnivores. Although the upward arrow nearest the middle indicates the transfer only of plant material to the top-level omnivores, food channels should be assumed leading to omnivores from all other trophic levels as well (people eat ants, jackrabbits, and snakes, as well as plants). The shaded arrows pointing downward, in turn, depict the passage of waste materials from all the other trophic levels down to the level of decomposers.

All arrows in Figure 4.3 extend across trophic levels. Not indicated is another kind of structural transformation that is confined to the level of decomposers itself. The role of decomposers in the ecosystem is to convert waste materials from other levels into chemical elements that serve as building blocks from which new plant materials is produced by photosynthesis. More will be said subsequently about the processes involved.

For now it is enough to note that the movement of material structure through the ecosystem actually constitutes a closed circle. As far as chemical elements are concerned, the same bits of matter might cycle through the system indefinitely.⁵ Although ecosystems might exchange materials with other ecosystems during the course of normal operations, this is not always necessary to keep a given ecosystem up and running. What *is* required to keep an ecosystem in operation is a constant input of solar radiation (Figure 4.2).

4.4 Functional interactions among biological components

We turn now to the nonphysical structure of ecosystems. The structure in question is nonphysical in that it has to do with the functional interactions of the organisms involved. For a simple parallel, think of a basketball going through a hoop. This is an interaction between physical objects (the ball and the hoop), but the interaction itself is not another physical object. Similarly, when several organisms cooperate in one or another biological process, there is an interaction among physical entities. But the functional relation among them is not an additional physical entity.

There are functional interactions among organisms on any given trophic level. For example, a mating pair of golden eagles might cooperate in raising young; or they might fight off other birds who threaten their territory. There are functional interactions also among organisms on different levels. A certain stand of plants might feed a population of prairie dogs, which in turn serves as food source for a pack of coyotes. And the decomposers of an ecosystem are functionally related as a group to organisms producing the waste material they help to break down.

In section 3.8, ecosystems were characterized as systems of prey and predators held together by biological feedback loops. But this description says nothing about how such systems themselves are organized. What the characterization leaves out is any indication of the functions served by these feedback interactions and of the way these functions relate to one another.

To remedy this lack, let us shift to a conception of an ecosystem as a network of functional interactions organized around its participating organisms. This is analogous to thinking of a road map as a system of lines (the roads) connected by dots (the towns) indicating how motorists can get from one place to another, as distinct from thinking of it as an arrangement of dots connected by lines which shows places one can reach as destinations. The conception of ecosystems in question focuses on the interactions among organisms (the lines) rather than on the organisms that participate in them (the dots). In brief, we are to think of an ecosystem as a network of interactions and the participating organisms as the nodes (connections) holding the network together.

The functional structure of an ecosystem may be defined as the overall configuration of functional interactions in which its constituent organisms participate. These configurations admit a variety of characteristic features. A given ecosystem will comprise interactions over a specific number of trophic levels, will include a certain number of populations among its primary consumers, will feature a top consumer sustained by a number of functional interactions with lower-level consumers, and so forth. As a consequence of such features, a given ecosystem might be more or less adaptive, more or less robust, and more or less vulnerable to environmental disturbances.

Like their resident organisms, ecosystems are in constant flux. Stability on the part of ecosystems is the equivalent of health on the part of their constituent organisms. Briefly characterized, a healthy organism is one capable of maintaining its organic structure while responding to changes in its living environment. In like fashion, an ecosystem is stable to the extent that it is able to maintain its functional structure in the face of environmental change.

For an individual organism to maintain its structure does not require that its biological functions remain wholly unaltered. An infant mammal does not lose its health in shifting from milk to more solid food. Similarly, an ecosystem does not inevitably become unstable with changing populations on its lower trophic levels. An ecosystem supporting a great horned owl as

top consumer would not necessarily lose its stability if chipmunks replace field mice in its diet on rodents.

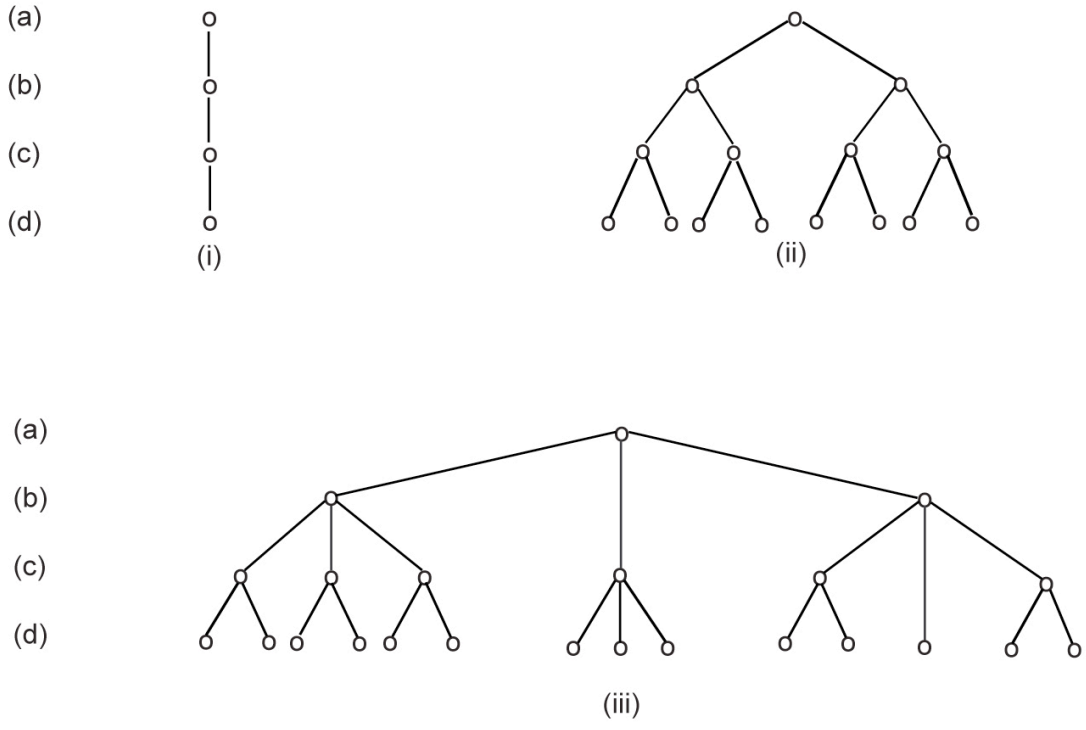
For present purposes, let us say that an ecosystem retains its structural stability as long as it provides a firm foundation of support for its top consumers.⁶ An unstable ecosystem, on the other hand, puts the continued sustenance of its top consumers in jeopardy. In thinking about this topic, we should bear in mind that the top consumers of the biosphere at large are living members of the human race. In the following discussion of factors responsible for an ecosystem's stability, we are in effect considering factors that influence the ability of the biosphere overall to provide continued support of its human population.

4.5 The contribution of nutritional diversity to ecosystem stability

To continue our discussion of Figure 4.1, we may observe that the segments signifying different trophic levels get narrower as they approach the top. With this in mind, we may think of the widths of these segments as representing comparative numbers of individual organisms functioning on a given trophic level. By way of illustration, a certain number of carnivores on level (b) will rely on nutritional input from a much larger number of herbivores on level (c). A single great horned owl, for instance, consumes many thousands of smaller birds and animals over a lifetime of 10 or so years. For another example, a standard size bison will take in around 30 pounds of plant material (at several hundred plants per pound) in a single day. And literally countless bacteria and other decomposers are required to break down the waste products of the animals that consume those plants.

On one hand, ecosystem stability requires ample populations on lower trophic levels to meet the needs of its top consumers. On the other, it also requires that these populations be distributed through a considerable variety of different species. What this latter requirement means in effect is that the functional stability of an ecosystem depends upon the availability of alternative pathways through which nutrients can flow from lower to upper trophic levels.

This effect can be demonstrated by comparing the following diagrams.



Ecosystem stability as a function of alternative nutrient pathways:
three cases for comparison

Figure 4.4

Each of the three diagrams in this figure represents the functional structure of a conceivable ecosystem. The diagrams are made up of circles, representing populations of organisms, and the lines between them, representing functional interactions among these populations. Trophic levels are labeled in the manner of Figure 1. The functional structure symbolized by (i), for instance, consists of an interactions between a plant population (d) and a population of herbivores (c), an interaction between (c) and a population of carnivores (b), and one between (b) and a population (a) of top consumers (other carnivores or omnivores, as in Figure 4.1). For simplicity, decomposer populations are left out of the picture.

Diagram (i) corresponds to a functional structure that is too unstable to exist in nature. A conceivable instance, nonetheless, would be a single population of jackrabbits (c) feeding on an isolated stand of clover (d), providing food in turn for a specific group of red-tailed hawks (b)

which are consumed by a single family of great horned owls (a). If any one of the lower populations were severely depleted, the ecosystem would promptly collapse and the owls at its top would die of starvation. This imaginary ecosystem would be highly unstable because of lack of diversity in the nutritional sources available to its upper-level populations.

An ecosystem structured in the manner of (ii) would provide alternative channels of nutrition at each trophic level, making it potentially more stable than an ecosystem patterned after (i). A conceivable instance might have a family of great horned owls as top consumer, feeding alternatively on a group of red-tailed hawks and a population of raccoons. The red-tailed hawks might have a diet of squirrels and rabbits, while the raccoons rely on song birds and mice. Squirrels and rabbits might have a diet of fruits and grains in turn, as might the song birds and the mice concerned. If one of these herbivore populations were to become severely diminished, the owls might still survive on nutrients channeled through alternative pathways.

We should note in passing that all the consumer species mentioned in illustrations (i) and (ii) actually have diets far more varied than the illustrations specify. Most herbivores (including mice and rabbits) eat more than fruits and grains. Red-tailed hawks feed on reptiles and smaller birds, as well as on a wide variety of rodents. Being omnivorous, raccoons feed on crayfish, insects, and frogs, along with various fruits and vegetables; and so forth.

Diagram (iii) is unrealistic in the same respect, and is included for purposes of comparison only. Whereas the top consumers in (i) and (ii) feed on carnivores exclusively, those in (iii) feed on carnivores (left), herbivores (middle), and omnivores (right). This contributes to the most important difference between (iii) and the other diagrams, which is that the ecosystem it represents contains substantially more nutritional pathways serving its upper trophic level. If several of these pathways were eliminated, the remainder might still provide adequate nourishment for its top consumers. In contrast with the others, ecosystem (iii) rests on a sufficiently broad base not to be severely affected by a few disturbances on its lower levels.

4.6 Biodiversity and stability

Maintaining a steady supply of nutrients is one among many services an ecosystem provides to its resident organisms. Any ecosystem of more than minimal complexity will probably involve symbiotic interactions (e.g., pollination of plants by insects), relationships of shelter (birds nesting in trees), of transport (seed spread in bird droppings), and so forth. Generally speaking, services like these will also be more reliable if provided by a variety of different species.

This brings us to the topic of biodiversity, and of its effect on ecosystem stability. Ecologists appear unanimous in viewing loss of biodiversity as a bad thing. It is regrettable aesthetically (the Ivorybilled Woodpecker must have been a magnificent sight). It is medicinally unpropitious (substances contained in extinct plants might have led to new medications). And it leaves fewer species for biologists to collect and study. Loss of these human benefits is certainly unfortunate.

A less anthropomorphic benefit was suggested by Eugene Odum in his book *Fundamentals of Ecology*, published more than fifty years ago.⁷ Odum's proposal was that the homeostatic (self-stabilizing) capacities of ecosystems increase with the diversity of networks through which energy can flow to upper trophic levels. His line of reasoning, basically that followed in section 4.5 previously, is that if adjacent levels of an ecosystem are linked by several parallel pathways, then loss of energy flow through one pathway can be compensated by increased flow through others.

Odum's hypothesis has obvious intuitive appeal, and numerous attempts have been made to test it empirically. Energy flows through ecosystems proved difficult to quantify,⁸ as did homeostasis on the part of ecosystems (the definition of homeostasis in section 3.6 does not carry over to ecosystems automatically, inasmuch as they are not biological organisms). This has made it difficult to establish a direct causal relation between number of species in an ecosystem and its overall stability.

On balance, however, it seems fair to say that enough empirical research has been done to show that ecosystem stability and biodiversity are positively correlated. Surveys of work in progress suggest that in some cases diversity is a source of ecosystem stability, while in other cases stability is an occasion for diversity instead.⁹ The upshot in either case is that loss of stability and loss of biodiversity go hand in hand. Particularly in ecosystems supporting top consumers that have extensive energy needs, severe loss of diversity can be a sign of potential collapse.

While thinking about this correlation, we should bear in mind that biodiversity is more than sheer number of species involved. An ecosystem's stability (or fragility) is an aspect of its functional structure. Considerations of biodiversity in an ecosystem are not addressed to numbers of species in isolation, but rather to the functional interactions to which resident species contribute. Stability and biodiversity both have to do with an ecosystem's structure in the nonphysical sense explained in section 4.4. Discussion of details in the following chapter will help us see that the nonmaterial status of an ecosystem's functional structure does not prevent loss of structure from counting as a form of entropy.

4.7 Ecosystems related by top consumers

Figure 4.1 shows the hierarchical arrangement among an ecosystem's various trophic levels. The occupants of the upper level comprise what we have been calling the ecosystems top consumers. An ecosystem's top consumers are those organisms whose nutritional needs are met within the system and who do not serve as prey for other constituent organisms. The top consumers of a given ecosystem need not be omnivores, as shown in the figure; but we are assuming that they are consumers as distinct from producers.

The hierarchy among trophic levels is internal to the ecosystem in question. There is an hierarchical arrangement of another sort (external) generally found among ecosystems themselves. With the exception of the biosphere at large, all ecosystems are included within

more comprehensive ecosystems. And all save the simplest have other ecosystems included within them in turn. Our present task is to explicate this mode of inclusion.

For an ecosystem to be included in another ecosystem is not for one to be *part* of the other. Consider an ecosystem supporting a colony of prairie dogs as top consumers, which is included in another whose top consumers are a pair of golden eagles. The prairie dogs are parts of their supporting ecosystem, along with the plants on which they feed, the decomposers that break down their waste materials, and so forth. The prairie dogs are also parts of the more comprehensive ecosystem supporting the golden eagles. But the *ecosystem* supporting the prairie dogs is not itself a part of this more comprehensive ecosystem. An ecosystem is an hierarchy of organisms ordered by trophic levels; and ecosystems themselves are not organisms occupying trophic levels.

In general, ecosystem A is included within ecosystem B if the top consumers of A are also components of B, but the top consumers of B are not among the organisms comprising A. Thus the ecosystem with the prairie dogs as top consumers is included within the ecosystem featuring the golden eagles. Likewise, an ecosystem supporting a group of bison as top consumers might be included in another ecosystem supporting a tribe of indigenous people. But since the people are not part of the former ecosystem, there is no inclusion in the other direction. The relation of inclusion is not reciprocal.

Inclusion nonetheless is a transitive relation. If ecosystem A is included in B, and B in C, then A is also included in ecosystem C. For example, the ecosystem featuring the bison is included in that featuring the native people; and inasmuch as the latter is included in the biosphere at large, the former is included in that most comprehensive of ecosystems as well.

This definition allows a single ecosystem to be included within two more comprehensive ecosystems at the same time. By way of illustration, an ecosystem supporting a colony of prairie dogs could be included simultaneously in one supporting a pack of coyotes and one supporting a pair of golden eagles. By reverse token, a single ecosystem might include several less

comprehensive ecosystems no one of which is included in any other. The ecosystem supporting the golden eagles as top consumers might include distinct ecosystems supporting prairie dogs and jack rabbits, respectively, without any relation of inclusion between the latter two.

This is the manner in which other, less inclusive, ecosystems are included in the biosphere at large. At this stage in geological history, the human race is the biosphere's dominant species. For all practical purposes, human beings function as the biosphere's top consumers. The biosphere includes all ecosystems meeting the nutritional needs of its human population, along with others meeting human needs that are no less essential. Among the latter are ecosystems maintaining a generally reliable supply of fresh air and clean water, others contributing materials for clothing and shelter, and yet others providing suitable contexts for social existence. Apart from their roles in the overall biosphere, however, these latter ecosystems tend not to be included within each other.

4.8 Ecosystems as processors of negentropy

As matters stand, consumers on all levels depend upon other organisms for food. This is shown clearly in Figure 4.1. As illustrated by producers like plants and algae, however, there are other ways of obtaining nourishment than eating living things. What Figure 4.1 does not show clearly is that upper-level consumers are *unavoidably* dependent upon other organisms for their livelihood.

All living creatures on the planet are ultimately reliant on solar radiation for energy to drive their metabolisms. Unlike plants and algae, however, consumer organisms are not equipped to receive metabolic energy from sunlight directly. The simple fact of the matter is that consumers such as jackrabbits, great horned owls, grizzly bears—and human beings—could not exist without other organisms to convert solar energy into forms their metabolisms can accommodate.

Let us recall (from section 3.3) Schroedinger's characterization of metabolism as a means of maintaining an organism's low level of entropy by "continually sucking orderliness from its environment." Since an organism's ecosystem effectively constitutes its environment, the upshot, again in Schroedinger's terms, is that "an organism feeds upon...negative entropy" provided by its ecosystem. The simple fact at hand is that the negentropy "sucked up" by consumer organisms (human beings included) must be altered from direct sunlight into forms capable of driving their metabolisms.

In effect, the negentropy that keeps these organisms alive must undergo preliminary processing before it can meet their metabolic needs. This preprocessing is the work of other organisms on lower trophic levels of their supporting ecosystems. Although performed externally to the upper-level organisms in question, the preprocessing provided by the ecosystem is an integral part of the vital processes by which they maintain their existence.

Maintaining an organism in existence requires both an external supply of energy to run its metabolism and external provisions for getting rid of the entropy produced by its vital processes. Again in Schroedinger's terms, the organism must have a way of "freeing itself from all the entropy it cannot help producing while alive." This amounts mainly to ways of dissipating the low-grade heat produced by its metabolism and means of discharging the waste materials resulting from its processes of growth and regeneration.

The organism's ecosystem thus plays a vital role both in transforming solar energy into forms usable by its metabolism and in getting rid of the entropy it produces in using this energy. The processes enabling an organism to maintain its vitality are not confined to the space occupied by the organism itself. These processes include functions performed within its supporting ecosystem as well.

Let us focus these observations upon the plight of the biosphere's top consumer specifically. We human beings are unavoidably dependent upon the biosphere at large both for converting solar energy into forms our metabolisms can accommodate and for getting rid of the

entropy produced as an essential part of maintaining our existence. If the biosphere ever reaches a point at which it is no longer capable of providing those services, human life as we know it will become extinct.

The stark reality of the matter is that this point might be nearer than most of us realize. As far as energy input is concerned, human ingenuity has been so successful in creating "processed" food that it may be hard to convince ourselves that we cannot "go it on our own" without the help of other species. What we must bear in mind in this regard is that there is no reasonable prospect whatever of our learning how to engineer food directly from solar energy.

As far as the disposition of entropy is concerned, there are compelling signs already that the biosphere is rapidly losing its capacity to get rid of the waste products created by human industry. Failure to reverse this development portends the end of human existence as we know it. The following chapter examines the details behind this threat.

Notes

1. The term 'trophic' comes from τροφός a Greek term meaning food or nourishment.
2. A highly relevant account of the Easter Island civilization may be found in Chapter 1 of Clive Ponting's *A Green History of the World* (Penguin Books, 1991).
3. Numerical estimates in this paragraph come from the Scientific American publication *The Biosphere* (1970), in particular the articles by A.H. Oort and G.M. Woodwell, and from "Biosphere" by D.M. Gates in *Encyclopedia Britannica*, 1974.
4. This is the "fifth extinction" relative to the namesake sixth of *The Sixth Extinction: Patterns of Life and the Future of Humankind* (Doubleday, 1995), by Richard Leakey and Roger Lewin; see pp. 52-56 esp. For a less technical account, see Tim Flannery, *The Eternal Frontier: An Ecological History of North America and its Peoples* (Atlantic Monthly Press, New York, 2001), ch. 1.

5. This recycling process is dramatized by Aldo Leopold in his story of the "Odyssey" of atom X in *A Sand County Almanac* (Oxford University Press, 1949; subsequently reprinted by Ballantine Books). After being locked in sedimentary rock for billions of years, X was pulled into the world of living things by the root of an oak, and began an uphill journey during which it passed through acorn, then deer, then hapless Indian, and again through buffalo chip, spiderwort, rabbit, and owl, until a fox caught a gopher and an eagle caught the fox, and X reached its zenith in an eagle's nest. After that, it was a quick trip downward, through cottonwood, beaver, coon, and crayfish, until X was finally caught in a freshet and rejoined the sea. Without life, X might have remained under the surface forever, but by joining life it "soared on eagle's wings."

6. Ecologists more commonly think of stability as the ability of an ecosystem to return to equilibrium quickly after perturbation. In point of fact, a stable ecosystem typically would provide a firm support for its top consumers. The definition adopted in the text focuses on that point directly.

7. Eugene P. Odum, *Fundamentals of Ecology* (Saunders, Philadelphia, 1953). In his later *Ecological Vignettes* (Harwood Academic Publishers, Amsterdam, 1998), Odum states categorically that, in addition to homeostasis, "redundancy—that is, more than one species or component capable of performing a given function—also enhances stability in ecosystems" (p. 121).

8. An early attempt to quantify trophic flows in ecosystems in terms of information theory (see the appendix to Chapter 2) was made by R. H. MacArthur in "Fluctuations of animal populations, and a measure of community stability" (*Ecology* 36: 533-536). Other attempts to apply information theory to the description of ecosystems may be found in R. Margalef, *Perspectives in Ecological Theory* (University of Chicago Press, Chicago, 1968); J. S. Wicken, *Evolution, Thermodynamics, and Information* (Oxford University Press, Oxford, 1987); Claudia Pahl-Wostl, *The Dynamic Nature of Ecosystems* (John Wiley & Sons, Chichester, 1995); and R. E. Ulanowicz, *Ecology, The Ascendent Perspective* (Columbia University Press, New York,

1997). An interesting analysis of the upshot of MacArthur's early attempt is offered by Ulanowicz, *op. cit.*, pp. 65-66.

9. For a summary overview, see Stuart Pimm, "The complexity and stability of ecosystems," *Nature*, Vol. 307, pp. 321-326, Jan. 26, 1984; and R. E. Ulanowicz, *Growth and Development*, pp. 117-118.