# Ecology of Natural Resources

François Ramade

# Ecology of Natural Resources

**François Ramade**

*Professor of Ecology and Zoology at the Université de Paris-Sud (Orsay)*
*Member of the IUCN Commission on Ecology (Gland, Switzerland)*

**Translated from the French by W. J. Duffin, University of Hull**

**JOHN WILEY & SONS**
Chichester . New York . Brisbane . Toronto . Singapore

First published under the title Ecologie des Ressources Naturelles by François Ramade.



*Library of Congress Cataloging in Publication Data:*

Ramade, François.
Ecology of natural resources.

Translation of: Écologie des ressources naturelles.
Bibliography: p.
Includes indexes.
1. Ecology. 2. Natural resources. I. Title.
QH541.R2513 1985 333.7′2 84–3678

ISBN 0 471 90104 0 (cloth)
ISBN 0 471 90625 5 (paper)

*British Library Cataloguing in Publication Data:*

Ramade, François
Ecology of natural resources.
1. Natural resources 2. Ecology
I. Title II. Ecologie des ressources naturelles. *English*
333.7 HC55

ISBN 0 471 90104 0 (cloth)
ISBN 0 471 90625 5 (paper)

Typeset by Pintail Studios, Ringwood, Hampshire
and printed by The Pitman Press, Bath, Avon

# Foreword

Reader, do you remember how, barely 10 years ago, futurologists and economic prophets were announcing to us all in a blaze of publicity that the major problem of tomorrow's citizens would be the occupation of their leisure time? And how the few pioneers in ecology who put forward quantitative evidence opposing this anaesthetizing myth were met with nothing but a disdainful silence from traditionalists on all sides?

Now the wind has changed. Shifts in the balance of world power and the resultant redrawing of the geopolitical map, the energy 'crisis' and upheavals in the Third World have put an end to the complacence of many of those holding the above opinion. We have passed from a smug optimism to a chronic pessimism, trying hard to ignore the future for the better enjoyment of the present. Après nous la fin du monde!

Such an attitude is just as irresponsible as the previous one, and this new book of François Ramade clearly demonstrates that, while the situation is serious, it is certainly not desperate—as long as we are willing to look beyond the end of our noses and draw the necessary conclusions in time. There *are* solutions to our problems but they must be willingly adopted or they will be violently imposed from outside. If the necessary measures are not taken in time, 'the Third World will only be able to advance by shattering the world's social order in one way or another' (Fernand Braudel, *Civilisation matérielle, économie et capitalisme*, Vol. 3, 1979, p. 469). At best, this would bring about a progressive collapse and decline of the civilization of which we are so proud; at worst, it would provoke a great march northward of the starving, and the dawn of the new Middle Ages.

What are these measures that seem forced on us by the inescapable laws of physics and biology?

First of all, it is more than ever necessary to put an end to the world's population explosion. Particularly urgent is the need to think at once about reducing the pressure in already overpopulated regions by freely accepted birth control: a measure that will undoubtedly require a colossal effort of education.

In parallel with that, the enormous wastage of renewable resources indulged in so freely by the West's consumer society should be reduced as far as is humanly possible and, at the same time, everything that can be recycled should be recycled.

The third, equally urgent, measure is the conservation of the potential biological productivity of land, sea and inland waters, and its rehabilitation in those environments where fertility has been thoughtlessly reduced through activities working against nature. This action must be accompanied by the preservation of the world's genetic stock of plants and animals, the fruit of hundreds of millions of years of evolution.

The final objective—and by no means the easiest to attain—is the need to learn how to share the available resources so as to reduce the most glaring inequalities between the 'haves' and the 'have nots'. Alas, no political movement of any importance dares for one moment to face this problem, because its solution necessarily implies some reduction in the standard of living of the present most wealthy countries.

It is greatly to be feared, therefore, that the inevitable unpopularity of many of the measures needed for an immediate response to the four requirements I have just outlined means that the necessary decisions will be taken too late and under the pressure of a 'crisis' that will have become endemic.

Moreover, things are not made any easier by the obsession of too many Third World leaders with a blind copying of models of development which were valid in other places and at other times, but which are ill-adapted to their current situation. Nor does the moral abdication on the part of too many 'elites' in wealthy countries help in any way. At a time when egocentricity, hedonism and laxity seem to have become the three Western pillars of wisdom, how can we hope to arouse in ourselves the great effort of imagination and research, the altruistic spirit and the sheer crusading attitude needed to take rapid decisions?

I hope that the pages which follow will nevertheless cause many future leaders of our society to reflect on such matters, and help to give their lives a new sense of direction. For all those who are not satisfied with the dullness of daily existence, there are as many exhilarating tasks to be undertaken today as there were yesterday. Knowing how to respond quickly and efficiently to the appeals of thousands of millions of the underprivileged presents a challenge that we must have the courage to accept as soon as possible.

François Bourlière,
*Honorary President of the International Union for the Conservation of Nature; President of the Société Nouvelle de Protection de la Nature and of the International Association for Ecology (INTECOL)*

# Acknowledgements

It gives me great pleasure to thank Professor J.-M. Pérès, Membre de l'Institut de France, who kindly offered to read the chapter on marine resources and suggested various modifications; Professor F. Bourlière, President of the International Association of Ecology (INTECOL), who was kind enough to contribute the foreword; and Professor M. Lamotte, Director of the Zoology Laboratory at the ENS, who allowed me to have access to a large volume of documentation on research into the ecology of the savannas carried out at Lamto.

I should also like to express my sincere thanks to my friends and colleagues, Y. Gillon, J. C. Moreteau and F. Terrasson, who have contributed to the illustration of this book by allowing me to use certain photographs from their personal collections.

# Introduction

Like all other living beings, humans require matter and energy. It is not being too sceptical about possible advances in science and technology to say that our species could obviously not set itself free from such requirements, whatever future progress might be envisaged.

Human beings are animals and are therefore heterotrophic organisms.[1] As such, their metabolic requirements are met by the air they breathe and by the water and organically derived food they ingest. Like other living species, they depend on the cosmic system from which they have descended: essentially the sun together with the ecosphere, the superficial part of our planet where the environmental conditions exist that make life possible.

However, continual advances in technology have caused other needs to appear in addition to those resulting from natural biological processes. The development of an ever more complex industrialized society in which the production of manufactured objects is incessantly growing entails a continually increasing use of primary energy and of organic and inorganic raw materials.

Just as metabolic processes involve the discharge of mineral and organic excreta, so the activities of a technological civilization release waste products into the environment. In both cases, the discharged material does not simply disappear from the environment that receives it: instead, it circulates in biological systems which can cease to function properly if their homeostatic mechanisms are overstretched.

Another feature of the contemporary world that arises from human activity and has a considerable impact on the ecosphere is the explosive growth in population. This, along with the unending increase in *per capita* consumption of manufactured goods, puts great pressure on nature and natural resources.

This takes us a long way from one of the fundamental concepts of industrial civilization, that of *Homo ecônomicus*, which regards humanity as the owner of all mineral and biological resources and thinks of these resources as inexhaustible and to be disposed of as we please. According to this idea, humanity is extraneous to the ecosphere and thus independent of any ecological changes in it that might be produced by human activity.

The very concept of a natural resource is worth some reflection. A resource can be defined simply as any form of energy or matter necessary to satisfy the physiological needs of humanity or to sustain all the various activities leading to production. The flow patterns of such resources through human civilization are very complex and so can be studied from several different angles.

Between the stage at which the resource is extracted and that of its use by a consumer, it undergoes many transformations, and these often have an impact on the overall functioning of the ecosystems in which the processes occur. A classic distinction is frequently made between non-renewable and renewable resources. Potential sources of energy such as hydrocarbons and fissile materials clearly come into the first category, but for other types of resource the distinction is often difficult to make. Even minerals could be allocated to the second category since they can theoretically be recycled from both domestic and industrial waste and this would circumvent the problem of their exhaustion.

Water and all resources of a biological origin are usually classified as renewable. Even when polluted, water is not chemically modified in any way by being used and so can be recycled after purification. Plant and animal resources, on the other hand, although potentially renewable, are very often so overexploited that the possibility of regeneration in many parts of the world has been greatly reduced and sometimes completely compromised by the destruction of the ecosystems on which they depend.

In reality, the natural resources of the ecosphere are being wastefully consumed at an increasing rate under the combined effect of population pressure and the dramatic increase in industrial production. The current rate of use takes absolutely no account of the real size of available reserves of minerals or fossil fuels, nor does it concern itself with the rate of renewal of plant or animal resources. The needs of future generations are similarly ignored. In addition to that, malnutrition is spreading in the Third World and, in a future that is closer than some people think, the industrialized and overpopulated countries of Europe and other continents will no longer be protected from shortages of animal protein.

1. See glossary, p. 222.

Another form of damage to the ecosphere which has very worrying ecological consequences is the overexploitation of the Earth's plant cover. The degradation of forests, quite apart from the decrease in timber production it brings, causes irreversible changes in climate and soil. The extension of deserts into grassland or open forests; the erosion of soils in mountainous terrain or in areas where fragile land has been irresponsibly cultivated—these all demonstrate the extent of the upheaval stemming from the overexploitation of natural resources indulged in by humanity.

Animal resources are even more threatened. During the last two centuries, more than 600 species of birds and mammals have become extinct because of human activity. As for marine ecosystems, whose biomass was long considered inexhaustible, these are now also showing disquieting signs of overfishing through excessive landings of the main species of economically valuable fish.

In what follows, therefore, I intend to analyse the ways in which the main categories of natural resource are exploited and to examine the major principles of methods for the rational management and conservation of such resources. Now, more than ever before, is the time for implementing a world strategy for the protection of nature in the cause of a lasting and stable world. The aim of this book is to explain the scientific foundations and methodological approach on which such a strategy must be based.

# Contents

## Chapter 1

# Ecological Concepts Related to Nature and Natural Resources

### 1.1 Ecosphere and Biosphere

The word *nature* is used in a good many senses and it includes ideas that vary widely according to the educational background of those using it and the amount of scientific training they have had, especially in biology. The concept of nature generally held by the non-specialist, the politician or the technocrat is undoubtedly only distantly related to that held by the ecologist. For that reason, I prefer in the following pages to use instead the terms *biosphere* and *ecosphere*, since these indicate the two regions of our planet which contain everything ordinarily understood as 'nature'.

The *biosphere* can be simply defined as that part of the Earth in which life is permanently possible and which contains all living organisms. It consists of the terrestrial oceans and the surfaces of the continents, together with the adjacent atmosphere (that is, the troposphere), with the exception of the polar ice caps and the higher mountain slopes above the snow line. These latter regions, described as parabiospheric, are included along with the biosphere itself in a larger system, the *ecosphere*, which also embraces the upper layers of the lithosphere and the whole of the atmosphere above the troposphere.

The aim of *ecology* is to investigate the relation of living organisms to each other and to their surroundings and it thus provides, more than anything else, an essential basis for any rational approach to the study of the biosphere. Since the ecosphere is the origin of all natural resources except solar energy, it is easy to appreciate the importance of ecological science to the understanding of problems caused by the consumption of such resources in our present technological civilization.

### 1.2 Fundamental Ecological Variables

The living world can be studied in ecological terms at various levels of organization having greater and greater complexity. The effects of the main factors typical of any given environment can be considered (a) on an individual taken in isolation (autecology or eco-physiology), (b) on the population of a given species (population ecology or demo-ecology), or (c) on the entire community of living organisms subject to the same environmental conditions (ecology of the ecosystem or synecology).

*The concept of an ecological factor*

Whatever the level of organization being studied, we are always led to consider the effects of a certain number of fundamental parameters called *ecological factors*: these are the typical physico-chemical or biological characteristics of each environment that are capable of acting *directly* on the living organisms. Thus, in a continental environment, the temperature and rainfall are ecological factors whereas the altitude is not: it can be divided up into a series of parameters (such as temperature, amount of daylight, atmospheric pressure, etc.) through which it exerts its influence and produces its effects.

Ecological factors can be classified in several different ways. First of all, we can distinguish between *abiotic factors* (climate, physico-chemical composition of the environment, for example) and *biotic factors* (such as parasitism, predation, food supply, etc.).

Then, some ecological factors can be said to be *independent of the population density* because they exert the same influences on the individual whatever the density of the population to which it belongs (temperature is an example). Other factors, such as the quantity of food available or the effect of predators, may be *dependent on the population density*.

The last method of classifying ecological factors, that of Mondchasky, takes into account the effect of cosmic phenomena on them. It is quite obvious that annual, seasonal and daily fluctuations connected with the Earth's movement in its orbit could have an influence on a whole series of ecological factors which would then vary cyclically, sometimes in a pronounced manner, sometimes less so.

*Table 1.1 Classification of ecological factors* (adapted from Dajoz, 1971)

| | | | |
|---|---|---|---|
| Abiotic factors | **Climatic factors**<br>temperature<br>amount of daylight<br>humidity<br>rainfall<br>others (wind, etc.) | Factors independent of population density | Primary periodic<br>Secondary periodic |
| | **Non-climatic physico-chemical factors**<br>*Aquatic environment*<br>pressure<br>concentration of mineral salts<br>concentration of dissolved oxygen<br>*Edaphic environment*<br>particle size<br>chemical composition | | Secondary periodic or aperiodic |
| | **Trophic factors**<br>concentration of inorganic nutrients<br>available food supply | Factors dependent on population density | Secondary periodic |
| Biotic factors | **Biotic factors**<br>*Intra-specific interactions*<br>*Inter-specific interactions*<br>competition<br>predation<br>parasitism<br>etc. | | Secondary periodic or aperiodic |

Mondchasky distinguishes *primary periodic factors* (such as temperature and amount of daylight, for example), where the connection with the Earth's movement is direct, from *secondary periodic factors*, where the cyclic variations are derived from those of the primary factors (like atmospheric humidity, plant food supply, etc.). In addition, there are *aperiodic factors*, some of which exhibit fluctuations that are both violent and unpredictable (an exceptional drought or a volcanic eruption are good illustrations). Also classified as aperiodic are those factors having such a slow variation that they can be considered as virtually constant (the concentration of nutrient minerals in soils is an example).

Table 1.1 shows the relation between these various methods currently used for the classification of ecological factors.

### *The concept of a fundamental ecological variable*

According to Watt (1973), the action of the many ecological factors can be reduced to a limited number of *fundamental ecological variables*, five in all: matter, energy, space, time and diversity. Any ecological phenomenon, no matter how complex, can be explained by the interplay of these five variables and, conversely, they must all be involved in the interpretation of such a phenomenon. I consider each of them in turn.

### 1.2.1 Matter

All living organisms consist of a certain number of chemical elements essential for the building of their biological molecules. In decreasing order of the amounts found in the human body, these are: oxygen, carbon, hydrogen, nitrogen, phosphorus, sulphur, etc., as indicated in Table 1.2. The table also shows that this order is very different from that of the relative abundances in the lithosphere and other large regions of the ecosphere. In all, about 40 chemical elements are found in living organisms, most of them being truly biogenic: in other words, they play a significant and precise role in the structure and/or the functioning of the organisms.

There are several fundamental principles governing the way matter is used by living organisms and the way that it circulates in ecological systems:

#### *The law of tolerance*

This law states that for each element there exists a range of concentrations, called the *interval of tolerance*, in which all physiological processes involving that element can take place normally. Consequently, it is only within this interval that life is possible for any particular plant or animal species. There is an optimum concentration in the interval, called the *preferendum*, for which metabolic processes occur at

*Table 1.2 Comparative proportions of principal chemical elements present in living matter and in the ecosphere generally*

| Element | Atomic number | Lithosphere, atmosphere, hydrosphere (%) | Human body (%) |
|---|---|---|---|
| Hydrogen | 1 | 0.95 | 9.31 |
| Carbon | 6 | 0.18 | 19.37 |
| Nitrogen | 7 | 0.03 | 5.14 |
| Oxygen | 8 | 50.02 | 62.81 |
| Fluorine | 9 | 0.10 | 0.009 |
| Sodium | 11 | 2.36 | 0.26 |
| Magnesium | 12 | 2.08 | 0.04 |
| Aluminium | 13 | 7.30 | 0.001 |
| Silicon | 14 | 25.80 | negligible |
| Phosphorus | 15 | 0.11 | 0.64 |
| Sulphur | 16 | 0.11 | 0.63 |
| Chlorine | 17 | 0.20 | 0.18 |
| Potassium | 19 | 2.28 | 0.22 |
| Calcium | 20 | 3.22 | 1.38 |
| Manganese | 25 | 0.08 | 0.0001 |
| Iron | 26 | 4.18 | 0.005 |

maximum speed. At concentrations less than the lower limit of the tolerance interval, death of the organism occurs through deficiency of the element concerned, while beyond the upper limit death occurs through excess (Figure 1.1).

Take as an example the case of nitrates in the soil. They are essential for the majority of plants, providing the source of inorganic nitrogen. The optimum growth of a plant like maize will occur for some definite concentration of these salts in the soil, other things being equal. Below a certain concentration, nitrogen deficiency will prevent the development of the plant, while at the other extreme an excess of nitrogen in the form of nitrates will cause inhibition of growth and even death through phytotoxicity.

### *The law of the minimum*

This law, discovered by Liebig in the last century, states that the growth of a plant is only possible as long as all essential elements are present in sufficient quantities; and that speed of growth is controlled by the essential element that is present in the lowest concentration: growth ceases if only one essential element is present in the environment in insufficient amounts.

This law can be generalized to cover all living organisms and the whole extent of the interval of tolerance. Clearly, at the other extreme, an element present in excessive amounts will be enough to prevent development because the threshold of toxicity has been reached. Similarly, there will be an optimum value for the concentration of *each* essential element at which the speed of growth will be a maximum.

If, now, *all* the elements necessary for the development of a given species are taken into account, it is possible to define what is called the ***ecological niche*** in matter space. If the interval of tolerance for each essential element is represented along a different axis as in Figure 1.2, the effect of all the various concentrations is combined in a multidimensional volume, or hypervolume, within which the organism will grow. The total extent of this ecological niche will in fact be represented by a hypervolume of $n + 1$ dimensions as shown in Figure 1.3, where $n$ is the number of physiologically essential elements for the species being studied. In Figure 1.3, $n = 2$.

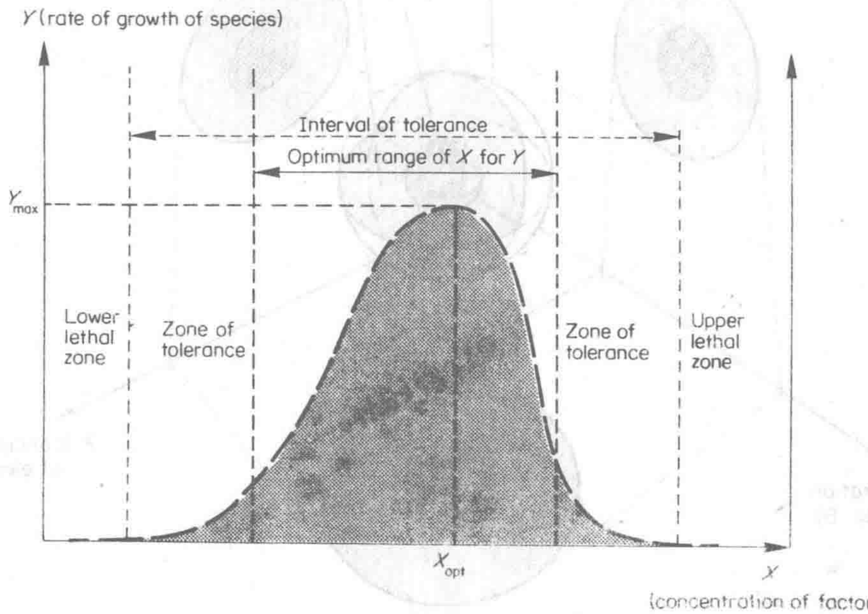


**Figure 1.1** Diagrammatic illustration of the law of tolerance. $X_{opt}$ is the preferendum, the concentration producing the maximum growth rate

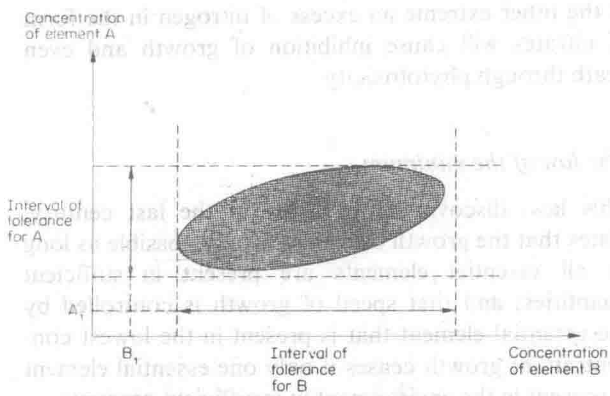


Figure 1.2 Application of the law of the minimum in the case of two elements considered simultaneously. The organism in question cannot grow or even survive with the concentrations denoted by $A_1$ or $B_1$, even if the other element has a sufficient concentration

*The law of the conservation of matter*

In ecological systems, matter never becomes a 'waste product' accumulating indefinitely in the surroundings. There is in fact an almost perfect and permanent recycling of matter, alternating between organic and inorganic forms, which is brought about by the three categories into which living organisms can be assigned: the primary photosynthetic producers (which are autotrophic), the animal consumers and the animal decomposers (both of which are heterotrophic). The cycle is illustrated in Figure 1.4.

### 1.2.2 Energy

All living systems, from the cell to the most complex ecological community, are energy converters more than anything else. At all levels of biological organization, processes exist which channel energy into the various activities of the living system in such a way that the flow of the energy is adapted and controlled. Not only that, but the utilization and the conversion of energy by biological systems are both quite remarkable in that they occur with the most extraordinary efficiency, greatly exceeding that of the most perfect machines of human design.

Energy is essential for all the vital processes at every level, from that of the most elementary cellular mechanisms to that of the entire biosphere. The body temperature of a mammal, the total number of organisms populating a biocoenosis, their speed of development, their rate of reproduction: all of these

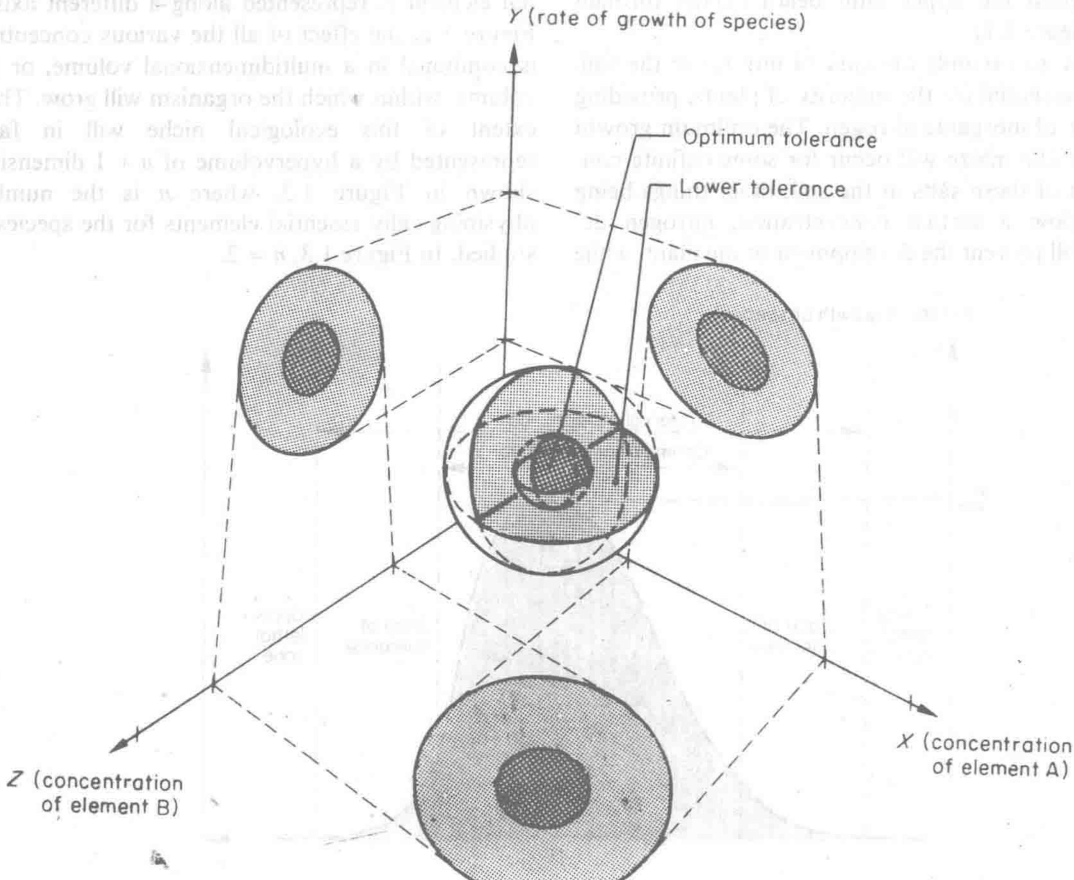


Figure 1.3 Representation of an ecological niche as a hypervolume in a space of three dimensions and its projections on the three planes which they define. (From Blondel and Bourlière, 1979, p. 350)

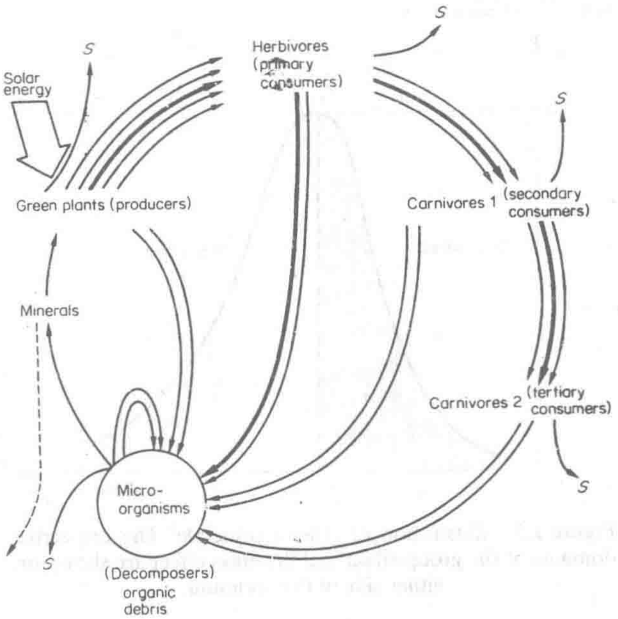


Figure 1.4 Illustrating the circulation of matter (thick lines) and the flow of energy (thin lines) in an ecosystem. $S$ = entropy. (Adapted from Lemée, 1967)

depend on the amount of energy available. It is important to realize, however, that the flow of energy in ecological systems is subject to the laws of thermodynamics as stated by Carnot and others, and we take a brief look at these before proceeding.

### *The first law: the principle of the conservation of energy*

Energy can be neither created nor destroyed, but only changed from one form to another. This principle can be expressed by the equation:

$$\Delta E = \Delta H - \Delta w \qquad (1)$$

where $\Delta E$ is the increase in the energy of the isolated system, $\Delta H$ the increase in heat (or enthalpy) of the system, and $\Delta w$ the amount of work done by the system on its surroundings.

Since the law is universally true, it certainly applies to all biological reactions, including those involving photosynthesis (the transformation of light energy to biochemical energy), muscular work (the transformation of biochemical energy to mechanical energy), neural conduction (the transformation of chemical energy to electrical energy) and so on. It also applies to processes involving energy flow that are appropriate to whole communities of living organisms, such as primary production and secondary production.

### *The second law: the principal of the degradation of energy*

The second law of thermodynamics states that no processes involving a transformation of energy can take place without a partial degradation of the energy, which passes from a concentrated, ordered form to one that is dilute and unusable (in other words, to heat at a low temperature). The loss of useful energy from a system during such processes is proportional to a quantity called the entropy, $S$.

The principle can be expressed by the equation

$$\Delta G = \Delta H - T\,\Delta S \qquad (2)$$

where $\Delta G$ is the change in usable energy (called the free energy)

$\Delta H$ is the exchange of heat with the surroundings

$\Delta S$ is the change in entropy

and $T$ is the absolute temperature at which the process occurs.

A corollary to this principle is that no biological process can take place with 100 per cent efficiency.

### *The unicyclic flow of energy*

Energy is quite different from matter in that it can only pass once through any given trophic level of the food chain. During such a single cycle of energy flow in an ecosystem, the second law shows that it is degraded as it progresses, so that it is gradually dispersed and lost to the surroundings in a non-usable form (entropy), as is illustrated in Figure 1.4.

The energy upon which all ecological systems depend has only one external source: the input from the sun. As a result, the structure and functioning of communities of living organisms inhabiting a particular region on the Earth's surface will be determined by the absolute values of the flux of solar radiation at each point, together with the size of their annual fluctuations. The distribution of large ecological units (macro-ecosystems or biomes) over the biosphere thus depends essentially on the characteristics of the solar radiation at different latitudes.

A *law of optimalization in the use of energy* exists both at the level of species and at that of communities. All species that occupy a particular ecological niche use the available energy more efficiently than other species having similar requirements but less well adapted to the environmental conditions appropriate to that niche.

In the same way, whole ecosystems tend to evolve naturally towards a structure consisting of communities that use the available energy most efficiently. This is expressed in terms of the ratio of the biomass $B$ of the community to the amount of energy $\mathscr{E}$ entering the biotope per unit surface area per unit time. Thus the biomass supported per unit of energy flow, $B/\mathscr{E}$, will increase as the ecosystem develops towards maturity. $B/\mathscr{E}$ ratios are low for cultivated land and natural grassland but become greater for shrublands and reach a maximum for ancient forests and, most clearly, for primeval forests and coral reefs.

*Lindemann's law*

An important consequence of the second law of thermodynamics concerns the transfer of energy in ecosystems: only a fraction of the energy reaching a given trophic level in a community is transmitted to a higher trophic level. As an example, if we consider the food chain:

plant → herbivore → carnivore 1 → carnivore 2

then as a general rule no more than 10 per cent of the energy corresponding to the herbivore level passes to that of carnivore 1, and so on....

In reality there are wide variations in the efficiency with which animals use energy. Their rate of consumption of energy per unit mass is generally higher, other things being equal, if they are smaller. This is because the loss of energy by radiation is directly related to the surface area $S$ of the body and this becomes greater in relation to the mass $M$ as the linear size $l$ decreases.

To show this more clearly, we have that

$$S = kl^2 \quad \text{and} \quad M = Kl^3$$

where $k$ and $K$ are constants. Thus

$$\frac{S}{M} = \frac{k/K}{l}$$

so that the ratio (surface area)/(body mass) increases as $l$ becomes smaller, thus leading to the higher energy loss.

It can be shown experimentally that the mass $M$ of an animal and its metabolic rate of energy consumption $E$ are related by

$$M = AE^{3/2}$$

where $A$ is a constant for the species under consideration.

### 1.2.3 Space

This is a fundamental ecological variable because the total mass of living organisms which can populate an ecosystem depends directly on the space available. In the first place, the available area determines the intensity of the competition within and between species, something that is particularly obvious in the case of cultivated plants. Here, the relation between the dry weight $P$ of a plant and the density $d$ of sowing (or the space available to each individual $S$, where $d = 1/S$) is

$$\log P = a - b \log(1/S) = a - b \log d$$

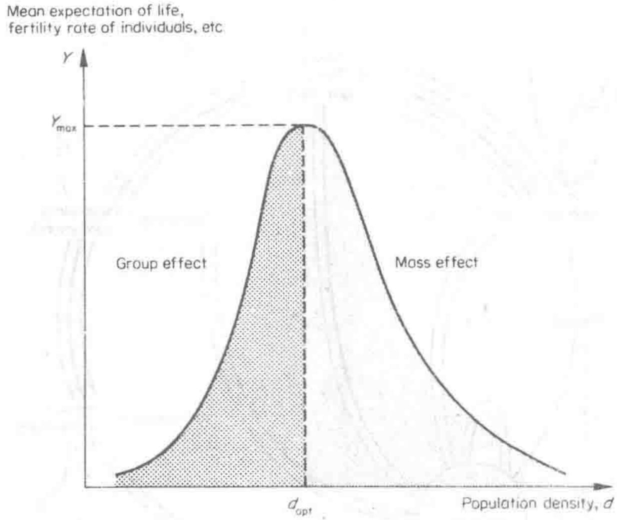


Figure 1.5 Illustration of Allee's principle. The respective domains of the group effect and the mass effect are shown on either side of the optimum

where $a$ and $b$ are constants. From field measurements that effectively yield values for $a$ and $b$, we obtain the general relations:

$$P = k'd^{-3/2} = k'S^{3/2}$$

where $k'$ is another constant.

In practice, the speed of growth, the individual weight, the fertility rate and other physiological factors do not vary monotonically as a function of population density either in plants or animals. There is a certain value of the density for which these factors are a maximum, and on both sides of which they consequently show a decrease. This condition is embodied in *Allee's principle*, according to which the density of population can be a *limiting factor* by being either too high or too low (Figure 1.5). On the other hand, in some cases the available space per individual can produce favourable effects if it is greater than or equal to the optimum (the effect of the group), and unfavourable effects when too low (the effect of the mass).

In the same way as with the overall density of population, the *distribution of the individuals* in each species over the available space also plays a fundamental ecological role. Classically, a distinction is made between distributions that are *random*, *clumped* or *uniform*. The degree of non-uniformity in a habitat is one of the chief factors governing the extent of its occupation by each living species. It has been noted, for example, that plant-eating forest insects proliferate much more easily in a homogeneous distribution of their host species than in discontinuous afforestation. Forests that are planted uniformly and monospecifically offer the most favourable conditions for population explosions among phyllophagous and xylophagous species.