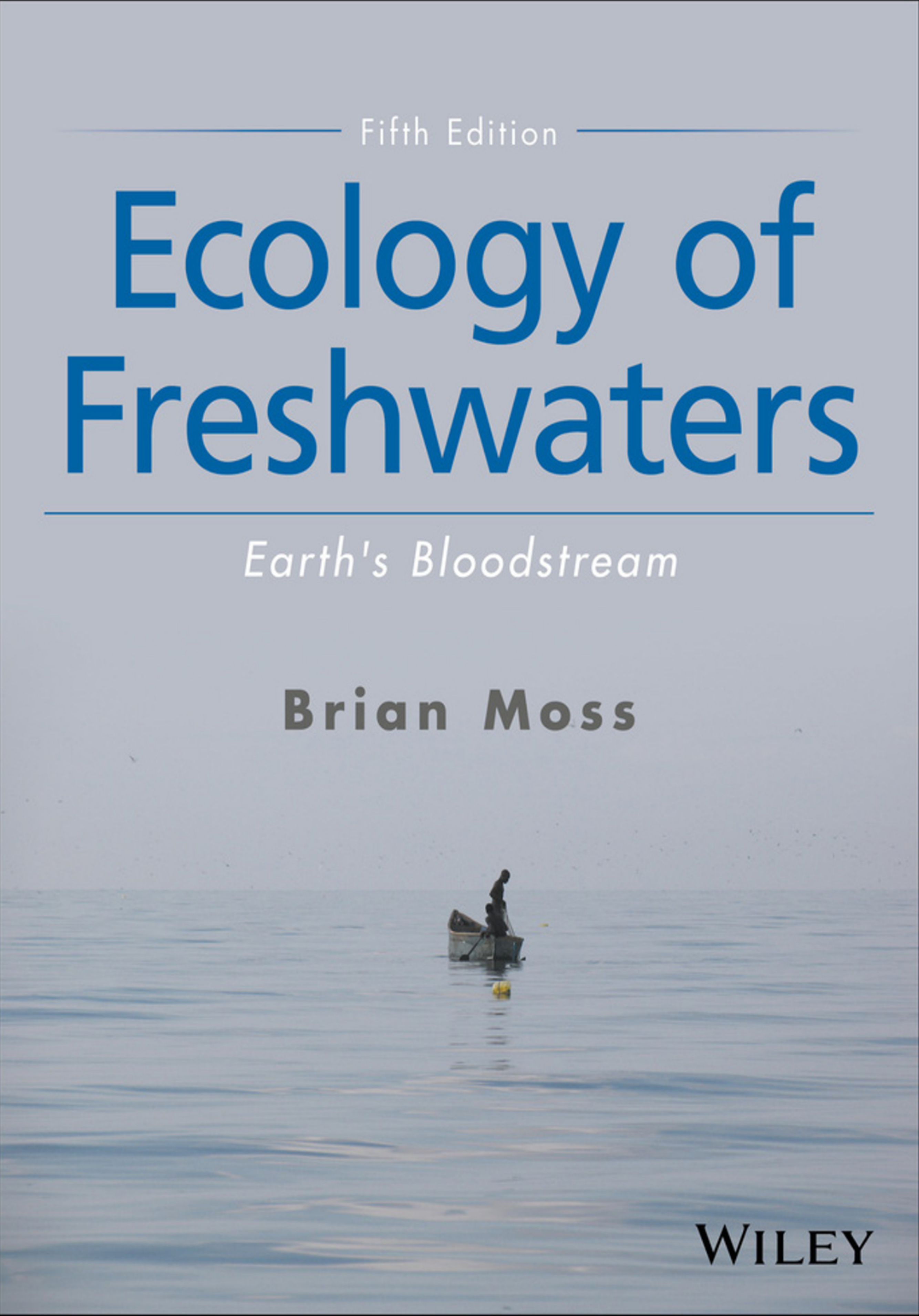
Fifth Edition

Ecology of Freshwaters

Earth's Bloodstream

Brian Moss



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Ecology of Freshwaters

Brian Moss 1943–2016

After receiving a terminal diagnosis, Brian reckoned that he would probably have enough time to complete this edition; he worked very hard, was very focussed, and he did finish the book. I thank Wiley for doing everything possible to speed the process of publication for Brian's special circumstances, and although he died sooner than expected and did not see his book printed, Brian was happy to know that publication was on track, and delighted that illustrations in colour would enhance this, his final, edition.

Joyce Simlett-Moss

(Photo courtesy of Rob Marrs)

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Earth's Bloodstream

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Brian Moss

Emeritus Professor, University of Liverpool, UK

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For my wife, Joyce, my daughter Angharad,
my friends and colleagues, particularly Tom Barker and Erik Jeppesen for their insight and generosity, and not least my former graduate students and post-doctorals, and all those who carry a banner for a need for change beyond any current political conception, if there is to be a comfortable human future

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Preface: why?

The word 'textbook' is a bit pompous. Yet many come from the passions of authors wanting to pass on their worldview and enthusiasms, reflected in the facts. But the relative importance of individual facts changes as understanding grows, and the amount of information increases. A huge volume appears in articles, books and websites on almost everything, and although there is a lot of repetition, the amount is nonetheless daunting. In the five years between 2010, when the last edition of this book appeared, and 2015, 26 596 papers with 'freshwater' appearing in the title or keywords were published in peer-reviewed journals. The complete literature on freshwaters for the five years will amount to several times this, perhaps as many as a quarter of a million articles.

Textbooks have to change to reflect this. Once they could be nearly comprehensive but remain of modest size; increasingly they have become near encyclopaedias, off-putting in bulk. I have come to the view with so much information, including most formal journal publications, available on the net, that a textbook should become a guide book, with the advantage that guide books can be much more attractive to read than encyclopaedias, and still give the fundamentals necessary for understanding. This is the fifth edition of this textbook. The previous editions have grown bigger and bigger so I decided to write a shorter fifth. Faced with so much information, however, this proved trickier than I had thought, but at least I have more or less held the line. I have had to be ruthless in avoiding giving several examples of everything, so as not to offend anyone, and I have had to discard some topics and many references that were dear to my heart and survived several previous editions. But a book is to be read. I have tried to make this one as accessible as I can. The web can be used for further reference.

Photographs taken from the first space missions in the late 1960s are said to have jolted our perceptions of our planet and ourselves. They showed a distant, delicately blue planet with wispy clouds. It was Planet Ocean rather than Planet Earth and the images inspired the environmental movement with the fragility that Earth appeared to have. That message of fragility is both right, when it comes to the conditions that make for a comfortable human existence, and wrong when a study of Earth's geological history reveals the vicissitudes that the biosphere, albeit occupied only by microorganisms for most of the time, has survived. The fragility message, though, has been forgotten. A plethora of beautiful satellite photographs that are too distant to reveal the details of destruction has diluted it. Many human activities continue to exploit the Earth's resources because of a roughly 200-year-old flawed economic model that assumes that lunches are free if the bill is not tendered immediately.

Environmental scientists and some economists have repeatedly pointed out that our present economic system can only be temporary, but the message has been ignored. We are ruled by those who know little outside the parochial worlds of finance and politics. Winston Churchill wrote that scientists should be on tap but not on top. Most would not wish to be on top, but the tap seems to have been screwed shut; and we must seek droplets of compromise from political plumbers determined to keep it that way.

Science, an account of the workings of energy and matter, and politics, that of the workings of human societies, are intertwined and it would be foolish to pretend otherwise. There has been no sentence, in any scientific book, ever written, that has not been immediately charged with the subjectivity of its author. But the self-critical, peer-policed world of academic investigation and experimentation, which I offer you here, gives the closest we have to objectivity, and is far superior to the nebulous and often self-serving dogmas of political theory, not least when it comes to the environment in which we must live. Our problem is to change the politics to reflect the science.

Brian Moss

1

The world as it was and the world as it is

1.1 Early ecological history

Our planet is old, around 4.53 billion years on current estimates, but we humans are very young. Only about 100 000 years have passed since we emerged distinctively as *Homo sapiens* from our previous ancestors. They had had comparatively little effect on the planet, and so did we until the last 15 000 years or so. Before then, the planet changed slowly but continually, under natural geological forces: volcanic eruption, plate separation and continental drift; natural cycles in the Earth's orbit around the Sun; and small changes in the rate at which the Sun emits energy. Its surface changed just as much because the inevitabilities of evolution were producing a succession of organisms that altered the chemistry of the atmosphere and oceans. Around 2 billion years ago, an atmosphere that had previously been free of molecular oxygen was steadily oxygenated because one group of bacteria, the Cyanobacteria (Fig. 1.1), had evolved the ability to use water as the hydrogen donor needed to reduce carbon dioxide in photosynthesis, and released oxygen as a by-product.

This created problems for a biosphere maintained by anaerobic bacteria, because free oxygen was toxic, but one consequence appears to have been the evolution of the eukaryotic cell, in which, through processes of symbiosis, host cells, probably Archaebacteria, engulfed other bacteria whose enzymes could function deep in the combined cell, away from the increasing oxygen concentrations in the environment. Oxygen then built up steadily in the atmosphere until concentrations were high enough (Fig. 1.2) for diffusion to be able to support bigger, multicellular organisation, between 500 and 600 million years ago. Multicellularity allows specialist systems to develop and was rapidly adopted. Multicellular systems could cope with conditions on land, and a biodiversity previously confined to water was joined by one that could take advantage of very high oxygen concentrations in the air. Oxygen is not very soluble in water (see Sections 5.2 and 5.3). On land there was also a greater supply of light energy (water absorbs the Sun's radiation very quickly; see Sections 7.2 and 7.3). In turn, these enhanced conditions allowed the eventual evolution of mammals that could start to modify conditions to their own ends through a high brain capacity. We were born.

The Earth is well supplied with the twenty or so elements that natural selection has used to produce and maintain living systems, but it has limited supplies, in available form at the surface, of some of them. The stock must be recycled. Moreover, liquid water is essential for living cells to function, and, from the end of the Hadean Period 4 billion years ago, when Earth had cooled sufficiently for water to condense from the steamy atmosphere of volcanic gases, there was established a water cycle. The essence of this is that water, evaporated from the oceans and land surfaces through solar heating, moves upwards or polewards in the atmosphere, cools and condenses. It falls as rain or snow, and runs off the land and back to the ocean.

Ecology of Freshwaters: Earth's Bloodstream, Fifth Edition. Brian Moss.

Figure 1.1 Cyanobacteria, which are now ubiquitous in soils, fresh and salt waters, had a pivotal role in the history of the biosphere. They evolved the ability to use water as a hydrogen donor in photosynthesis, thus releasing molecular oxygen as a by-product. Individual cells of cyanobacteria (inset) are generally very small (around 1–2 µm) but may aggregate in much bigger filaments and colonies, sometimes occurring so abundantly as to colour the water prominently, as in this temple tank in Nepal. Ancient fossils suggest that the range of forms of cyanobacteria have not changed greatly since they first evolved. (Reproduced with permission of K. J. Irvine. Inset reproduced with permission of Matthew J. Parker.)

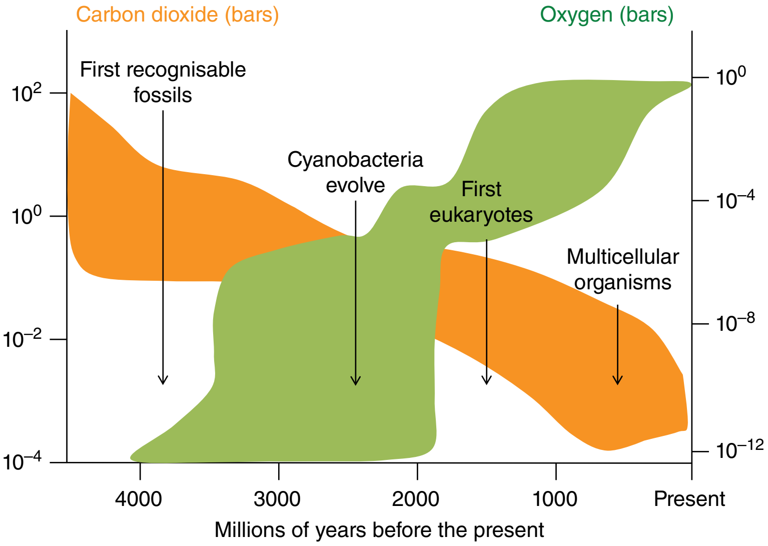

Figure 1.2 Reconstructed changes in oxygen and carbon dioxide concentrations in the Earth's atmosphere over geological time. The envelopes indicate the variation calculated from different geological models, but the trends are clear. Major events in evolution are also shown. A bar is the unit of atmospheric pressure. Current total pressure is close to 1 bar (or 10^0 on the logarithmic scale used). (Based on Mojzsis 2001.)

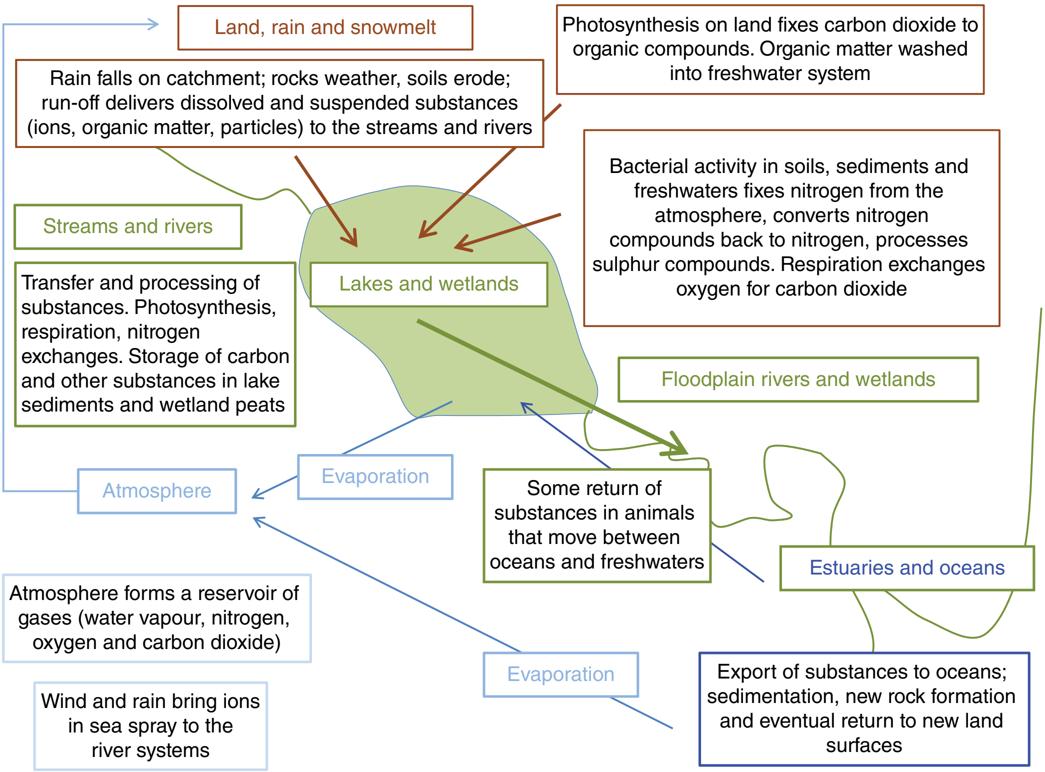

Figure 1.3 Linkages among parts of the freshwater system, the catchment area of the land, the atmosphere and the water cycle.

In doing so, it is retained for a time in a continuous system of hilly streams and rivers, groundwaters, pools, wetlands and lakes, and then in floodplain rivers and estuaries that connect them with the coastal seas and oceans (Fig. 1.3). Water dissolves a huge range of substances and carries them with it during the liquid phases of this cycle. Some are absorbed by aquatic organisms; others, like nitrogen compounds, are converted quickly to gases by bacteria and returned to the atmosphere, and yet others contribute to the saltiness of the ocean or are precipitated out into sediments and newly forming rocks. Recycling of these latter elements is long term. Movements of the Earth's plates against one another raise new mountains over millions of years and weathering slowly re-releases substances usable by organisms. Recycling of many essential elements, however, has to be much more rapid and depends on biological processes. Water thus acts like a bloodstream for the Earth (Fig. 1.4), its rivers and lakes the equivalents of arteries and veins, its evaporative surfaces a sun-driven heart that pumps the water around, and its basins, especially lakes and wetlands, its digestive and excretal systems, foci of biological activity that shuttle dissolved substances between organisms and the water.

There appears to be some overall linkage of these activities, though we have no idea how it is achieved. The oxygen and carbon dioxide concentrations in the atmosphere and the saltiness of the sea have been maintained for a long time within limits that allow the persistence of liquid water and of multicellular organisms, despite geological forces that could threaten this. Carbon dioxide remained between 190 and 260 ppm by volume for at least a million years until very recently – a period that included a number of advances of the polar and mountain glaciers – and oxygen concentrations have been

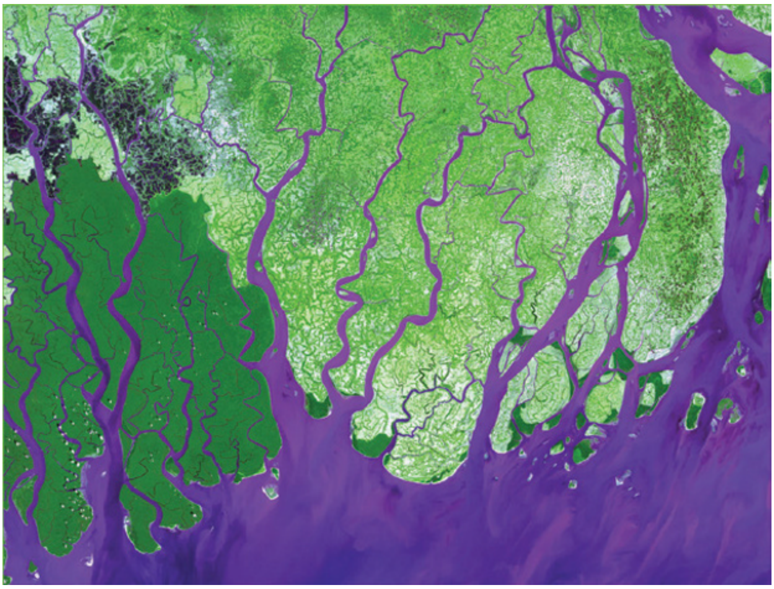

Figure 1.4 Seen from space, the freshwater systems of the Earth support the analogy that they are the bloodstream of the biosphere. The many mouths of the River Ganges shown here discharge into the Indian Ocean. (Reproduced with permission of USGS EROS Data Center Satellite Systems Branch.)

Table 1.1 Composition of the Earth's atmosphere, compared with those of its closest planets, Mars and Venus. Equilibrium Earth is calculated from chemical models that assume that all possible reactions are allowed to run to equilibrium. Present-day composition is as measured on Earth, and for Mars and Venus is deduced from spectroscopic measurements. (Based on Lovelock 1979. Reproduced with permission of Oxford University Press.)

	Venus	Equilibrium Earth	Mars	Earth as it is
Carbon dioxide (%)	98	98	95	0.03
Nitrogen (%)	1.9	1.9	2.7	79
Oxygen (%)	Trace	Trace	0.13	21
Argon (%)	0.1	0.1	2	1
Surface temperature (°C)	477	290	−53	13
Total pressure (bars)	90	60	0.0064	1

around 21% for at least as long. Carbon dioxide was prevented from rising much higher through the storage of carbon compounds in waterlogged soils, peats and lake sediments, whilst gases produced by living organisms, such as methane and dimethyl sulphide, react with oxygen and temper its concentration downwards. Much higher oxygen concentrations would promote uncontrollable forest and grassland fires and indeed this had happened earlier in geological history. The chemistry of both seawater and the atmosphere is maintained in a non-equilibrium state by the activities of living organisms (Table 1.1). Without them, we would have a much hotter planet and possibly no liquid water, and then only with a crushing atmospheric pressure. But how this system is maintained in an apparently orderly way is a mystery. There appears to be cooperation, but cooperation and natural selection do not easily fit together.

1.2 The more recent past

We know a great deal about the ecology of our planet but the detail is greater for the past few million years, and particularly for the last few tens of thousands of years, than for any time previously. This latter time embraces the final melting back of the ice sheets that had advanced and retreated over the previous several million years. As ice advances, it bulldozes the land surfaces, widens pre-existing river valleys and changes the former courses of rivers. It scrapes out new basins for eventual lakes, and changes the outlines and depths of previous ones if they were large enough for their basins still to be recognisable. When ice melts, enormous amounts of fractured rock, gravel, sand and finer sediments wash out from under the glaciers, and may be deposited as moraines or in extensive washout plains. Organisms from previous periods of retreat, when the land was exposed and ecological communities developed, do survive, but they are a small proportion of the former communities.

We are not talking about a few metres of ice and snow, the consequences of even a severe blizzard. Over the land in the upper forty degrees of latitude in both the southern and the northern hemispheres, we must imagine ice several kilometres in thickness. We must hear the deafening noise of crashing bergs and roaring floods at the ice front; and towards the Equator, we must see lands that were frosted in winter, melting only in summer for their rivers to flow. Closer to the Equator, there was not such devastation, but it was cooler and wetter: one of the reasons for ice to advance is that the Earth's orbit is slightly farther from the Sun than at other times and its tilt on its axis slightly less extreme. Heating and evaporation were reduced; droughts were still frequent in arid areas, but lakes were bigger, rivers flowed more prolifically. And eventually, from a reservoir of species in the now warmer lands, came a steady migration of organisms polewards as the ice retreated and the now temperate and polar lands were re-exposed.

The final advance of the ice and its melting back did not completely re-set ecological history, even for the temperate and polar lands, but particularly not for the regions that were not covered by ice. There continued a long process of evolutionary change since the times that they too may have been devastated by even more severe glaciations some hundreds of millions of years before, and particularly following the impact of collision with a large meteor in what is now Mexico 66 million years ago. At that time, the continents were approaching their present positions but were still on the move. North and South America had not yet joined up, India was yet to smash into Asia and cause the upthrust of the Himalayas, and Australia was only just separating from Antarctica and moving equatorward, whilst Antarctica moved farther south. The land surfaces that were to become the present tropics and warm-temperate regions were mostly ancient, having been subjected to millions of years of weathering down to flat plains (Fig. 1.5), whose soils were deep and had been leached for long periods, in contrast to the glaciated regions where new soils were formed from rock freshly plucked and scoured by the ice (Fig. 1.6).

There were to be immense consequences for freshwaters, because the minerals that leach out from the soils determine the nature of the water that fills the basins. And cutting across this simple picture of ancient, un-iced surfaces and new just-glaciated ones, was the legacy of past plate movements. There were (and still are) huge mountain chains along the western edges of the Americas, continuing across the arc of the Aleutian Islands around the far side of the Pacific through Russia and Japan, and dwindling into South East Asia. Sixty-six million years ago, the Himalayas were yet to form, but the Carpathians, the Alps and the Appalachians, formed by earlier plate collisions, were still high features. In many places, even under the ice, the effects of plate movement continued to be reflected in volcanic activity. The flat continent of Africa acquired, only a million or two years ago, deep basins, the rift valleys,

Figure 1.5 Mount Conner, Northern Territory, Australia. Ancient land surfaces have been planed flat by erosion, often have deep but infertile soils, from which minerals have long been leached, leaving only bright iron oxides and quartz with little organic matter. Such landscapes are now mostly found in the warm temperate and tropical regions. (Reproduced with permission of Gabriele Delhay.)

Figure 1.6 Youthful landscapes are those where rock has been exposed by volcanic action or scoured and ground by ice. Soils are shallow and still forming but are rich in minerals, which leach to the streams and rivers. In glaciated landscapes like this near Cader Idris in Wales, with Cregennan Lake in the foreground, the northerliness and dampness of the climate also promotes the build-up of organic matter in the soils.

in which rest the East African Great Lakes. Volcanoes continued to erupt, leaving isolated high mountains, Kenya and Kilimanjaro, for example, with dozens of streams and small tarns. Lakes like Kivu (Fig. 1.7) were formed as lava flows dammed the rivers. Nothing has rested for very long.

We enter the last 20 000 years, even the last few million years, on a still changing stage but one that would be easily recognisable to a

Figure 1.7 Fishing on Lake Kivu, which is shared between the Democratic Republic of the Congo and Rwanda. The lake was formed by the damming of the River Rutshuru sometime before 15 000 years ago, when the Virunga volcanoes to the north erupted and filled the rift valley between Lake Edward and Lake Tanganyika with lava flows. This changed the drainage so that the lake overflows now to the south whereas previously the flow was northwards into Lake Edward. The lake is very deep and does not mix from top to bottom and so has accumulated very large stocks of carbon dioxide and methane in its deeper layers. (Reproduced with permission of Steve Evans.)

modern biologist. The groups of organisms that are now familiar to us were by then already dominating. We are not dealing with trilobites and dinosaurs, huge trees of the fern families, or even exotic microorganisms. Indeed there has been a great turnover in individual species and genotypes, even over a hundred thousand years, but all the groups with which we are now familiar were established before the disruption of the meteorite collision 66 million years ago. In freshwaters, the bacteria, algae and protozoans, though now reclassified into seven or so new kingdoms that would be unfamiliar to a biologist trained just twenty-five years ago, are old groups.

1.3 Characteristics of freshwater organisms

The freshwater invertebrates have been dominated by the annelid worms, molluscs, crustaceans and insects for many millions of years, and the flowering plants, birds and mammals had established their dominance over the ferns and mosses, amphibians and reptiles long previously. But it is, and was, a highly changing world. Freshwaters contain only a very small proportion of the world's water. Most water is contained in a set of linked oceans that has been a permanent body of water (though greatly changing its shape) since water first condensed out of the atmosphere around 4 billion years ago. The next most abundant source is in the polar and mountain glaciers, then the soil and groundwaters. Only a tiny fraction, a percentage point or two, is stored in lakes or flowing through rivers at any one time, but with the even tinier proportion in the atmosphere, this water maintains the movements and exchanges of nutrients and minerals throughout the land. Its amounts in any given place are basically determined by climate, but within the climatic zones, weather has an immense effect. There are droughts and floods; lake levels can rise and fall; streams, even rivers, can move sideways,

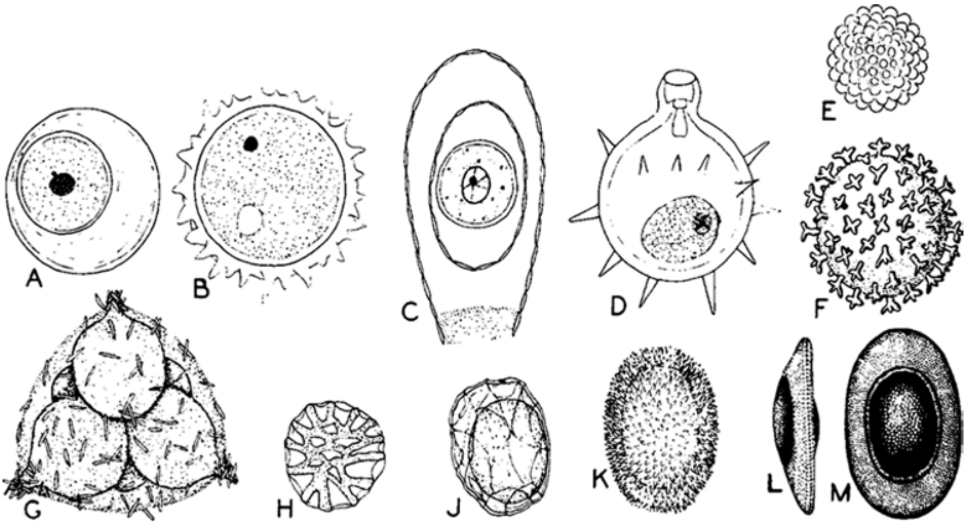

Figure 1.8 Freshwater animals often produce structures that allow them to survive drought or other difficult conditions by reducing their metabolism in protective shells or spores. A–D are cysts of protozoans; E and F are resting eggs of tardigrades (water bears). G shows dispersive structures (gemmules) of a freshwater sponge; H is a resting egg of a freshwater shrimp (*Eulimnadia*); and J and K the resting eggs of rotifers. L and M are side and front views of a statoblast of a bryozoan. (Based on Pennak 1985. Reproduced with permission of Oxford University Press.)

even dry up, and there is little detailed predictability from year to year. The loss and re-formation of the entire system in the polar and temperate regions during the recent glaciations is a manifestation of this. Unless it lives in a particularly big lake, a freshwater organism can rely on little. Its habitat may be very different next year.

Freshwater communities are well adapted to change and disturbance. They might produce resting stages to survive a dry period; they might be very efficient at dispersal as spores or cocoons (Fig. 1.8) or by flood or on the wing. They generally have high tolerance of varying habitat conditions and they invest more energy in reproduction and replacement than in developing liaisons among different species, in breeding colours or elaborate behaviours. When these features are prominent, the organisms will usually be in one of the more stable basins: a large, deep tropical lake for example. In contrast, marine organisms can rely on a permanent water body. Tides vary but highly predictably; ocean currents involve such huge volumes of water that they can be relied upon; and below a shallow surface layer is a steady habitat, tranquil even, that supports multicoloured animals that have developed many mutually supportive symbioses (Fig. 1.9). As in freshwaters, the open-water planktonic habitat in the oceans is hazardous, but the bottom is steadier and that is where most of the biodiversity lies. Marine organisms are generally fussy. It is much easier to maintain a freshwater aquarium than a marine one.

1.4 Freshwater biodiversity

Freshwaters are sometimes thought of as Cinderellas when it comes to richness of diversity. Apparently they have many fewer species, though not necessarily families, than the land, or especially the oceans. But the more valid comparison is in richness compared with extent of habitat. Freshwaters occupy a tiny proportion of the land space or total water space, but have broadly comparable diversities in terms of order of magnitude

Figure 1.9 Marine animals are frequently brightly coloured compared with freshwater ones. The ocean is a much more predictable habitat than freshwaters and investment in warning or breeding colours is worthwhile, whereas in freshwaters, more energy is invested in reproduction in a habitat where death rates are often high. (Reproduced with permission of Mark Peter.)

Table 1.2 Relative biodiversity of fishes in marine and freshwater habitats. NA, not applicable. (Based on Cohen 1970; Horn 1972; and Balian *et al*. 2008.)

Habitat	Area (million km^2)	Volume (million km^3)	Mean depth	Species number (percentage)	Species per million km^2	Species per million km^3
Fish						
Oceans	361	1371	3.8 km	18 000 (58)	49.9	13.1
Freshwaters	1.5	0.13	87 m	13 000 (41)	8667	100 000
Total animals						
Oceans	361	1371	3.8 km	349 000 (26.8)	967	255
Freshwater	1.5	0.13	87 m	126 000 (9.7)	84 000	969 200
Land	149	NA	NA	827 000 (63.5)	5550	NA

to land or marine biota (Table 1.2). Speciation has been much more vigorous in freshwaters, perhaps because of the continual moderate and occasionally high disturbance that they experience. The continually shifting habitat means continual evolutionary adjustment. Freshwater fish are especially diverse.

After the ice retreated, there was plentiful water flow in the rivers, and on flat, long-eroded landscapes, irregularities held water and created extensive networks of shallow wetlands or deeper ponds and lakes. Rivers meandered over wide floodplains, carrying silt from the uplands, depositing it in the spring or wet season floods, and creating a mosaic of habitats. The land was covered in natural vegetation: forests of many kinds, grasslands in drier areas, deserts in the most arid. But most deserts had some vegetation and plant-lined ephemeral streams ran