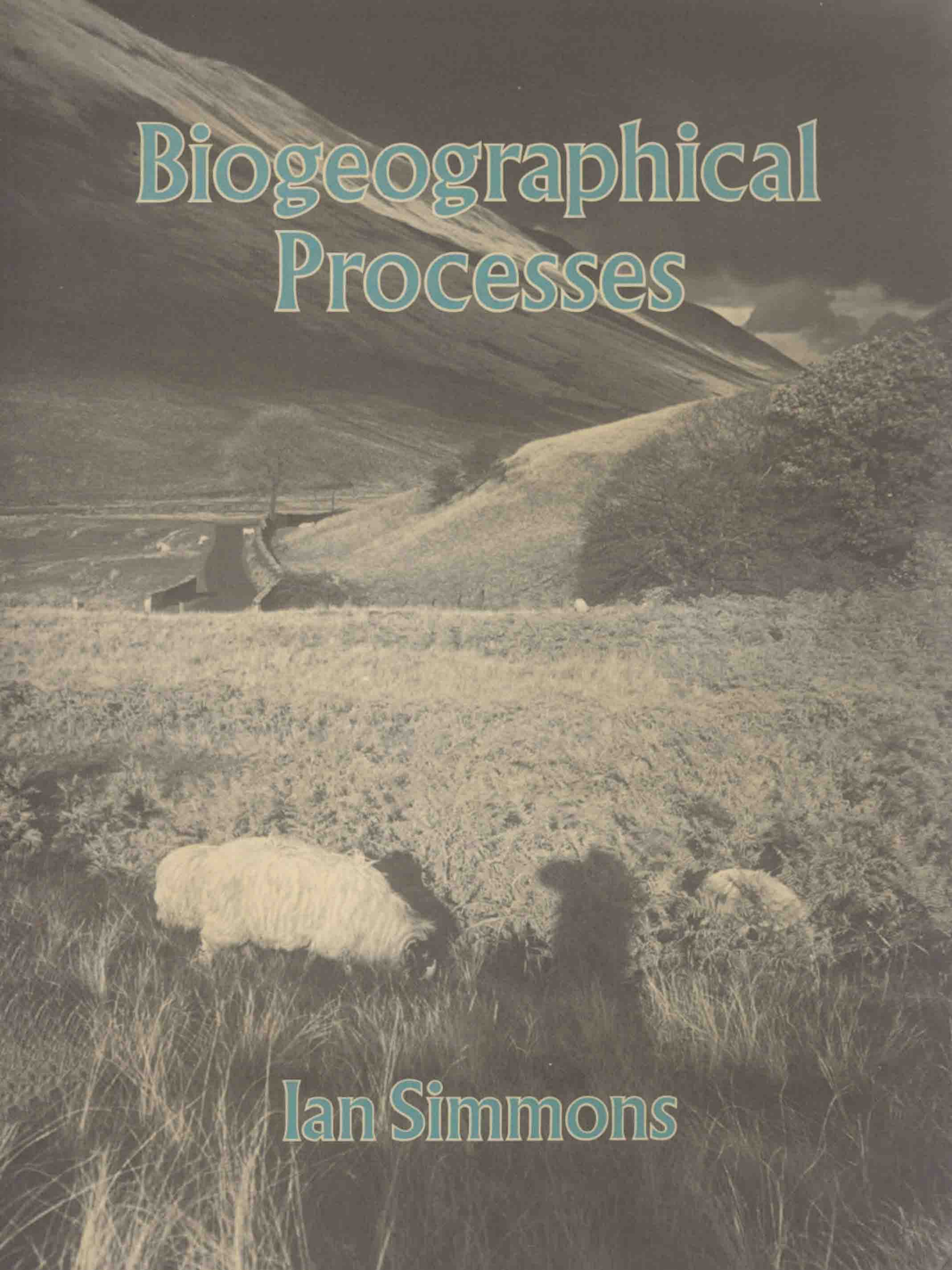
Biogeographical Processes

Ian Simmons



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Preface

It is perhaps unusual for professors to write school books nowadays but I can assure my colleagues that it is a salutary and stimulating exercise. What has worried me is that, unlike the other books in this series, no practising school teacher could be found to write this book. One of my hopes is that by doing it myself I shall help to make sure that eventually such a situation is corrected.

My thanks are due to everybody who helped with the production, and especially to Mrs Macey and Mrs Southcott who did most of the typing. I am very grateful to Darrell Weyman, the general editor of this series, who provided a great deal of constructive comment on the early drafts. The other teachers to whom a draft was sent for review also provided a great deal of comment, much of it quite useful.

The text was written during a period of low teaching load made possible by an informal arrangement with my colleagues at Bristol University and my particular thanks go to Professor Peter Haggett, then Head of the Department, for making this possible.

I. G. SIMMONS
Bristol, December 1980

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Introduction

'There is no wealth but life'

(John Ruskin)

In many schools biogeography is one of the Cinderellas of geographical society. It is taught usually with physical geography and so suffers from juxtaposition with the considerably more popular geomorphology. Even when biology is part of the curriculum in the last two years of secondary school, the overlap and synthesis which are possible seem to happen rather rarely. One reason for the status of biogeography is that the teachers know relatively little about it, or at any rate do not value it as highly as, for example, geomorphology. This state of affairs probably reflects their own experiences as students, for biogeography was often relegated to a back seat in universities, polytechnics and colleges; only recent graduates of these institutions are likely to have found it ranked more or less equally with other branches of the discipline. Another possible reason for its unpopularity is perhaps that it is seen as uninteresting compared with competitors for limited school time. I find this difficult to believe: there is the intellectual challenge of mastering unfamiliar material, the contact with the ideas of eminent scientists past and present, the interest in hearing about faraway places, the opportunity to carry out field and laboratory work (and indeed the chance still to make original observations), and above all to study a field in which the systems of nature and the systems created by man meet. For biogeography cannot be studied realistically only as a branch of physical geography, since man has altered too many of the plants and animals and their habitats for it to be solely a 'natural' study. Neither, of course, can it be a totally 'social' study, for biological organisms do have their own lives outside human minds. So it can be an 'interface' subject with roots both in natural and social sciences but transcending both to become a very difficult but pioneering subject with, of course, a relevance to today's problems, and in this regard it is a microcosm of the discipline of geography where the whole is always something more than the sum of its parts. I hope something of the flavour of today's biogeography has found its way into this book: not only the excitement and the relevance but also (to be realistic) some of the hard concentration required to master basic material; like all intellectual achievement there has to be perspiration as well as inspiration.

What is biogeography?

It is not possible to give a simple definition of biogeography, for the word has been used in a number of different ways. Common to them all, perhaps, is the idea that biogeography is the study of the distribution of plants and animals over the surface of the Earth. This study has two main phases: description, in which we try to identify meaningful patterns in the distributions we observe; and explanation, in which we try to say how and why these patterns have come about. The attempt to identify patterns of distribution on a large scale (e.g. the world or a continent) is usually called **phyto-** or **zoogeography** (depending on whether it deals with plants or with animals) and these sciences together make up biogeography as it is understood by biologists. The study of pattern may take place also at a regional or local scale and the groups of organisms described are usually referred to as **communities,** their physical environment being called the **habitat.** Complementary to this view are investigations which attempt to link together plants and animals and their environment: to study the effect each has upon the other. Such an approach is essentially that of **ecology,** and the unit recognised is the **ecosystem,** which can be studied at any scale from a drop of water to the entire planet. This way of thinking is essentially functional, i.e. it emphasises how the systems work. The environment of plants and animals includes factors of a physical nature, such as climate, water and soil, but nowadays often comprises man as well. Our species has not only altered or removed many ecosystems but has changed the genetic material in many groups of plants and animals so that the outcome of their reproduction is more to our liking. These considerations have led one scholar to suggest that a geographer's approach to biogeography could be focused on the ideas (a) that man creates new **genotypes** (i.e. breeds plants and animals which perpetuate different characteristics from their ancestors), and (b) that he creates new ecosystems in all kinds of ways – by covering them over, by simplifying natural communities, by replacing wild species with tame ones and in many other ways. In order to assess the effect of our species under these two headings, it is essential to have information about conditions before we intervene and so historical biogeography is clearly an important study.

Framework

We start by considering some of the fundamental processes which determine why plants and animals grow where they do, noting particularly that although we have to single out each process for description, in reality many processes are operating simultaneously. Some of this material will be familiar to those taking parallel studies in biology and they may feel able to skip the first pages and join the story at p. 18. This first section ends with the concept of an interactive system of plants, animals and their non-living environment – the ecosystem – and we go on to discuss the way in which an ecosystem functions at a local scale. So the flows of energy and matter, changes in the populations of organisms and the rate of production of living matter in an ecosystem are described. The ecosystem concept can be used at larger scales and so a major block of material deals with the major world formations of climate, soil, plant and animal life (e.g. forests, grasslands, the oceans) as they would be if they were in a natural condition; however, we have to note in passing that many of these formations (called **biomes**) have been modified by human activity. This in turn leads us to an examination of the main categories of human impact upon plants, animals and their ecosystems, using a simple classification of the processes involved. Lastly, there is a short section devoted to a discussion of the alternative future relationships of man and other living organisms. So far as is possible, each of the major sections is free standing, i.e. it can be read without the others as prerequisites; this lessens the possibility of intellectual progression but means that parts only of the book can be read if time does not permit detailed study of it all.

Contents

Chapter 1

Distributional Processes

'No pleasure endures unseasoned by variety'
(Publilius Syrus, 1st century BC)

Our starting point must be the enormous variety of life on Earth; the ability of living organisms to grow and reproduce in so many different habitats and to take such different forms. The basic classificatory unit of this variety is the **species,** which may be thought of conveniently as comprising all those individuals which can breed among themselves but which cannot breed at all freely with individuals from other groups. We currently recognise about 2 million species, and Table 1.1 gives some idea of the classification of different groups of living things. It is important to remember that it is unlikely for all members of one species to be identical and this characteristic of **variation** is important in the evolutionary change of plants and animals. Changes in the species present at various periods of Earth's history are shown by the fossil record, from which we know that some species are of quite recent origin, whereas others have had a very long span of tenure. We also know that many life forms have become extinct (the dinosaurs are the most obvious example), although the reasons for their demise are often far from clear. What is normally accepted is that constant change in the characteristics of species has been brought about by **natural selection.** By this we mean the way in which the environment of a plant or animal (including other organisms) exerts a pressure which ensures that the individuals most fitted to the environment survive and reproduce. Hence the importance of variation (e.g. of size or behaviour) within a species (Fig. 1.1), for amongst the variety of individuals there will be some which are more likely to survive (especially in times of relatively rapid environmental change such as that of climate) than others and these are the ones which will reproduce. Their offspring may be different from their ancestors and so a drift in characteristics will occur; this may eventually result in a

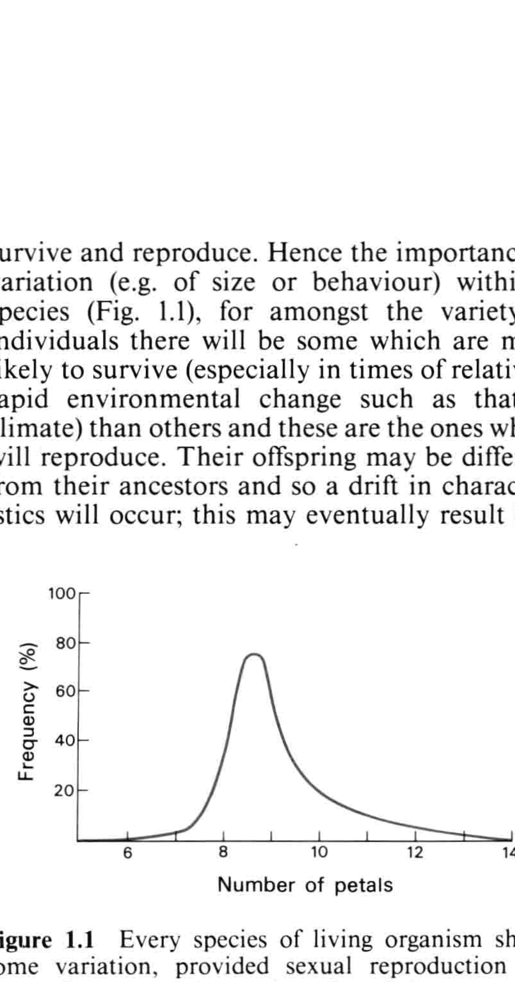
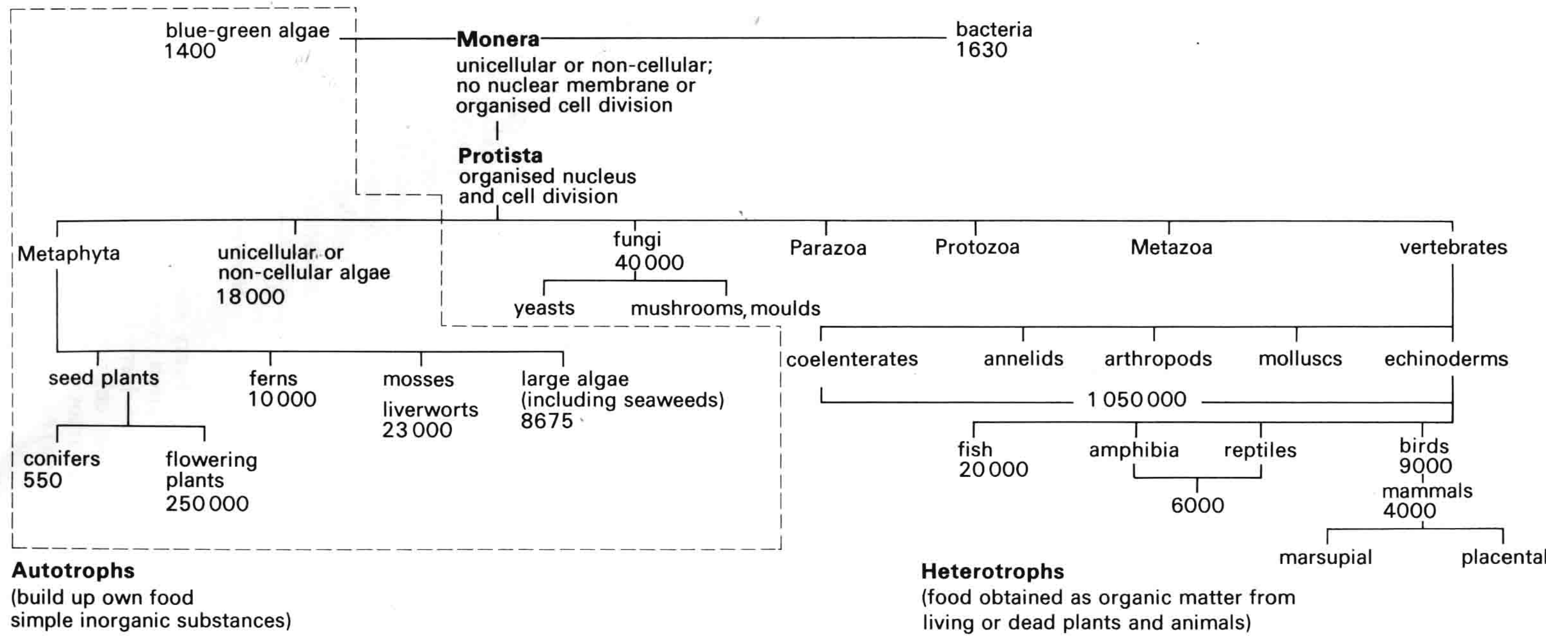


Figure 1.1 Every species of living organism shows some variation, provided sexual reproduction has taken place. Here, the number of petals in a sample of the lesser celandine (*Ranunculus ficaria*) exhibits a typical amount of variance; most individuals (about 80 per cent) have eight petals, but the range is from six to 14.

Table 1.1. Simplified schemes of plant and animal classification. Numbers are estimates of the number of species in each group.



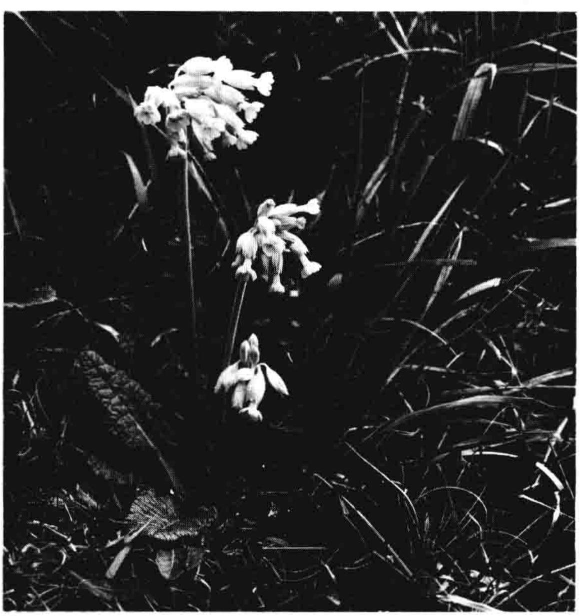
Steps in animal classification

kingdom	Animalia	
subkingdom	Metazoa	many-celled animals
phylum	Vertebrata	possessing a backbone
class	Mammalia	young fed on milk
order	Carnivora	flesh eating
family	Canidae	long muzzle, four toes on hind foot, non-retractable claws
genus	*Canis*	dogs
species	*Canis lupus*	wolf
species	*C. familiaris*	domestic dog

Steps in plant classification

kingdom	Plantae	
subkingdom	Metaphyta	many-celled plants
class	seed plants	conifers and flowering plants
order	Angiospermae	flowering plants
family	Compositae	tubular corolla, milky juice in tissues
genus	*Bellis*	daisies
species	*Bellis perennis*	common daisy
genus	*Taraxacum*	dandelion
species	*Taraxacum officinale*	common dandelion

Below this level sub-species can be developed in both plants and animals



Photograph 1 Two different plant species of the same genus. *Primula veris* and *P. elatior* (cowslip and oxlip respectively). The differences are not easily distinguished in these photographs but they are anatomically distinct, though clearly related closely. They are sufficiently close for hybrids to be formed when the two species grow together.

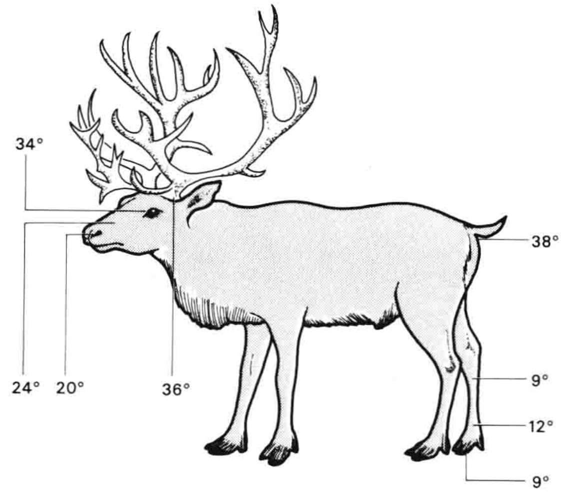


Figure 1.2 This sketch shows the temperatures on the body of a caribou when the air temperature around the animal is −30°C. The extremities of the body are able to tolerate quite low temperatures, but the fur and blood supply combine to keep parts such as the head distinctly warm.

parent group giving rise to reproductively isolated successors and so a new species has been formed. If a species is to avoid extinction, it must adapt to the prevailing conditions and there are many ways in which this has been achieved. The most obvious is **morphological** adaptation of gross order, such as the development of wings which enabled birds to occupy a range of habitats previously unoccupied by such large creatures, or the shape of fish which enables them to swim through water with the most economical use of energy. At a lower order of magnitude we might cite adaptations such as the webbed feet of aquatic animals, or the coats of Arctic animals which permit them to survive in very cold places (Fig. 1.2). More spectacular perhaps are the co-evolutionary adaptations, as for example where the reproductive parts of an orchid and the mouth-parts of an insect are developed to ensure both cross-pollination of the plant and a food source for the animal: the Late Spider Orchid, beautifully illustrated in the BBC book of *Life on Earth* (p. 84), is an example. But adaptation may not be so obvious: there are, for example, strains within plant species which show **physiological** differences in various environments. The mountain and high latitude plant *Oxyria digyna,* for example, comes out of its winter dormancy at different day-lengths in Arctic and mountain

Photograph 2 The flower of the fly orchid, *Ophrys insectifera.* This plant mimics the anatomy of an insect and cannot set seed unless visited by bees or flies which transfer pollen and cross fertilize the plants. If possible, compare the mimicry with late spider orchid in *Life on Earth*, p. 84.

habitats; Arctic plants have higher concentrations of **chlorophyll** and reach peak rates of physiological processes at lower temperatures than their mountain equivalents. But the plants of both habitats remain of the same species. Another method of adaptation is **behavioural:** some desert rats and mice, for example, are not very different in their anatomy and physiology from their temperate relatives but may behave differently. Many of them are nocturnal and spend the day in burrows where they can avoid over-exposure to the levels of solar radiation which would cause so much water loss that they would die. The movement of the whole organism from one habitat to another (migration) is another example of a behavioural adaptation: birds which fly long distances so as to remain in a temperate climate all year (e.g. by summering in the tundra and wintering in mid-latitudes) are another example. It is possible, too, for plants to exhibit behavioural adaptations, for some desert plants simply shed whole branches during periods of extreme drought.

The conclusions we must draw from this discussion of variety and adaptation are twofold. Firstly, that different species have different environmental **tolerances,** i.e. one species can grow and reproduce under conditions where another would be excluded (Fig. 1.3) – thus we have an uneven distribution of species over the surface of the Earth. Secondly, that even within one species, response to the environment is likely to be uneven because of the variation in individuals. There is therefore always the potential for evolutionary change. This adaptive capability may be absolutely essential to maintain life if the environmental conditions change.

1.1 Environmental factors in plant and animal growth

Many factors of the physical environment condition the distribution of an individual organism. Taken together they constitute the potential range of a species, i.e. all those places where it

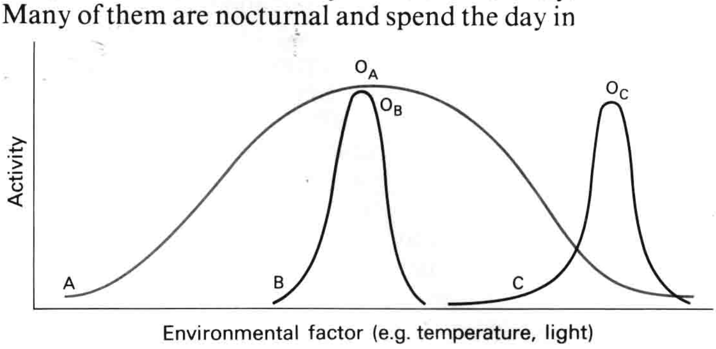


Figure 1.3 The patterns of tolerance for three species of living organisms are plotted on this graph. 'Activity' is a measure of successful adaptation to the environment, some measure of which (e.g. temperature or light) is plotted on the x axis. Species A has a wide tolerance, though best adapted at O_A – its optimum conditions. Species B has its optimum conditions (O_B) at the same value as O_A but its tolerances are much more narrow. Species C is also a narrow-tolerance species, but its optimum at O_C is quite different from the other two. A and B, however, may well compete for resources around the values of their optima, but are unlikely to compete with C.

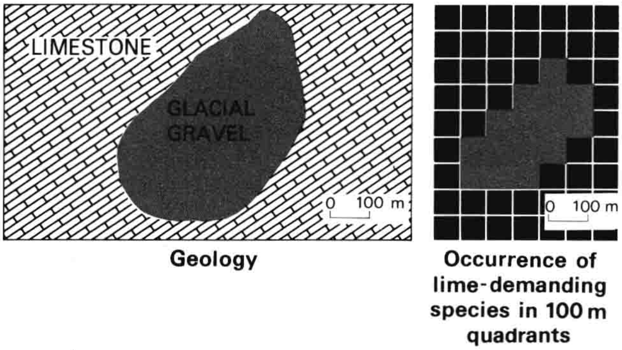


Figure 1.4 The distribution of an imaginary plant which is a calcicole, i.e. requires a high level of calcium-containing mineral nutrition. The geology on the left shows a patch of glacial gravel with an acid reaction overlying limestone with a calcareous reaction. On the right the presence or absence of the calcicole plant is recorded for every 100-metre square: it is virtually absent from the patch of glacial gravel.

might be potentially found. But this potential is rarely realised since the species' evolutionary history may, for example, be too recent for it to have dispersed into all the potential space; again, the environmental history of a locality may have ensured that the place is now beyond the limits of tolerance of a particular species. For instance, if glaciation has left a patch of gravel in a largely limestone area, then **calcicoles** (plants found in areas with a high calcium carbonate content in the soil, as above limestones for example) will probably be absent from the gravel area (Fig. 1.4).

If we look in more detail at contemporary environmental factors, then we must begin with the contribution of the Sun in providing *light* and *warmth*. Solar radiation of a particular wavelength is, of course, the basis of **photosynthesis** in which the radiant energy of the Sun is fixed as chemical energy in plant tissue – a process which is fundamental to most (but not all) forms of life. Not all the Sun's light is suitable for photosynthesis – only certain wavelengths – but in the course of a 'normal' day, most plants are saturated with light once the intensity of sunlight is above 10 000 lux (Fig. 1.5). The absence of light emphasises its importance: consider the very few species that grow on the floor of a forest with a dense canopy, or the filtering effect of water on light so that all the photosynthesis in water takes place in a zone less than 200 m deep. This is shallow compared with the depth of the oceans which are commonly 7000 m deep away from the continental shelves.

Warmth is another product of the Sun's radiation and is measured as a meteorological element and often expressed as a climatic pattern. Clearly, there are temperatures above and below which no organism can live at all (mice have lived and reproduced in a cold-store at –12°C; bacteria can be found at 90°C and their spores can survive 140–180°C), but most plants have an optimum temperature around 25°C and can function well between 10°C and 35°C. There may be critical times in life cycles: a certain temperature may be needed to ripen a seed or to end the **hibernation** of a pollinating insect and in certain years the critical value may not be reached. On a larger scale, it is notable that the northernmost limit of tree growth coincides more or less with the July isotherm for 10°C, and that reptiles are not found in the Arctic and relatively few species of this group are seen in temperate latitudes. In broad terms, the number of species per unit area diminishes away from the Tropics and towards the Poles (Table 1.2).

Since *water* is essential for life, its available quantity and seasonality (and sometimes its quality) also act as differentiating factors in plant and animal distribution. Under the wettest conditions there are the adaptations to an aquatic environment seen in several groups of animals,

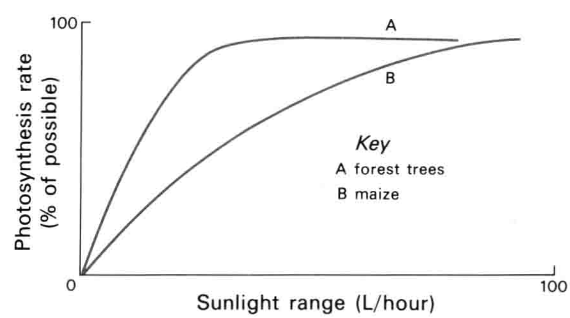


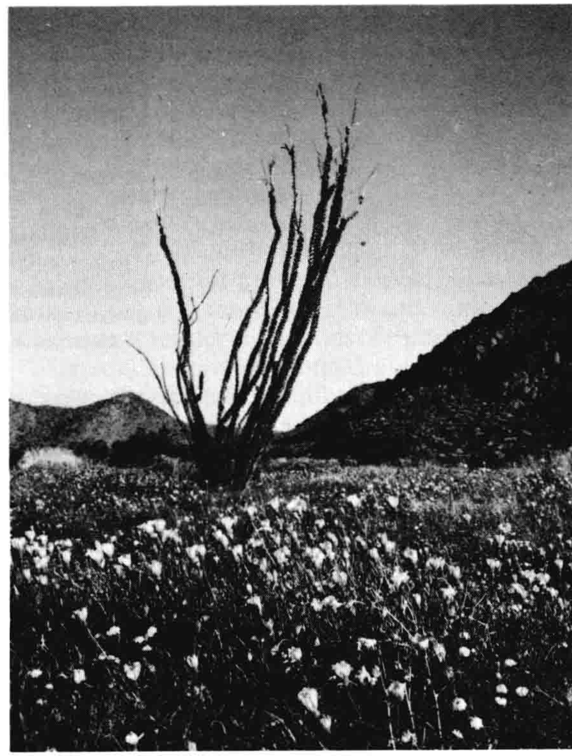
Figure 1.5 The photosynthetic rate as a percentage of the total photosynthesis possible (i.e. at 100 per cent the plant cannot carry out the process any faster), plotted against the quantity of incoming sunlight (L = lux), for (a) a forest tree and (b) maize. The forest tree reaches high levels of photosynthetic rate at a lower level of sunlight than the maize, thus producing much more organic matter per unit of time.

Table 1.2 General increase in species diversity with decreasing latitude in North America.

	Number of species:			
	Florida	*Massa-chusetts*	*Labrador*	*Baffin Island*
beetles	4000	2000	169	90
land snails	250	100	25	0
reptiles	107	21	5	0
amphibians	50	21	17	0
flowering plants	2500	1650	390	218

and water plants may possess adaptations such as an airtight compartment in a stem which then confers buoyancy on a leaf or flowering head. On land, the lowland equatorial climates are the main factors which have allowed the growth of luxuriant forests (pp. 53–5), the physiology of whose trees could not be maintained without a year-round input of rainfall. At the other end of the scale, lack of moisture produces adaptations in both plants and animals: the succulent habit of desert plants such as cacti is well known. Less obvious, perhaps, are modifications such as the ability to put down very deep roots: the root of a tamarisk shrub is reputed to have been traced some 30 m down during the excavation of the Suez Canal. Desert animals are frequently black (nobody quite knows why) and may possess the ability to store water, as in the case of the camel. Some arid-land plants, known as **ephemerals,** complete their whole life cycle from dormancy back again in a very short period after rains and an animal's breeding cycle may well result in the production of young at the time of maximum food availability after seasonal rains. Within such broad-scale considerations, moisture will produce different patterns of distribution of species, for example the lower limits of conifers on mountains in western North America seem to be affected by the sensitivity to drought of particular species (Table 1.3).

Other factors of the physical environment which may place an overall limit on life, or which may produce a selective response from species or individuals, include gases such as oxygen and carbon dioxide. Since carbon dioxide is essential for photosynthesis, there can be little life without it. This gas is not likely to be severely limiting in the air but can be so in water since it enters the water mainly by mixing in the surface layer. Oxygen is essential for animal life and again may



Photograph 3 A perennial desert plant (the ocotillo cactus) of the Mojave Desert of California is surrounded by ephemeral plants which respond quickly to the winter rains and complete their life-cycle in a few weeks, from germination to setting seed.

be limiting in aquatic habitats in a sewage-contaminated river the bacteria may use up all the dissolved oxygen during their fast growth on the sewage, leaving very little for the fish which may then die (Fig. 1.6). But there are forms of life adapted to live without these gases, since we find

Table 1.3 **Lower limits of pine species on mountains in the USA.** Note. Since rainfall increases with latitude, the knobcone pine has become adapted to low precipitation levels and is not, therefore, sensitive to drought. The sugar pine normally grows where precipitation is highest and so is susceptible to long dry periods. The Coulter pine falls between the two.

	Lower limit (m)	*Drought sensitivity*
knobcone pine	850	least
Coulter pine	1200	intermediate
sugar pine	1600	most

bacteria which live in sulphur springs and also apparently in petroleum at depths of 4000 m.

We see later (pp. 20–3) that plants receive their combined mineral nutrition from the soil and so the quantity of these elements in a given soil may act as a differentiating factor. For example, soils which have lost most of their minerals due to **leaching** by soil water percolation will support only those plants which can tolerate very low supplies of the nutritive elements. In Britain, the growth of heather (*Calluna vulgaris*) on moorland soils is an example of this process at work. Soils derived from parent materials with a diversity of minerals and which have not subsequently lost them in runoff may support a much wider variety of flora. Soils which are very high in mineral salts, as in deserts or at the sea's edge, present special problems of growth to plants and those which are adapted to be salt tolerant are called **halophytes.**

Fire may be an element of the natural environment. Animals have to adapt to it by fleeing it or by migration in dry periods, but some plants have evolved a very thick bark which keeps the growing cells alive and these are called **pyrophytes.** Other plants have seeds which will only germinate after they have been burnt and a number of pines have cones which only open and release the seeds after burning. These adaptations suggest the presence of fire over many millenia and are not found when fire appears to be a recent phenomenon due to human presence.

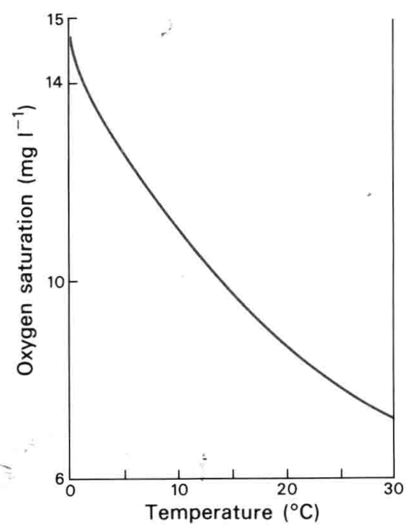


Figure 1.6 The oxygen saturation curve of water at different temperatures. The quantity of oxygen dissolved in water falls with rising temperature. The quantity of oxygen available, for example to fish, would thus drop off in summer in a temperate climate. If fast-growing organisms were then to compete for oxygen (e.g. bacteria from pollution) the fishes' chance of survival is much lower when the water is warm than when it is cold.

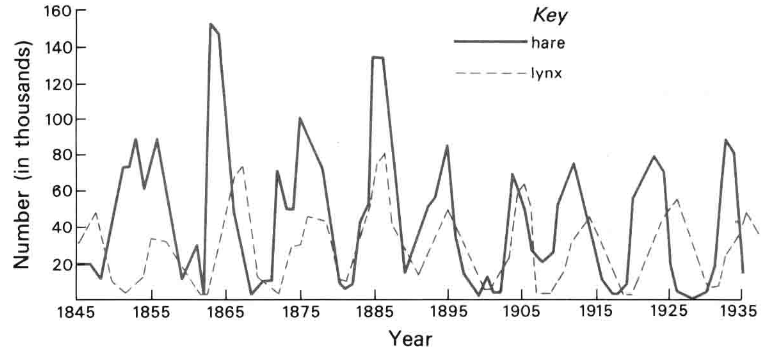
Photograph 4 A sulphur spring at Yellowstone. Even in environments like this, bacteria can flourish: some species can use the inorganic chemicals as sources of energy.

1.2 Community factors in distributions

It is not only factors of the physical environment which determine the presence and abundance of organisms, for the individuals interact among themselves: one of the most frequent relationships is **predation.** Mice may eat grass, for example, and in turn be eaten by owls. This may affect the growth of the grass and the numbers of mice and owls but is unlikely to account for the total absence of any of them unless the system gets out of balance. For instance, if the owls are exterminated, the mice become so abundant that they eat all the grass until they then all starve. But such predator–prey systems are usually finely tuned to avoid such extreme occurrences, just as a successful parasite may debilitate its host but will not kill it as this would deprive it of a home and sustenance (Fig. 1.7).

Competition is another form of community relationship and occurs between species (inter-specific competition) and between individuals of the same species (intra-specific competition). Inter-specific competition may occur when, for example, two species may potentially occupy the same habitat (e.g. bracken fern and heather on a hillside) but where one factor, or a combination of

Figure 1.7 Changes in the abundance of lynx and snow-shoe hare, determined from skins received by Hudson's Bay Company. The peaks in numbers of the hares are followed, after a slight lag, by peaks in numbers of their predator – the lynx. However, the lynxes are never so efficient that they wipe out their food source altogether.



Photograph 5 An area of heathland in Sussex, England. The dominant vegetation is mostly heather but in the foreground and middle ground areas of bracken can be seen. The bracken and heather are competing in the same habitat. Apart from the contemporary dynamics of the vegetation (e.g. the colonisation by bracken), we need to remember that this was once woodland, relics of which can still be seen.

factors, may give one the edge over the other. The ability to withstand grazing by domestic animals such as sheep, the occurrence of fire, or the availability of nutrients, are examples. Intra-specific competition occurs in plants, for example, in germination when the emerging seedlings jostle for light, water and nutrients, with survival going to the most vigorous. In animals there is competition between males (including fighting) for the privilege of breeding, which seems to ensure that the 'best' genetic traits are passed to the next generation. Thus intra-specific competition is a potent force that exerts a strong

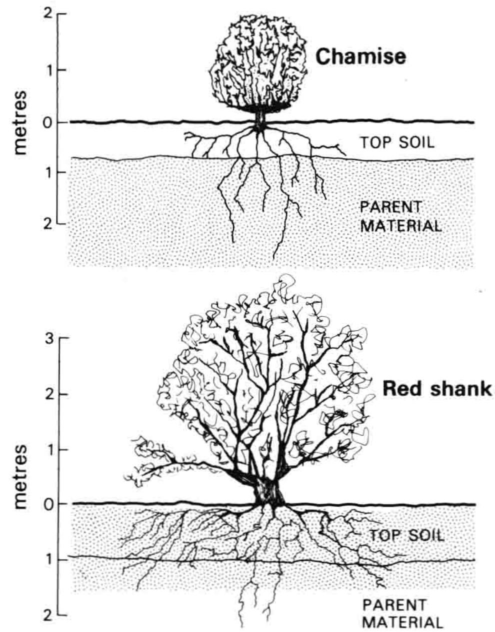


Figure 1.8 The separation of two closely growing desert species – chamise and red shank. The roots of chamise are sparse in the top soil, but penetrate some distance into the subsoil; those of red shank are nearly all in the top soil. Thus, although water is scarce, these two plants can grow closely together without competing for the small quantities of water that become available.

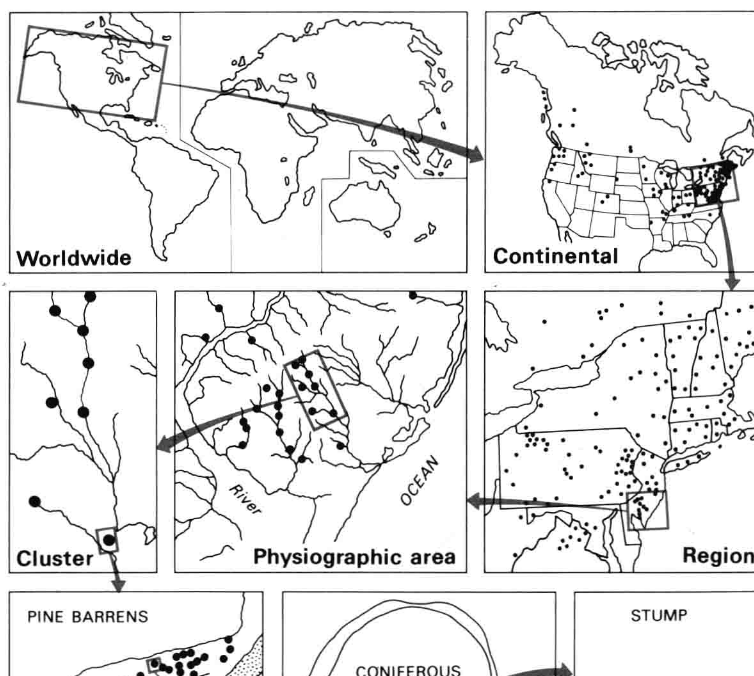


Figure 1.9 An American moss (*Tetraphis*) plotted at different levels of distribution, from the world (top left) to the clump (bottom right) which shows that it can only grow on the stable soils at the foot of conifer tree stumps. The more difficult question to investigate would be 'why is it only found in North America?'.

selective pressure on populations and it forces them in the direction of evolving differences that allow them to evade the competition for resources, i.e. to coexist rather than to compete (Fig. 1.8). Such selective processes are likely eventually to produce different species.

1.3 How can we characterise the distribution of organisms?

Given that an organism is unlikely to be evenly distributed in the world, for the various reasons sketched in above, it becomes essential to be able to characterise its distribution. Of considerable importance here is the scale at which we wish to work: Figure 1.9 shows very well how the distribution of a moss (*Tetraphis*) may be mapped on a number of scales: its world distribution is limited (for reasons unknown) to North America; within that continent, temperature and moisture provide the main constraints on its distribution. Locally, its moisture relations are highly important, as is its inability to grow on **unstable soils,** so that it is confined to the presence of conifer tree stumps.

At a world scale, it is possible to recognise certain groups of plant species. There are, for example, groups which appear to have continuous worldwide distributions providing that suitable conditions are present: the palms are a tropical and subtropical example of such a group. Another example is given by a saxifrage species which is virtually continuous in the circumpolar zone but exhibits outliers in temperate mountains, where broadly similar conditions are to be found. Within the British Isles there are a few plants, e.g. the daisy (*Bellis perennis*) and the ribwort plantain (*Plantago lanceolata*) (Fig. 1.10), which exhibit a continuous distribution to the point of being found in every 1-km grid square, although obviously not necessarily continuously within that unit. On the other hand, there are numerous examples of discontinuous distributions where a plant is found in widely scattered places. Some examples are given in Figure 1.11 and the fascinating part is not so much the scatter

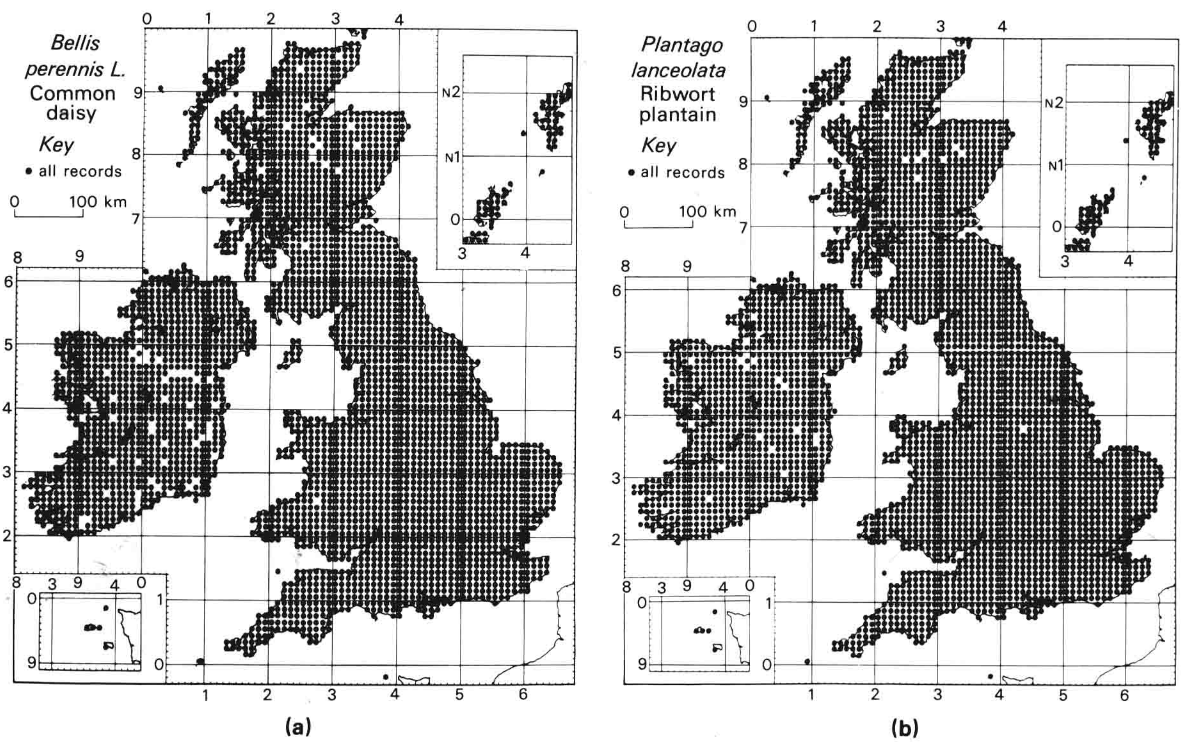


Figure 1.10 The presence or absence of two plants, recorded for every 1-km grid square in the British Isles. The plantain and the daisy are so common that they are found in almost every square. The blanks in Highland Scotland could be environmental, but what might be the cause of the single gap in the Midlands for the plantain? Are there really no daisies in lowland Gwent?